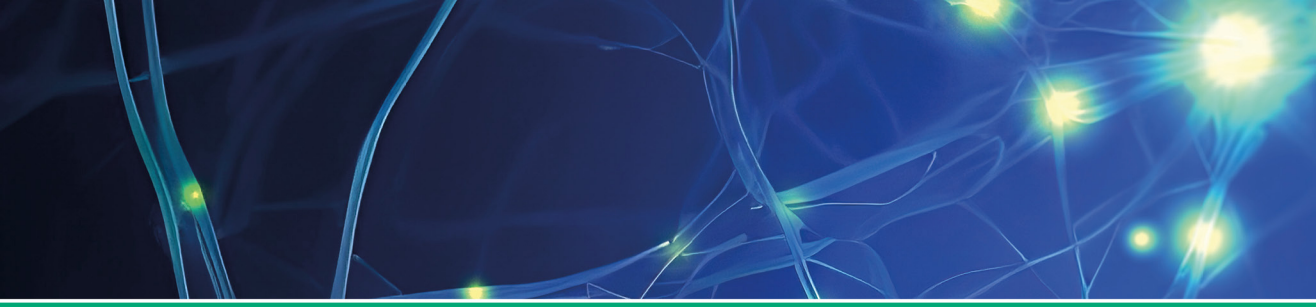
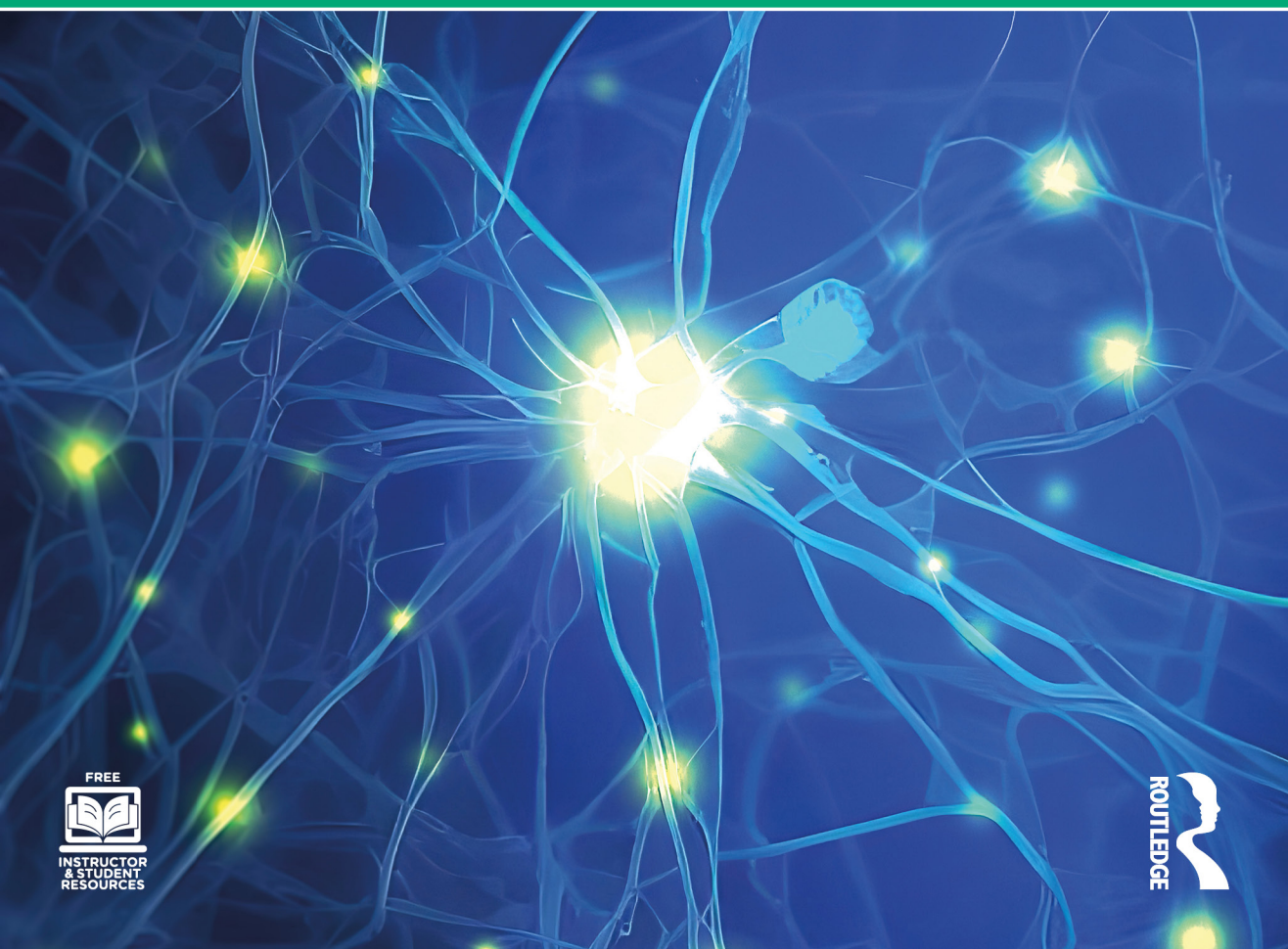


JAMIE WARD

The Student's Guide to Cognitive Neuroscience

FIFTH EDITION



'The fifth edition of *The Student's Guide to Cognitive Neuroscience* builds on the impressive strengths of the outstanding previous editions. Jamie Ward provides a clearly written introduction to cognitive neuroscience that will both engage and inform students. He thoughtfully integrates findings and ideas from neuropsychology, neuroimaging, and cognitive psychology, and has added new cutting-edge content and novel pedagogy to the fifth edition. I highly recommend this excellent new edition.'

Daniel L. Schacter, *William R. Kenan, Jr. Professor of Psychology, Harvard University, USA*

'This new textbook represents an invaluable resource for students at all levels of study. The clearly-written chapters are complemented by video recordings of Jamie's lectures and an abundance of other materials for students, including interviews with key figures in the field of Cognitive Neuroscience. This is more than a textbook, it is a compendium.'

Ben Parris, *Professor of Psychology, Bournemouth University, UK*

'*The Student's Guide to Cognitive Neuroscience* has long been my choice of textbook for teaching undergraduates and beginning graduate students. The 5th edition retains all the virtues of earlier editions – clear and engaging explanations of key theories, methods and findings – with new sections on emerging issues such as replicability and robust research practices.'

Martha J. Farah, *Director of the Center for Neuroscience & Society, Walter H. Annenberg Professor in the Natural Sciences, University of Pennsylvania, USA*

‘In *The Student’s Guide to Cognitive Neuroscience* (5th edition) Jamie Ward successfully guides the reader through the fascinating world of cognitive neuroscience in an accessible and engaging manner. The author weaves together insights from neurobiology, psychology, and cognitive science, presenting with great precision the latest research discoveries on the complexity of the brain, all enriched by key examples from clinical neuropsychology. I have used previous editions of this book for teaching and plan to continue using the new edition, as its clarity and value for both experts and newcomers are undeniable.’

Manuela Sellitto, *Assistant Professor of Neuropsychology and Cognitive Neuroscience at the University of Pavia, Italy*

‘Jamie Ward’s *The Student’s Guide to Cognitive Neuroscience* (5th edition) provides a comprehensive introduction to the field. The text includes an excellent integration of research from cognitive psychology, neuroscience, and neuropsychology, with a strong emphasis placed on explaining the diverse methodologies integral to the field. A particular strength of this book is the balance between accessible writing with skillful discussions of research. The inclusion of foundational studies and recent research, with clear explanations of the relevance of the findings to current topics is remarkable.’

Jocelyn R. Folk, *Associate Professor and Associate Chair at the Department of Psychological Sciences, Kent State University, USA*

The Student's Guide to Cognitive Neuroscience

Reflecting recent changes in the way cognition and the brain are studied, this thoroughly updated fifth edition of this bestselling textbook provides a comprehensive and student-friendly guide to cognitive neuroscience. Jamie Ward provides an easy-to-follow introduction to neural structure and function, as well as all the key methods and procedures of cognitive neuroscience, with a view to helping students understand how they can be used to shed light on the neural basis of cognition.

The book presents a comprehensive overview of the latest theories and findings in all the key topics in cognitive neuroscience, including vision, hearing, attention, memory, speech and language, numeracy, executive function, social and emotional behavior, and developmental neuroscience. Throughout, case studies, newspaper reports, everyday examples, and student-friendly pedagogy are used to help students understand the more challenging ideas that underpin the subject. This edition features expanded coverage of consciousness, a combined chapter on literacy and numeracy, and increased coverage of brain networks and computational approaches.

Written in an engaging style by a leading researcher in the field and presented in full color including numerous illustrative materials, this book will be invaluable as a core text for undergraduate modules in cognitive neuroscience. It can also be used as a key text on courses in cognition, cognitive neuropsychology, biopsychology, or brain and behavior. Those embarking on research will find it an invaluable starting point and reference.

This textbook is supported by an extensive collection of free digital resources for students and instructors, including lectures by leading researchers, links to key studies and interviews, multiple-choice questions, and interactive flashcards to test your knowledge. Visit the Instructor & Student Resources website at routledgelearning.com/wardcognitiveneuroscience.

Jamie Ward is Professor of Cognitive Neuroscience at the University of Sussex, UK. He is the author of a number of books on social and cognitive neuroscience and on synesthesia and is President of the British Association of Cognitive Neuroscience.

THE STUDENT'S GUIDE TO COGNITIVE NEUROSCIENCE

Fifth Edition

JAMIE WARD

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About the author

Jamie Ward is Professor of Cognitive Neuroscience at the University of Sussex, UK. He completed degrees at the University of Cambridge (1991–1994) and the University of Birmingham (1994–1997). He subsequently worked as Research Fellow at the University of Sussex (1997–1999) and as Lecturer and Senior Lecturer at University College London (1999–2007). His principal research interest lies in the cognitive neuroscience of synesthesia, although he has published on many other topics, including frontal lobe function, memory and disorders of reading and spelling. His research uses a number of methods in cognitive neuroscience, including human neuropsychology, functional imaging, EEG, and TMS. His other books include *The Frog Who Croaked Blue: Synesthesia and the Mixing of the Senses* and *The Student's Guide to Social Neuroscience*. He is the founding editor of the journal *Cognitive Neuroscience* and is currently President of the British Association of Cognitive Neuroscience (BACN).

Preface to the fifth edition

The motivation for writing this book came out of my experiences of teaching cognitive neuroscience. When asked by students which book they should buy, I felt that none of the existing books would satisfactorily meet their needs. Other books in the market were variously too encyclopedic, too advanced or not up to date, or gave short shrift to explaining the methods of the field. My brief for writing this textbook was to provide a text that presents key ideas and findings but is not too long, that is up to date, and that considers both method and theory. I hope that it will be useful to both lecturers and students.

In writing a book on cognitive neuroscience I had to make a decision as to how much would be "cognitive" and how much would be "neuroscience." In my opinion, the theoretical underpinnings of cognitive neuroscience lie within the cognitive psychology tradition. Some of the most elegant studies using methods such as fMRI and TMS have been motivated by previous research in cognitive psychology and neuropsychology. The ultimate aim of cognitive neuroscience is to provide a brain-based account of cognition, and so the methods of cognitive neuroscience must necessarily speak to some aspect of brain function. However, I believe that cognitive neuroscience has much to learn from cognitive psychology in terms of which theoretically interesting questions to ask.

In Chapter 1, I discuss the current status of cognitive neuroscience as I see it. Some of the topics raised in this chapter are directly aimed at other researchers in the field who are skeptical about the merits of the methodologies including, in this revised edition, concerns about the replication of cognitive neuroscience findings. I hope that students who are new to the field will approach the topic with open-mindedness and a sense of optimism that the best is yet to come.

Chapter 2 is intended primarily as a reference source that can be referred back to. It is deliberately pitched at a need-to-know level.

Chapters 3 to 5 describe in detail the methods of cognitive neuroscience. The aim of an undergraduate course in cognitive neuroscience is presumably to enable students to critically evaluate the field, and in my opinion, this can only be achieved if the students fully understand the limitations of the methods on which the field is based. I also hope that these chapters will be of use to researchers who are starting out in the field.

Chapters 6 to 16 outline the main theories and findings in the field. I hope that they convey something of the excitement and optimism that currently exists. This fifth edition represents a substantial update in the form of a new chapter called The Conscious Brain (Chapter 15). This deals with topics such as levels of consciousness (coma, sleeping and dreaming, etc.), theories of consciousness (such as those derived from contrasting conscious and unconscious perception), and awareness of internal states (including mind-wandering). The previous chapters on Literacy and Numeracy have been merged into a single one (Chapter 13) with good integration between them and more focus on the core themes at undergraduate level.

The other significant addition is a revamp of the online material and the way in which it can be accessed from within the book itself (via QR codes). I have created a set of 15 minute "bitesize" videos that closely relate to content of the book. These are supplemented by "Short and Sweet" videos on closely related topics that are easy to digest (e.g., TED talks) and "Deeper Dive" longer, lecture-style talks by the leaders in this field. These sit alongside an updated set of pedagogical features such as flashcards and quizzes.

Jamie Ward
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Brighton, UK, July 2024

CHAPTER 1

Introducing cognitive neuroscience

CONTENTS

Between 1928 and 1947, Wilder Penfield and colleagues carried out a series of remarkable experiments on over 400 living human brains (Penfield & Rasmussen, 1950). The patients in question were undergoing brain surgery for epilepsy. To identify and spare regions of the brain involved in movement and sensation, Penfield electrically stimulated regions of the cortex while the patient was still conscious. The procedure was not painful (the surface of the brain does not contain pain receptors), but the patients did report some fascinating experiences. When stimulating the occipital lobe one patient reported, "a star came down toward my nose." Upon stimulating a region near the central sulcus, another patient commented, "those fingers and my thumb gave a jump." After temporal lobe stimulation, another patient claimed, "I heard the music again; it is like the radio." She was later able to recall the tune she heard and was absolutely convinced that there must have been a radio in the operating theater. Of course, the patients had no idea when the electrical stimulation was being applied – they couldn't physically feel it or see it. As far as they were concerned, an electrical stimulation applied to the brain felt pretty much like a mental/cognitive event.

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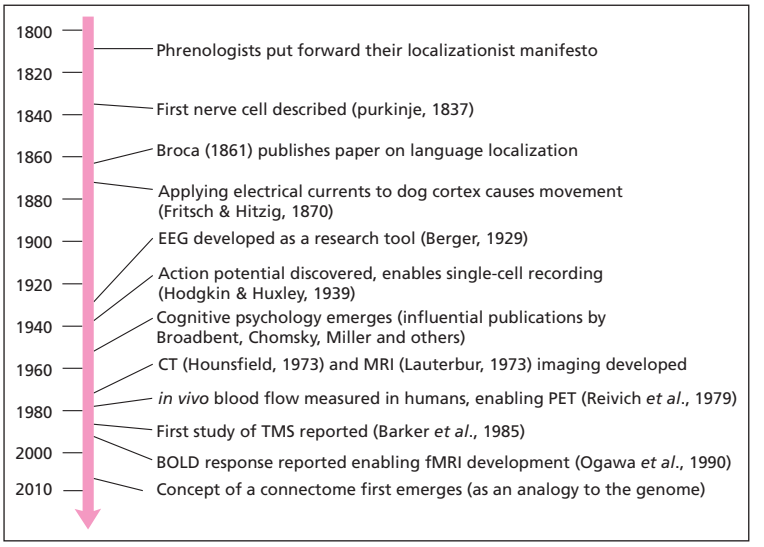

FIGURE 1.1: A timeline for the development of methods and findings relevant to cognitive neuroscience, from phrenology to present day.

KEY TERMS

Cognition
A variety of higher mental processes such as thinking, perceiving, imagining, speaking, acting, and planning.

Cognitive neuroscience
Aims to explain cognitive processes in terms of brain-based mechanisms.

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To discover more about Wilder Penfield and his pioneering research, watch the videos found on the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience).

This book tells the emerging story of how mental processes such as thoughts, memories, and perceptions are organized and implemented by the brain. It is also concerned with how it is possible to study the mind and brain and how we know what we know. The term **cognition** collectively refers to a variety of higher mental processes such as thinking, perceiving, imagining, speaking, acting, and planning. **Cognitive neuroscience** is a bridging discipline between cognitive science and cognitive psychology, on the one hand, and biology and neuroscience, on the other. It has emerged as a distinct enterprise only recently and has been driven by methodological advances that enable the study of the human brain safely in the laboratory (see Figure 1.1). It is perhaps not too surprising that earlier methods, such as direct electrical stimulation of the brain, failed to enter into the mainstream of research.

This chapter begins by placing a number of philosophical and scientific approaches to the mind and brain in a historical perspective. The coverage is selective rather than exhaustive, and students with a particular interest in these issues might want to read more deeply elsewhere (Wickens, 2015). The chapter then provides a basic overview of the current methods used in cognitive neuroscience. A more detailed analysis and comparison of the different methods is provided in Chapters 3 to 5. Finally, the chapter attempts to address some of the criticisms of the cognitive neuroscience approach that have been articulated and outlines how it can move forward.

COGNITIVE NEUROSCIENCE IN HISTORICAL PERSPECTIVE

Philosophical approaches to mind and brain

Philosophers, as well as scientists, have long been interested in how the brain can create our mental world. How is it that a physical

substance can give rise to our sensations, thoughts, and emotions? This has been termed the **mind–body problem**, although it should more properly be called the mind–brain problem, because it is now agreed that the brain is the key part of the body for cognition. One position is that the mind and brain are made up of different kinds of substance, even though they may interact. This is known as **dualism**, and the most famous proponent of this idea was René Descartes (1596–1650). Descartes believed that the mind was nonphysical and immortal, whereas the body was physical and mortal. He suggested that they interact in the pineal gland, which lies at the center of the brain and is now considered part of the endocrine system. According to Descartes, stimulation of the sense organs would cause vibrations in the body/brain that would be picked up in the pineal gland, and this would create a nonphysical sense of awareness. There is little hope for cognitive neuroscience if dualism is true because the methods of physical and biological sciences cannot tap into the nonphysical domain (if such a thing were to exist).

Even in Descartes' time, there were critics of his position. One can identify a number of broad approaches to the mind–body problem that still have a contemporary resonance. Spinoza (1632–1677) argued that mind and brain were two different levels of explanation for the same thing, but not two different kinds of thing. This has been termed **dual-aspect theory**, and it remains popular with some current researchers in the field (Velmans, 2000). An analogy can be drawn to wave–particle duality in physics, in which the same entity (e.g., an electron) can be described both as a wave and as a particle.

An alternative approach to the mind–body problem that is endorsed by many contemporary thinkers is **reductionism** (Churchland, 1995; Crick, 1994). This position states that, although cognitive, mind-based concepts (e.g., emotions, memories, attention) are currently useful for scientific exploration, they will eventually be replaced by purely biological constructs (e.g., patterns of neuronal firings, neurotransmitter release). As such, psychology will eventually reduce to biology as we learn more and more about the brain. Advocates of this approach note that there are many historical precedents in which scientific constructs are abandoned when a better explanation is found. In the seventeenth century, scientists believed that flammable materials contained a substance, called *phlogiston*, which was released when burned. This is similar to classical notions that fire was a basic element along with water, air, and earth. Eventually, this construct was replaced by an understanding of how chemicals combine with oxygen. The process of burning became just one example (along with rusting) of this particular chemical reaction. Reductionists believe that mind-based concepts, and conscious experiences in particular, will have the same status as phlogiston in a future theory of the brain. Those who favor dual-aspect theory over reductionism point out that an emotion would still *feel* like an emotion even if we were to fully

KEY TERMS

Mind–body problem
The problem of how a physical substance (the brain) can give rise to our sensations, thoughts, and emotions (our mind).

Dualism
The belief that mind and brain are made up of different kinds of substance.

Dual-aspect theory
The belief that mind and brain are two levels of description of the same thing.

Reductionism
The belief that mind-based concepts will eventually be replaced by neuroscientific concepts.

understand its neural basis and, as such, the usefulness of cognitive, mind-based concepts will never be fully replaced.

Scientific approaches to mind and brain

Our understanding of the brain emerged historically late, largely in the nineteenth century, although some important insights were gained during classical times. Aristotle (384–322 BC) noted that the ratio of brain size to body size was greatest in more intellectually advanced species, such as humans. Unfortunately, he made the error of claiming that cognition was a product of the heart rather than the brain. He believed that the brain acted as a coolant system: the higher the intellect, the larger the cooling system needed. In the Roman age, Galen (circa AD 129–199) observed brain injury in gladiators and noted that nerves project to and from the brain. Nonetheless, he believed that mental experiences themselves resided in the ventricles of the brain. This idea went essentially unchallenged for well over 1,500 years. For example, when Vesalius (1514–1564), the father of modern anatomy, published his plates of dissected brains, the ventricles were drawn in exacting detail, whereas the cortex was drawn crudely and schematically (see Figure 1.2). Others followed in this tradition, often drawing the surface of the brain like the intestines. This situation probably reflected a lack of interest in the cortex rather than a lack of penmanship. It is not until one looks at the drawings of Gall and Spurzheim (1810) that the features of the brain become recognizable to modern eyes.

Gall (1758–1828) and Spurzheim (1776–1832) received a bad press, historically speaking, because of their invention and advocacy of **phrenology**. Phrenology had two key assumptions: first, that different regions of the brain perform different functions and are associated with different behaviors; and second, that the size of these regions produces distortions of the skull and correlates with individual differences in cognition and personality. Taking these two ideas in turn, the notion of **functional specialization** within the brain has effectively endured into modern cognitive neuroscience, having seen off a number of challenges over the years (Flourens, 1824; Lashley, 1929). The observations of Penfield and coworkers on the electrically stimulated brain provide some striking examples of this principle. However, the functional specializations of phrenology were not based on controlled experiments and were not constrained by theories of cognition. For example, Fowler's famous phrenologist's head had regions dedicated to "parental love," "destructiveness," and "firmness" (Figure 1.3). Moreover, skull shape has nothing to do with cognitive function.

Although phrenology was fatally flawed, the basic idea of different parts of the brain serving different functions paved the way for future developments in the nineteenth century – the most notable of which are Broca's (1861) reports of two brain-damaged patients. Broca documented two cases in which acquired brain damage had impaired the ability to speak but left other aspects of cognition rel-

KEY TERMS

Phrenology
The failed idea that individual differences in cognition can be mapped onto differences in skull shape.

Functional specialization
Different regions of the brain are specialized for different functions.

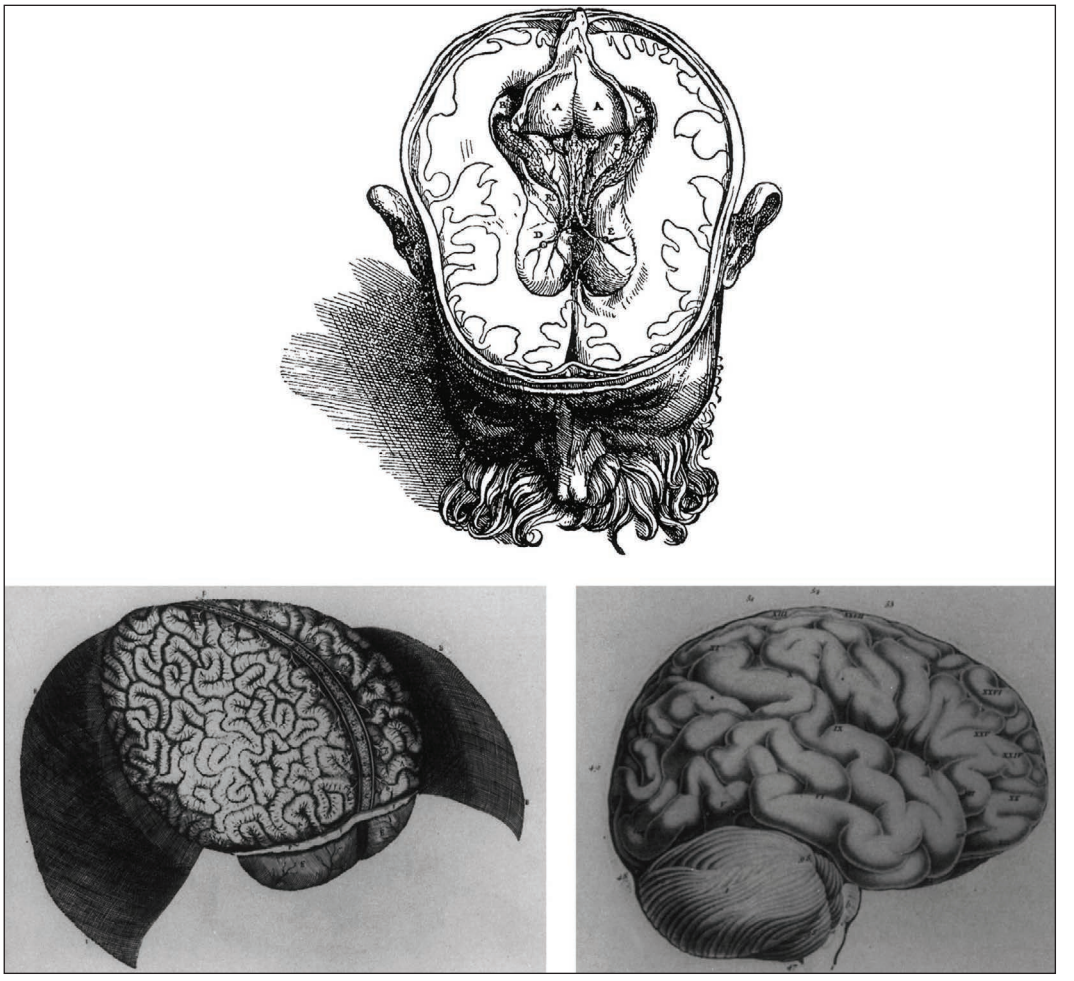

FIGURE 1.2: Drawings of the brain from Vesalius (1543) (top), de Viessens (1685) (bottom left), and Gall and Spurzheim (1810) (bottom right). Note how the earlier two drawings emphasized the ventricles and/or misrepresented the cortical surface.

atively intact. He concluded that language could be localized to a particular region of the brain. Subsequent studies argued that language itself was not a single entity but could be further subdivided into speech recognition, speech production, and conceptual knowledge (Lichtheim, 1885; Wernicke, 1874). This was motivated by the observation that brain damage can lead either to poor speech comprehension and good production, or good speech comprehension and poor production (see Chapter 12 for full details). This suggests that there are at least two speech faculties in the brain and that each can be independently impaired by brain damage. This body of work was a huge step forward in terms of thinking about mind and brain. First, empirical observations were being used to determine the building blocks of cognition (is language a single module?) rather than listing them from first principles. Second, and related, they were

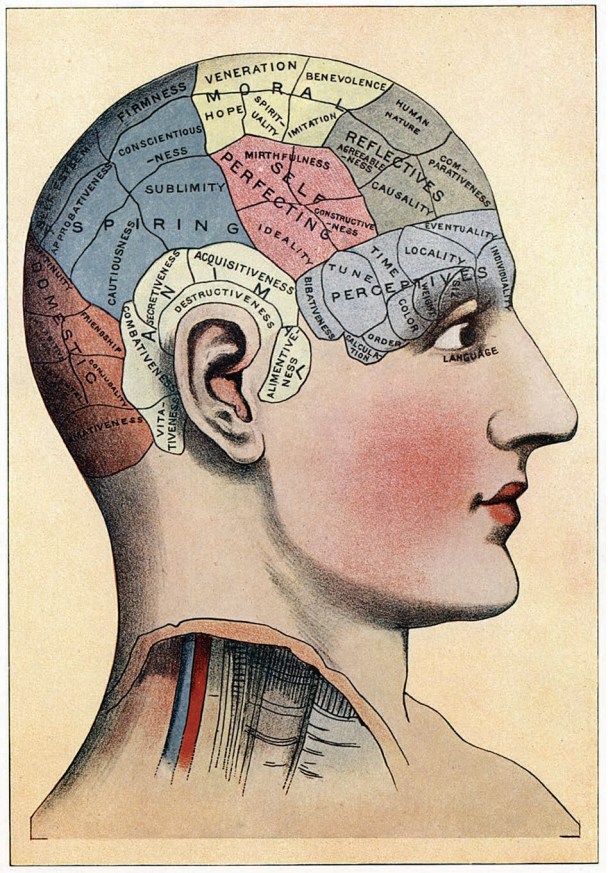

FIGURE 1.3: The phrenologist's head was used to represent the hypothetical functions of different regions of the brain.

World History Archive/Alamy Stock Photo

developing models of cognition that did not make direct reference to the brain. That is, one could infer that speech recognition and production were separable without necessarily knowing *where* in the brain they were located, or *how* the underlying neurons brought these processes about. The approach of using patients with acquired brain damage to inform theories of normal cognition is called **cognitive neuropsychology** and remains influential today (Chapter 5 discusses the logic of this method in detail). Cognitive neuropsychology is now effectively subsumed within the term "cognitive neuroscience," where the latter phrase is seen as being less restrictive in terms of methodology.

Whereas discoveries in the neurosciences continued apace throughout the nineteenth and twentieth centuries, the formation of psychology as a discipline at the end of the nineteenth century took the study of the mind away from its biological underpinnings. This did not reflect a belief in dualism. It was due, in part, to some pragmatic constraints. Early pioneers of psychology, such as William James and Sigmund Freud, were interested in topics like consciousness, attention, and personality. Neuroscience has had virtually nothing to say about these issues until quite recently. Another reason for the schism between psychology and biology lies in the notion that one can develop coherent and testable theories of cognition that do not make claims about the brain. The modern foundations of cognitive psychology lie in the computer metaphor of the brain and the **information-processing** approach, popular from the 1950s onwards. For example, Broadbent (1958) argued that much of cognition consists of a sequence of processing stages. In his simple model, perceptual processes occur, followed by attentional processes that transfer information to short-term memory and thence to long-term memory (see also Atkinson & Shiffrin, 1968). These were often drawn as a series of box-and-arrow diagrams (e.g., Figure 1.4). The implication was that one could understand the cognitive system in the same way as one could understand the series of steps performed by a computer program, and without reference to the brain.

The idea of the mind as a computer program has advanced over the years along with advances in computational science.

KEY TERMS

Cognitive neuropsychology
The study of brain-damaged patients to inform theories of normal cognition.

Information-processing
An approach in which behavior is described in terms of a sequence of cognitive stages.

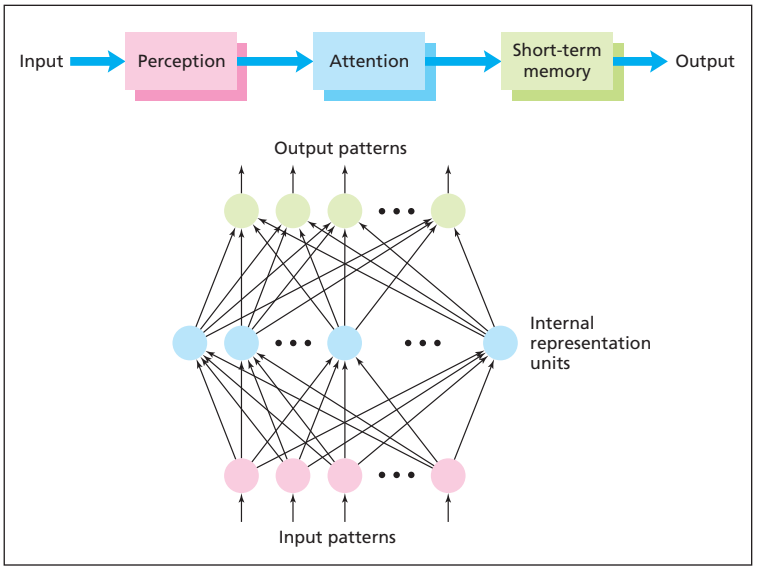

FIGURE 1.4: Examples of box-and-arrow and connectionist models of cognition. Both represent ways of describing cognitive processes that need not make direct reference to the brain.

For example, many cognitive models contain some element of interactivity and parallel processing. **Interactivity** refers to the fact that stages in processing may not be strictly separate and that later stages can begin before earlier stages are complete. Moreover, later stages can influence the outcome of early ones (**top-down processing**, in contrast to **bottom-up processing**). **Parallel processing** refers to the fact that lots of different information can be processed simultaneously (by contrast, serial computers process each piece of information one at a time). Although these computationally explicit models are more sophisticated than earlier box-and-arrow diagrams, they, like their predecessors, do not always make contact with the neuroscience literature. The same debates concerning biological plausibility hold true for the latest iterations of these models which are based on deep learning (Richards et al., 2019), where "deep" refers to the fact that there are multiple layers trying to predict and learn from each other.

The notion that the brain contains different regions of functional specialization has been around in various guises for 200 years. However, one particular variation on this theme has attracted particular attention and controversy – namely, Fodor's (1983, 1998) theory of **modularity**. First, Fodor makes a distinction between two different classes of cognitive process: central systems and modules. The key difference between them relates to the types of information they can process. Modules are held to demonstrate **domain specificity** in that they process only one particular type of information (e.g., color, shape, words, faces), whereas central systems are held to be domain independent in that the type

KEY TERMS

Interactivity
Later stages of processing can begin before earlier stages are complete.

Top-down processing
The influence of later stages on the processing of earlier ones (e.g., memory influences on perception).

Bottom-up processing
The passage of information from simpler (e.g., edges) to more complex (e.g., objects).

Parallel processing
Different information is processed at the same time (i.e., in parallel).

Modularity
The notion that certain cognitive processes (or regions of the brain) are restricted in the type of information they process.

Domain specificity
The idea that a cognitive process (or brain region) is dedicated solely to one particular type of information (e.g., colors, faces, words).

KEY TERMS

Neural network models
Computational models in which information processing occurs using many interconnected nodes.

Nodes
The basic units of neural network models that are activated in response to activity in other parts of the network.

of information processed is nonspecific (candidates would be memory, attention, executive functions). According to Fodor, one advantage of modular systems is that, by processing only a limited type of information, they can operate rapidly, efficiently, and in isolation from other cognitive systems. An additional claim is that modules may be innately specified in the genetic code. Many of these ideas have been criticized on empirical and theoretical grounds. For example, it has been suggested that domain specificity is not innate, although the means of acquiring it could be (Karmiloff-Smith, 1992). Moreover, systems like reading appear modular in some respects but cannot be innate because they are recent in evolution. Others have argued that evidence for interactivity suggests that modules are not isolated from other cognitive processes (Farah, 1994).

COMPUTATIONAL AND CONNECTIONIST MODELS OF COGNITION

In the 1980s, powerful computers became widely accessible as never before. This enabled cognitive psychologists to develop computationally explicit models of cognition (that literally calculate a set of outputs given a set of inputs) rather than the computationally inspired, but underspecified, box-and-arrow approach. One particular way of implementing computational models has been very influential; namely, the **neural network**, connectionist, or parallel distributed processing (PDP) approach (McClelland et al., 1986). These models are considered in a number of places throughout this book, notably in the chapters dealing with memory, speaking, and literacy.

Connectionist models have a number of architectural features. First, they are composed of arrays of simple information-carrying units called nodes. **Nodes** are information-carrying in the sense that they respond to a particular set of inputs (e.g., certain letters, certain sounds) and produce a restricted set of outputs. The responsiveness of a node depends on how strongly it is connected to other nodes in the network (the "weight" of the connection) and how active the other nodes are. It is possible to calculate, mathematically, what the output of any node would be, given a set of input activations and a set of weights. There are a number of advantages to this type of model. For example, by adjusting the weights over time as a result of experience, the model can develop and learn. The parallel processing enables large amounts of data to be processed simultaneously. A more controversial claim is that they have "neural plausibility." Nodes, activation, and weights are in many ways analogous to neurons, firing rates, and neural connectivity, respectively. However, these models have been criticized for being too powerful in that they can learn many things that real brains cannot (Pinker & Prince, 1988). A more moderate view is that connectionist models provide examples of ways in which the brain *might* implement a given cognitive function, and they generate new predictions that can then be tested. Whether or not the brain actually *does* implement cognition in that particular way will ultimately be a question for empirical research in cognitive neuroscience.

The latest wave of these models are **deep neural networks**, where the term "deep" denotes that fact that they have many layers. These are routinely used in everyday machine learning (/artificial intelligence) applications such as image recognition (e.g., to recognize that a photograph which has never been encountered before contains an elephant). In this example, although the network is trained on a set of images (elephant v. not elephant) the detailed operation of the deep layers is not hard-coded but emerges via experience. The responsiveness of nodes in different layers resembles, to some degree, the hierarchical nature of biological visual systems in which lower layers respond to simple features (e.g., edges) and higher ones to more complex ones (e.g., a trunk) (Güçlü & van Gerven, 2015).

The birth of cognitive neuroscience

KEY TERM

Deep neural networks
A neural network model containing multiple layers, typically producing a simple-to-complex hierarchy of information processing.

It was largely advances in imaging technology that provided the driving force for modern-day cognitive neuroscience. Raichle (1998) describes how brain imaging was in a "state of indifference and obscurity in the neuroscience community in the 1970s" and might never have reached prominence if it were not for the involvement of cognitive psychologists in the 1980s. Cognitive psychologists had already established experimental designs and information-processing models that could potentially fit well with these emerging methods. It is important to note that the technological advances in imaging not only led to the development of functional imaging but also enabled brain lesions to be described precisely in ways that were never possible before (except at postmortem).

Present-day cognitive neuroscience is composed of a broad diversity of methods. These will be discussed in detail in subsequent chapters. At this juncture, it is useful to compare and contrast some of the most prominent methods. The distinction between *recording* methods and *stimulation* methods is crucial in cognitive neuroscience. Direct electrical stimulation of the brain in humans is now rarely carried out as a research tool, although it has some therapeutic uses (e.g., in Parkinson's disease). The modern-day equivalent of these studies uses stimulation across the skull rather than directly to the brain (i.e., transcranially). This includes transcranial magnetic stimulation (TMS) and transcranial electrical stimulation (tES). These will be considered in Chapter 5, alongside the effect of organic brain lesions. Electrophysiological methods (EEG/ERP and single-cell recordings) and magnetophysiological methods (MEG) record the electrical and magnetic properties of neurons themselves. These methods are considered in Chapter 3. In contrast, functional imaging methods (PET, fMRI, and fNIRS) record physiological changes associated with blood supply to the brain, which evolve more slowly over time. These are called hemodynamic methods and are considered in Chapter 4.

Aside from stimulation versus recording, the methods of cognitive neuroscience can be placed on a number of other dimensions (see Figure 1.5):

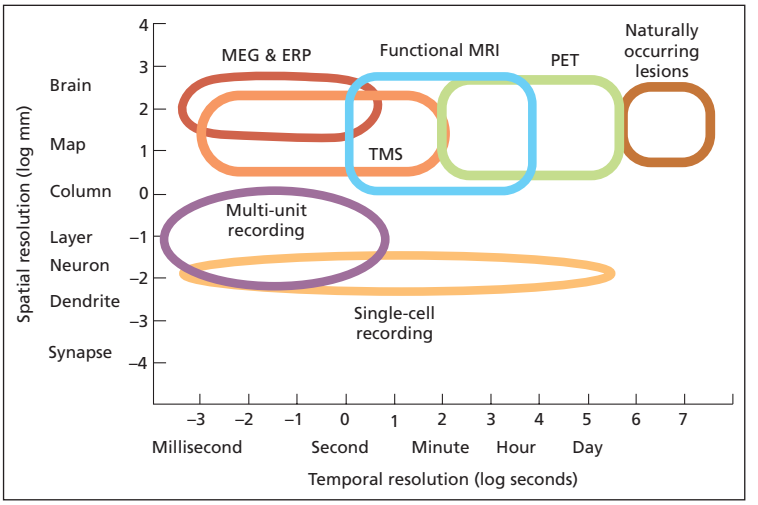

FIGURE 1.5: The methods of cognitive neuroscience can be categorized according to their spatial and temporal resolution.

Adapted from Churchland and Sejnowski (1988).

KEY TERMS

Temporal resolution
The accuracy with which one can measure when an event (e.g., a physiological change) occurs.

Spatial resolution
The accuracy with which one can measure where an event (e.g., a physiological change) is occurring.

- The **temporal resolution** refers to the accuracy with which one can measure *when* an event is occurring. The effects of brain damage are permanent and so this has no temporal resolution as such. Methods such as EEG, MEG, TMS, and single-cell recording have millisecond resolution. fMRI has a temporal resolution of several seconds that reflects the slower hemodynamic response.
- The **spatial resolution** refers to the accuracy with which one can measure *where* an event is occurring. Lesion and functional imaging methods have comparable resolution at the millimeter level, whereas single-cell recordings have spatial resolution at the level of the neuron.

THE DIFFERENT METHODS USED IN COGNITIVE NEUROSCIENCE

Method	Method type	Invasiveness	Brain property used
EEG/ERP	Recording	Noninvasive	Electrical
Single-cell (and multi-unit) recordings	Recording	Invasive	Electrical
TMS	Stimulation	Noninvasive	Electromagnetic
tES	Stimulation	Noninvasive	Electrical
MEG	Recording	Noninvasive	Magnetic
PET	Recording	Invasive	Hemodynamic
fMRI	Recording	Noninvasive	Hemodynamic
fNIRS	Recording	Noninvasive	Hemodynamic

- The *invasiveness* of a method refers to whether the equipment is located internally or externally. PET is invasive because it requires an injection of a radio-labeled isotope. Single-cell recordings are performed on the brain itself and are normally only carried out in nonhuman animals.

DOES COGNITIVE PSYCHOLOGY NEED THE BRAIN?

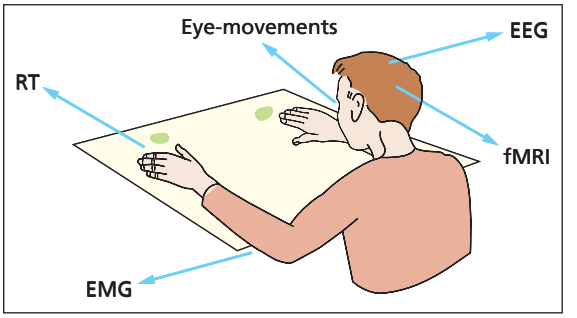

FIGURE 1.6: One could take many different measures in a forced-choice response task: behavioral (reaction time [RT], errors, eye-movements) or biological (electromyographic [EMG], BOLD response in fMRI or electrical activity in EEG). All measures could potentially be used to inform cognitive theory.

Adapted from Henson (2005). By kind permission of the Experimental Psychology Society.

As already noted, cognitive psychology developed substantially from the 1950s, using information-processing models that do not make direct reference to the brain. If this way of doing things remains successful, then why change? Of course, there is no reason why it should change. The claim is not that cognitive neuroscience is replacing cognitive psychology (although some might endorse this view), but merely that cognitive psychological theories can inform theories and experiments in the neurosciences and vice versa. However, others have argued that this is not possible by virtue of the fact that information-processing models do not make claims about the brain (Coltheart, 2004b; Harley, 2004).

Coltheart (2004b) poses the question:

> Has cognitive neuroscience, or if not might it ever (in principle, or even in practice), successfully used data from cognitive neuroimaging to make theoretical decisions entirely at the cognitive level (e.g. to adjudicate between competing information-processing models of some cognitive system)? (p. 21)

Henson (2005) argues that it can in principle and that it does in practice. He argues that data from functional imaging (blood flow, blood oxygen) comprise just another dependent variable that one can measure. For example, there are a number of things that one could measure in a standard forced-choice reaction-time task: reaction time, error rates, sweating (skin conductance response), muscle contraction (electromyograph), scalp electrical recordings (EEG), or hemodynamic changes in the brain (fMRI) – see Figure 1.6. Each measure will relate to the task in some way and can be used to inform theories about the task.

To illustrate this point, consider an example. One could ask a simple question such as, does visual recognition of words and letters involve computing a representation that is independent of case? For

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example, does the reading system treat "E" and "e" as equivalent at an early stage in processing, or are "E" and "e" treated as different letters until some later stage (e.g., saying them aloud)? A way of investigating this using a reaction-time measure is to present the same word twice in the same case (e.g., RADIO-RADIO) or different case (e.g., radio-RADIO) and compare this with situations in which the word differs (e.g., mouse-RADIO, MOUSE-RADIO). One general finding in reaction-time studies is that it is faster to process a stimulus if the same stimulus has recently been presented. For example, if asked to make a speeded decision about RADIO (e.g., is it animate or inanimate?), performance will be faster if it has been previously encountered. Dehaene et al. (2001) investigated this mechanism by comparing reaction-time measures with functional imaging (fMRI) measures. In this task, the first word in each pair was presented very briefly and was followed by visual noise. This prevented the participants from consciously perceiving it, and hence, one can be sure that they are not saying the word. The second word was consciously seen and requires a response. Dehaene *et al.* found that reaction times were faster to the second word when it follows the same word, irrespective of case. Importantly, there was a region in the left fusiform cortex that shows the same effect (although in terms of "activation" rather than response time). This is shown in Figure 1.7. In this concrete example, it is

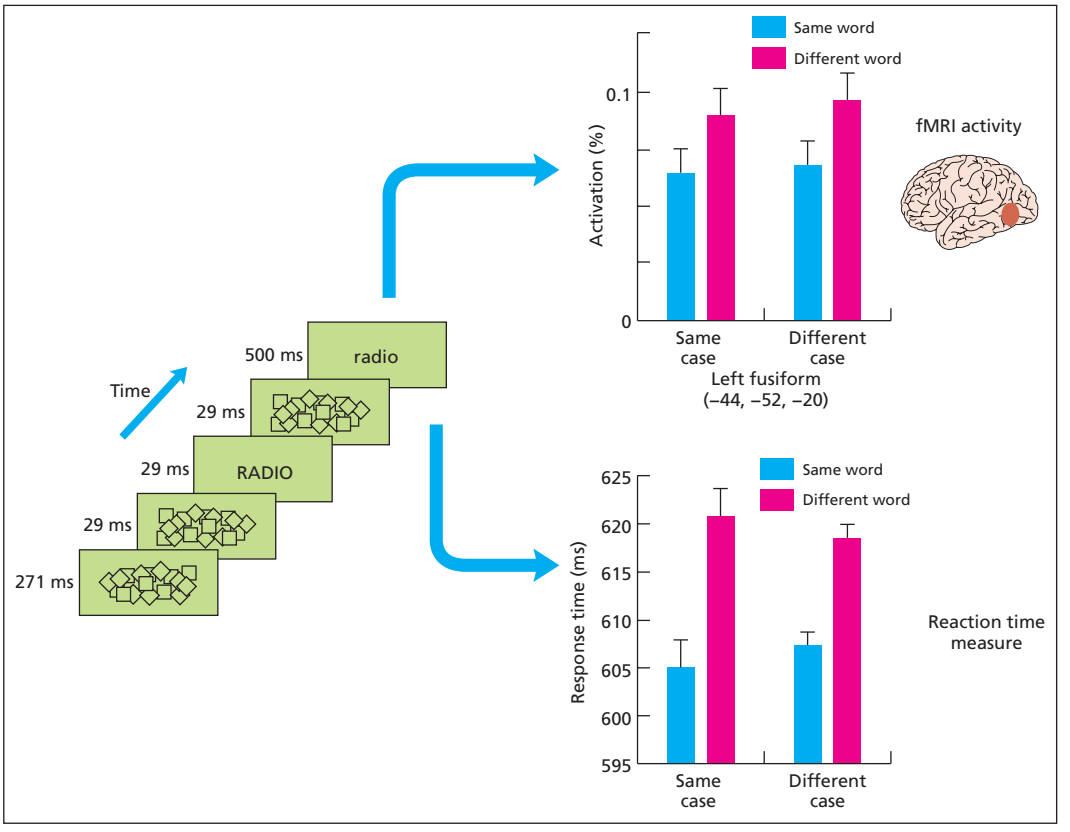

FIGURE 1.7: Both reaction times and fMRI activation in the left fusiform region demonstrate more efficient processing of words if they are preceded by subliminal presentation of the same word, irrespective of case.

Adapted from Dehaene et al. (2001).

meaningless to argue that one type of measure is "better" for informing cognitive theory (to return to Coltheart's question) given that both are measuring different aspects of the same event. One could explore the nature of this effect further by, for instance, presenting the same word in different languages (in bilingual speakers), presenting the words in different locations on the screen and so on. This would provide further insights into the nature of this mechanism (e.g., what aspects of vision does it entail? Does it depend on word meaning?). However, both reaction-time measures and brain-based measures could be potentially informative. It is not the case that functional imaging is merely telling us *where* cognition is happening and not *how* it is happening.

Another distinction that has been used to contrast cognitive psychology and cognitive neuroscience is that between software and hardware, respectively (Coltheart, 2004b; Harley, 2004). This derives from the familiar computer analogy in which one can, supposedly, learn about information processing (software) without knowing about the brain (hardware). As has been shown, to some extent this is true. But the computer analogy is a little misleading. Computer software is written by computer programmers (who, incidentally, have human brains). However, information processing is not written by some third person and then inscribed into the brain. Rather, the brain provides causal constraints, honed by evolution, on the nature of information processing. This is not analogous to the computer domain in which the link between software and hardware is arbitrarily determined by a computer programmer. To give a simple example, one model of visual word recognition suggests that words are recognized by searching words in a mental dictionary one by one until a match is found (Forster, 1976). The weight of evidence from cognitive psychology argues against this serial search, and in favor of words being searched in parallel (i.e., all candidate words are considered at the same time). But *why* does human cognition work like this? Computer programs can be made to recognize words adequately with both serial search and parallel search. The reason why human information processing uses a parallel search and not a serial search probably lies in the relatively slow *neural* response time (acting against serial search). This constraint does not apply to the fast processing of computers. Thus, cognitive psychology may be sufficient to tell us the structure of information processing, but it may not answer deeper questions about why information processing should be configured in that particular way. The biological constraints imposed by the brain shape the nature and limitations of cognition.

DOES NEUROSCIENCE NEED COGNITIVE PSYCHOLOGY?

It would be no exaggeration to say that the advent of techniques such as functional imaging has revolutionized the brain sciences.

FIGURE 1.8: The media loves to simplify the findings of cognitive neuroscience. Many newspaper stories appear to regard it as counterintuitive that sex, pain, and mood would be products of the brain.

Sunday Times, 21 November 1999; *Metro*, 5 January 2001; *The Observer*, 12 March 2000.

For example, consider some of the newspaper headlines that have appeared over the years (Figure 1.8). Of course, it has been well-known since the nineteenth century that pain, mood, intelligence, and sexual desire are largely products of processes in the brain. The reason headlines such as these are extraordinary is because now the technology exists to be able to study these processes *in vivo*. Of course, when one looks inside the brain one does not "see" memories, thoughts, perceptions, and so on (i.e., the stuff of cognitive psychology). Instead, what one sees is gray matter, white matter, blood vessels, and so on (i.e., the stuff of neuroscience). It is the latter, not the former, that one observes when conducting a functional imaging experiment. Developing a framework for linking the two will necessarily entail dealing with the mind–body problem either tacitly or explicitly. This is a daunting challenge.

Is functional imaging going to lead to a more sophisticated understanding of the mind and brain than was achieved by the phrenologists? Some of the newspaper reports in Figure 1.8 suggest it might not. One reason why phrenology failed is because the method had no real scientific grounding; the same cannot be said of functional imaging. Another reason why phrenology failed was that the psychological concepts used were naïve. It is for this reason that functional imaging and other advances in neuroscience do require

the insights from cognitive psychology to frame appropriate research questions and avoid becoming a new phrenology (Uttal, 2001).

The question of whether cognitive, mind-based concepts will eventually become redundant (under a reductionist account) or coexist with neural-based accounts (e.g., as in dual-aspect theory) is for the future to decide. But for now, cognitive, mind-based concepts have an essential role to play in cognitive neuroscience.

THE FUTURE OF COGNITIVE NEUROSCIENCE

What does the future of cognitive neuroscience look like? Although nobody knows for sure, there are clues from the current directions of travel. This final section will consider two shifts within the field: one theoretical and one more practical. In terms of a theoretical shift, there is a greater focus on understanding the mind and brain as a network. On a practical level there is a shift towards big data and more synthesizing approaches (such as meta-analyses) that are motivated by a desire to protect future cognitive neuroscience research from the so-called replication crisis. The **replication crisis** refers to systemic difficulties in being able to independently reproduce published results that have been documented in many scientific fields, which has eroded confidence in evidence and theories.

KEY TERMS

Replication crisis
Systemic difficulties in being able to independently reproduce published results that have been documented in many scientific fields.

Connectome
A comprehensive map of neural connections in the brain that may be thought of as its "wiring diagram."

From modules to networks

A network is a dynamically changing pattern of activity over several brain regions. Rather than thinking of the brain as a single network, there might be a multitude of different networks which are, themselves, switched on or off depending on the kind of thought or behavior that is needed. Thus, not only do brain regions have a degree of functional specialization, but entire networks may also have some specializations. This network approach is exemplified by current efforts to map the human **connectome** (Sporns, 2011). The Human Connectome Project was launched in 2010 at a cost of over $40M. The aim is to try to map out the pattern of connectivity in the human brain at a macro, that is, millimeter, scale (rather than the micro level of individual synapses). The project is based on MRI techniques that measure structural connectivity (essentially white matter fibers) and functional connectivity (essentially correlated patterns of brain activity between regions). By scanning and testing thousands of people it will be possible to identify differences in the connectome that are linked to disease and also, of particular relevance here, to understand how these networks support cognitive function. This can be done by, for instance, linking individual differences in the connectome to individual differences in specific cognitive abilities (Barch et al., 2013). Thus, it is not just an enterprise for biologists and neuroimagers – it also requires the input of psychologists who understand cognition.

KEY TERM

Graph theory
A mathematical technique for computing the pattern of connectivity (or "wiring diagram") from a set of correlations.

ONLINE RESOURCES

Delve deeper into the Human Connectome Project (humanconnectome.org) and watch TEDx talks on connectomics by Jeff Lichtman and David van Essen. Visit the Instructor & Student Resources website at routledgelearning.com/wardcognitiveneuroscience.

A complementary approach is to map the connectome at the micro scale of individual synapses. This is a daunting prospect as there are 10^{10} neurons linked by 10^{14} synaptic connections (Azevedo et al., 2009). By comparison, the size of a human genome is far smaller (3×10^{9}). Aside from the sheer scale of this challenge, there is no obvious way of interpreting the connectome "code" (unlike the genome where there is a simple mapping between the DNA code and the proteins they create).

Of course, networks are nothing new. Networks were there from the start in the form of black-box-and-arrow diagrams. However, the contemporary and emerging landscape looks very different from this. Firstly, the network architecture that supports cognition is derived from biologically based observations of the structural and functional connectome. This is supported by advanced mathematical tools such as **graph theory** (Bullmore & Sporns, 2009). This essentially creates a wiring diagram, rather like a subway map, in which some brain regions act as central hubs within the network (where several subway lines cross, in that analogy), and other regions are less connected (the suburbs, in that analogy). Secondly, there has been a shift away from conceptualizing the hubs in the network as highly specialized units. Instead, brain regions might perform a range of different functions depending on which other parts of the brain they are communicating with. A good example is Broca's region itself, which, whilst everyone agrees it is important for language, seems to also be involved in other cognitive processes such as detecting musical violations (Koelsch et al., 2006). So it may flexibly switch between processing language versus other kinds of information depending on the source of inputs at a given point in time.

Does this mean that the era of functional specialization, stretching from phrenology through to Broca and Penfield, is now over? This is certainly not the case. It has even been argued on first principles that if the brain is a network, then the different hubs in the network *must* have different functional specializations (Sporns & Betzel, 2016), except in the hypothetical scenario that all regions in the network connect equally strongly to each other (in which case each hub is identical). However, the function assigned to a region may be harder to map onto simple cognitive concepts in this new framework. For instance, the function of a brain region may be something like "integrating vision and speech" rather than "a store of words."

Thus, the central challenge for cognitive neuroscience for the future is to develop new ways of describing the relationship between brain structure (notably connectomics) and function (i.e., cognition and behavior). Barrett and Satpute (2013) offer a useful summary of three different approaches, as shown in Figure 1.9. In the first scenario (a), there is a very simple one-to-one mapping between different brain regions and different cognitive functions. Few researchers would endorse such a view. In the second scenario (b), there is still a high degree of specialization of brain regions, but multiple regions need to interact to generate a cognitive function. In the third scenario (c)

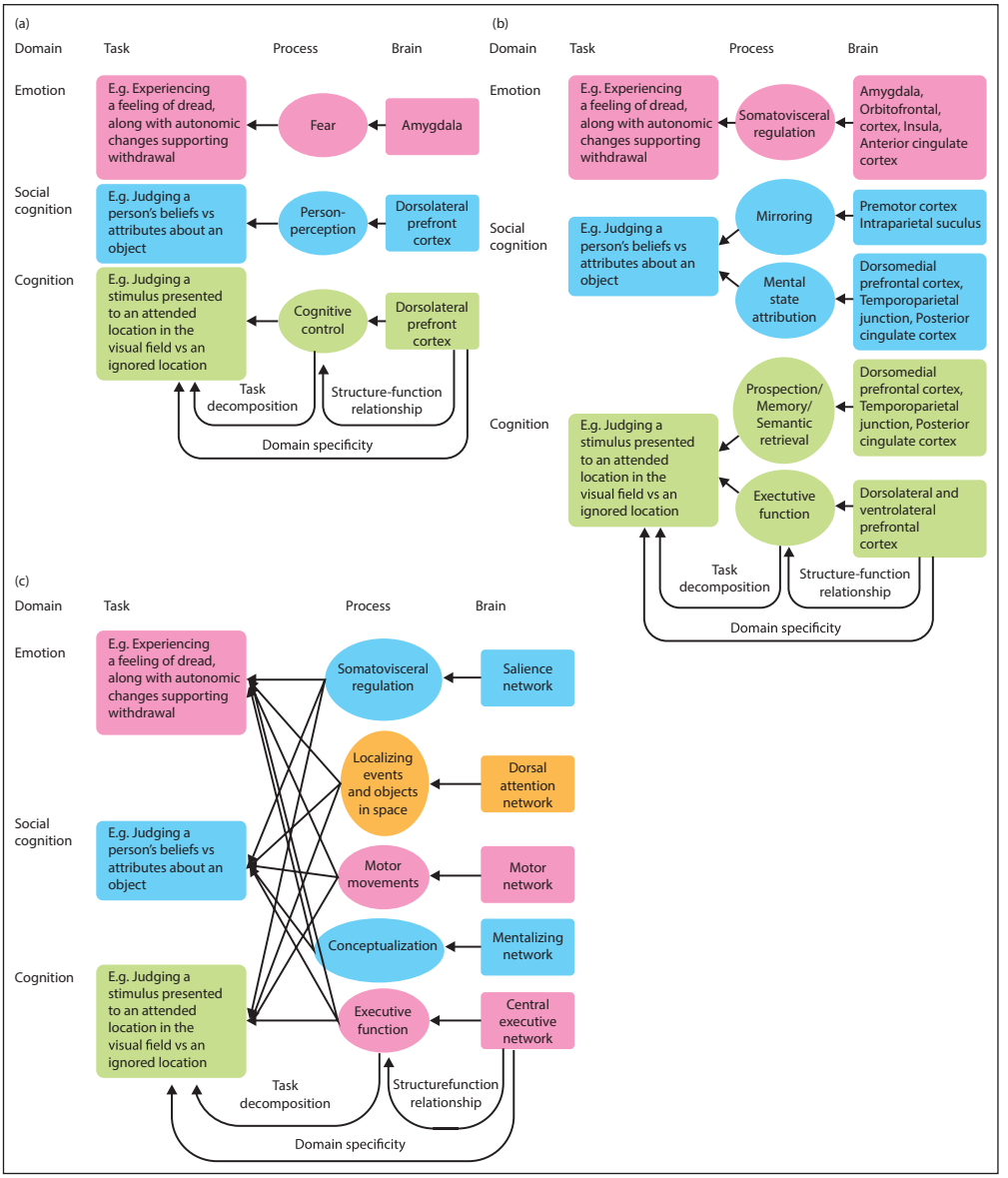

FIGURE 1.9: Three different ways in which different brain structures might be mapped to different functions (tasks and processes). In (a) there is a one-to-one association between brain structure and function whereas in both (b) and (c) a network of regions may make different contributions to a given function. In (b) the network consists of specialized units that interact, but in (c) the network consists of interactions between nonspecialized units.

From Barrett and Satpute (2013).

there is far less specialization of regions, and cognitive functions are generated by the interaction of multiple networks (with each network having some specialization). Barrett and Satpute (2013) favor this third option, although others argue that the cognitive architecture of the brain is more like the second option (Vytal &

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KEY TERMS

Reproducibility
Ability to examine and validate an existing set of analyses.

Replicability
Ability to repeat an experimental design and analysis on an independent sample and achieve the same results.

A power analysis
A statistical method for determining a required sample size given a likely effect size (whether a variable is strong or weak) and the probability of detecting it (due to sample variability).

Meta-analysis
A statistical method for pooling across equivalent datasets (based on a weighted average of effect sizes).

Hamann, 2010). The next generation of cognitive neuroscientists may be able to resolve these debates or propose new ways of understanding cognition in terms of the specializations and network-based structures of the brain.

Research reform in cognitive neuroscience

There are significant concerns around the ability to replicate and reproduce scientific findings (Ioannidis, 2005; Korbmacher et al., 2023), including those relating to cognitive neuroscience. **Reproducibility** refers to being able to examine and validate an existing set of analyses, and **replicability** refers to being able to repeat an experimental design and analysis on an independent sample and achieve the same results. To some extent variability in findings are to be expected: we are not all the same, and even within individuals, our behavior is never perfectly consistent. There can be random fluctuations, or uncontrolled variables like mood or time of day. As such, there is an element of judgment as to how much variability one can expect and how much one is willing to tolerate. If one is trying to detect a small effect in the brain, then this would be harder to detect against the background noise (random and uncontrolled variability), and one would need a larger sample so that the noise would be averaged out. But a larger effect would stand out more against this background noise and a smaller sample may suffice. **A power analysis** is one formal way of estimating, in advance, the size of the sample needed to produce the size of the effect that is expected (effect size) and the likelihood of finding it, if it exists (termed power). The smaller the effect size that one is trying to detect, then the larger the sample size that one will need to reliably detect it.

If a published finding replicates only half of the time, then we may be tempted to dismiss it as junk. But that conclusion is too hasty. One needs to remember that a judgment of statistical significance is indeed just a judgment rather than a statement of fact. We commonly apply a statistical threshold such as $p < .05$ meaning that there is a less than a 5 percent probability that it is a purely junk finding (also called a type 1 error). If someone did publish such a junk finding, then others would be able to replicate it only 1 in 20 times just by chance ($p < .05$ is equivalent to 1 in 20). So a result that replicates half of the time (i.e., 1 in 2 successful replications) could be considered good odds! On what basis could we have confidence in drawing conclusion from a conflicting set of evidence? One possibility is to pool all the datasets (significant and nonsignificant) into a **meta-analysis**. A meta-analysis calculates a weighted average of all the effects (so a study with a larger sample gets weighted more) and then tests the significance of this aggregate data. It also increases statistical power by increasing the overall size of the sample. A significant result in a meta-analysis would give confidence in the overall finding. But even here there can still be room for doubt. Imagine that for every 20 labs that run the experiment, only one gets a significant result (they publish it),

and the other 19 labs find nothing at all. One lab publishes a null result and the other 18 labs put it in the file-drawer – this is called the **file-drawer problem**. In this scenario it would also appear like 1 in 2 studies have produced a positive finding, but that is untrue. The possible solutions to the file-drawer problem are as follows: try to search for unpublished results when running a meta-analysis; reform the publishing system to be more accepting of nonsignificant findings; engage in more collaborative multi-lab studies from the outset (so the level of replicability is explicitly measured). Of course, there could also be interesting reasons why a study does not replicate, such as cross-cultural differences, sampling differences in age or gender, and so on. The bottom line: lack of replication is a real problem, and it can occur for many reasons, not all of which reflect bad science or require a wholesale rejection of the findings.

Variability in research findings can also occur because the person conducting the analysis has been confronted with a large number of arbitrary analysis choices. These include the criteria on which trials or participants are excluded, the exact choice of statistical test, and so on. Neuroimaging analyses can have lots of these kinds of decisions, and some of these arbitrary decisions may result in statistical significance and others not. Of course, there could easily be 20+ permutations of an analysis pipeline with the result that meaningless data can appear as statistically significant but have no hope of independent replication (except by chance). **P-hacking** is said to have occurred if a researcher has analyzed the data in multiple ways but has chosen to publish a favorable, statistically significant analysis. The famous example here comes from putting a dead salmon in an MRI scanner and showing the subject two different kinds of images (Figure 1.10). (Bennett et al., 2009). Given the "right" choice of analysis, the dead salmon's brain appeared active when comparing the two conditions! Of course, this "experiment" was set up to illustrate the principle of p-hacking rather than as an attempt at serious science. The recommended practice for avoiding p-hacking, or any insinuation of p-hacking, is to put the analysis plan in the public domain before running it, and ideally before collecting any data at all. This is referred to as a **pre-registration** or

KEY TERMS

File-drawer problem
The tendency for non-significant results to be unpublished.

P-hacking
Analyzing the data in multiple ways and choosing to publish a single favorable analysis.

Pre-registration
An open set of hypotheses and analysis plan that is posted prior to conducting the analysis.

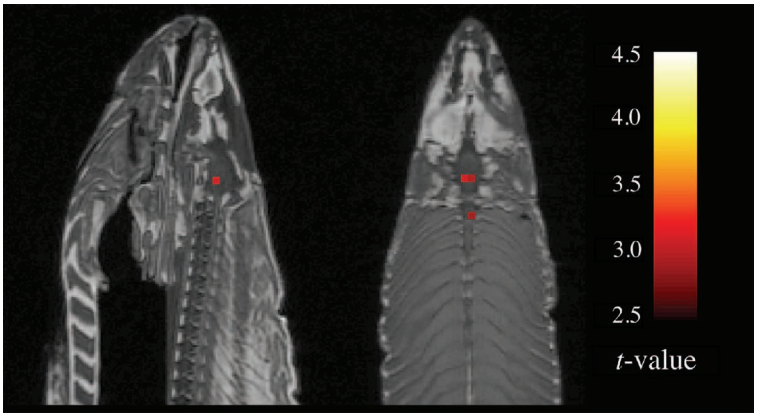

FIGURE 1.10: fMRI activity from a dead salmon? No way! But if you analyze a complex dataset enough times, with a hypothesis to prove, you could generate the expected results. Bennett et al. (2009).

KEY TERMS

Registered report
Peer-reviewed scientific paper in which hypotheses, methods, and analysis are reviewed prior to data collection.

HARKing
Hypothesizing after the results are known.

Multiverse analysis
Performing multiple analyses of the same dataset across all reasonable options for excluding, transforming, and coding data.

a **registered report** (where the latter refers to a method and analysis plan that has been peer-reviewed). Registering your hypotheses before analyzing the data also guards against changing one's hypotheses in light of the results or so-called **HARKing**, or hypothesizing after the results are known (Kerr, 1998).

One important study examined the reproducibility (note: as opposed to replicability) of a neuroimaging finding by giving 70 teams of researchers the same dataset and the same stated hypotheses but no detailed guidance on the analysis plan (Botvinik-Nezer et al., 2020). No two teams produced identical analysis workflows, and there was considerable variability in the exact results. Nevertheless, a meta-analytic approach identified a core set of similar findings that were common across approaches. Some lessons from this exercise include the importance of sharing analysis code (and not just data) to ensure reproducibility and the possible benefits of trying multiple analyses, providing this is done in a transparent way. This kind of approach is sometimes called a **multiverse analysis** (Steegen et al., 2016) and can be used to assess the robustness of findings against arbitrary choices in analysis.

TOP TIPS FOR A MORE ROBUST COGNITIVE NEUROSCIENCE

- Open science involves making all your research material freely available for reuse. This is the key to reproducibility and for creating larger, aggregated datasets (e.g., for a meta-analysis).
- Transparency in the hypotheses and analysis plan (ideally before data collection and certainly before data analysis) protects the field against p-hacking and HARKing.
- Justify your sample size formally (e.g., with a power analysis), and don't just rely on previously published sample sizes.
- Replicate your own results before you publish them.
- A nonsignificant result could be weak or inconclusive evidence (as opposed to evidence of absence). There are ways of testing the null hypothesis that don't rely on p-values (Dienes, 2014).

In summary, it is important to approach research findings with a healthy skepticism but not to be overly dismissive of variability in findings. Some variability is to be expected and can occur for interesting reasons. There are good grounds to be optimistic given that there is now a strong consensus on best practice including more transparency, prior to analysis, and data sharing and pooling. These kinds of developments may lead to a step change, or Cognitive Neuroscience 2.0 (Yarkoni et al., 2010).

SUMMARY AND KEY POINTS OF THE CHAPTER

- The mind–body problem refers to the question of how physical matter (the brain) can produce mental experiences, and this remains an enduring issue in cognitive neuroscience.
- To some extent, the different regions of the brain are specialized for different functions.
- Functional neuroimaging has provided the driving force for much of the development of cognitive neuroscience, but there is a danger in merely using these methods to localize cognitive functions without understanding how they work.
- Cognitive psychology has developed as a discipline without making explicit references to the brain. However, biological measures can provide an alternative source of evidence to inform cognitive theory, and the brain must provide constraining factors on the nature and development of the information-processing models of cognitive science.
- Attempting to map the human connectome, and link it to cognition, is the greatest challenge for the next generation of cognitive neuroscientists. Although old concepts will remain (e.g., the idea of functional specialization), they may be understood in entirely new ways.
- There are concerns about the extent to which findings in cognitive neuroscience will replicate or reproduce (as in most disciplines), but there are now agreed methods to tackle this.

EXAMPLE ESSAY QUESTIONS

- What is the "mind–body problem" and what frameworks have been put forward to solve it?
- Is cognitive neuroscience the new phrenology?
- Does cognitive psychology need the brain? Does neuroscience need cognitive psychology?
- What are the challenges and solutions for producing reproducible and replicable research findings in cognitive neuroscience?

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CHAPTER 2

Introducing the brain

CONTENTS

It is hard to begin a chapter about the brain without waxing lyrical. The brain is the physical organ that makes all our mental life possible. It enables us to read these words and to consider thoughts that we have never considered before – or even to create thoughts that no human has considered before. This book will scratch the surface of how this is all possible, but the purpose of this chapter is more mundane. It offers a basic guide to the structure of the brain, starting from a description of neurons and working up to a description of how these are organized into different neuroanatomical systems. The emphasis is on the human brain rather than the brain of other species.

STRUCTURE AND FUNCTION OF THE NEURON

All **neurons** have basically the same structure, as shown in Figure 2.1. They consist of three components: a **cell body** (or soma), **dendrites**, and an **axon**. Although neurons have the same basic structure and function, it is important to note that there are

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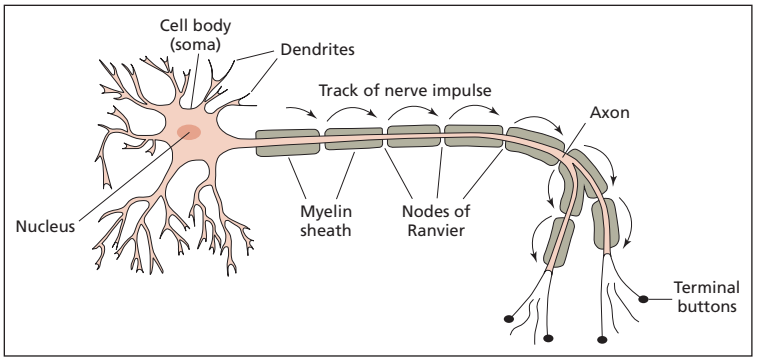

FIGURE 2.1: Neurons consist of three basic features: a cell body, dendrites that receive information, and axons that send information. In this diagram the axon is myelinated to speed the conduction time.

KEY TERMS

Neuron
A type of cell that makes up the nervous system and supports, among other things, cognitive function.

Cell body
Part of the neuron containing the nucleus and other organelles.

Dendrites
Branching structures that carry information from other neurons.

Axon
A branching structure that carries information to other neurons and transmits an action potential.

some significant differences between different types of neurons in terms of the spatial arrangements of the dendrites and axon.

The cell body contains the nucleus and other organelles. The nucleus contains the genetic code, and this is involved in protein synthesis. Proteins serve a wide variety of functions from providing scaffolding to chemical signaling (they can act as neurotransmitters and receptors in neurons). Neurons receive information from other neurons, and they make a "decision" about this information (by changing their own activity) that can then be passed on to other neurons. From the cell body, a number of branching structures called dendrites enable communication with other neurons. Dendrites receive information from other neurons in close proximity. The number and structure of the dendritic branches can vary significantly depending on the type of neuron (i.e., where it is to be found in the brain). The axon, by contrast, sends information to other neurons. Each neuron consists of many dendrites but only a single axon (although the axon may be divided into several branches called collaterals).

TEN INTERESTING FACTS ABOUT THE HUMAN BRAIN

(1) There are 86 billion neurons in the human brain (Azevedo et al., 2009).
(2) Each neuron connects with around 10,000 other neurons. As such, there are over 3,000 times as many synapses in one person's brain than there are stars in our whole galaxy.
(3) If each neuron connected with every single other neuron, our brain would be 12.5 miles in diameter (Nelson & Bower, 1990). This is the length of Manhattan Island. This leads to an important conclusion – namely, that neurons only connect with a small subset of other neurons. Neurons tend to communicate only with their neighbors in what has been termed a "small-world" architecture (Sporns & Zwi, 2004). Long-range connections are the exception rather than the rule.
(4) The idea that we only use 10 percent of the cells in our brain is generally considered a myth (Beyerstein, 1999). It used to be thought that only around 10 percent of the cells in the brain were neurons (the rest being cells called glia), hence a plausible origin for

the myth. This "fact" also turns out to be inaccurate, with the true ratio of neurons to glia being closer to 1:1 (Azevedo et al., 2009). Glia serve a number of essential support functions; for example, they are involved in tissue repair and in the formation of myelin.

(5) The brain makes up only 2 percent of body weight.

(6) It is no longer believed that neurons in the brain are incapable of being regenerated. It was once widely believed that we are born with our full complement of neurons and that new neurons are not generated. This idea is now untenable, at least in a region called the dentate gyrus (for a review, see Gross, 2000).

(7) On average, we lose a net amount of one cortical neuron per second. A study has shown that around 10 percent of our cortical neurons perish between the ages of 20 and 90 years – equivalent to 85,000 neurons per day (Pakkenberg & Gundersen, 1997).

(8) Identical twins do not have anatomically identical brains. A comparison of identical and nonidentical twins suggests that the three-dimensional cortical gyral pattern is determined primarily by non-genetic factors, although brain size is strongly heritable (Bartley et al., 1997).

(9) People with autism have larger brains in early life (Abell et al., 1999). They also have large heads to accommodate them (Redcay & Courchesne, 2005). There is unlikely to be a simple relationship between brain size and intellect, and brain efficiency may be unrelated to size.

(10) Men have larger brains than women, but the female brain is more folded, implying a relative increase in surface area that may offset any size difference (Luders et al., 2004). The total number of cortical neurons is related to gender, but not overall height or weight (Pakkenberg & Gundersen, 1997).

The terminal of an axon flattens out into a disc-shaped structure. It is here that chemical signals enable communication between neurons via a small gap termed a **synapse**. The two neurons forming the synapse are referred to as presynaptic (before the synapse) and postsynaptic (after the synapse), reflecting the direction of information flow (from axon to dendrite). When a presynaptic neuron is active, an electrical current (termed an **action potential**) is propagated down the length of the axon. When the action potential reaches the axon terminal, chemicals are released into the synaptic cleft. These chemicals are termed **neurotransmitters**. (Note that a small proportion of synapses, such as retinal gap junctions, signal electrically and not chemically.) Neurotransmitters bind to receptors on the dendrites or cell body of the postsynaptic neuron and create a synaptic potential. The synaptic potential is conducted passively (i.e., without creating an action potential) through the dendrites and soma of the postsynaptic neuron. These passive currents form the basis of EEG. These different passive currents are summed together, and if their summed activity exceeds a certain threshold when they reach the beginning of the axon in the postsynaptic neuron, then an action potential (an *active* electrical current) will be triggered in this neuron. In this way, different neurons can be said to be

KEY TERMS

Synapse
The small gap between neurons in which neurotransmitters are released, permitting signaling between neurons.

Action potential
A sudden change (depolarization and repolarization) in the electrical properties of the neuron membrane in an axon, which forms the basis for how neurons code information (in the form of the rate and synchrony of action potentials).

Neurotransmitters
Chemical signals that are released by one neuron and affect the properties of other neurons.

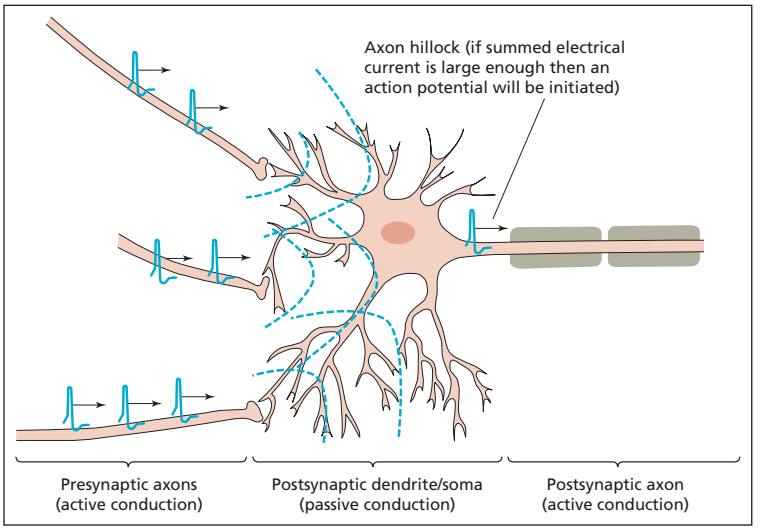

FIGURE 2.2: Electrical currents are actively transmitted through axons by an action potential. Electrical currents flow passively through dendrites and soma of neurons but will initiate an action potential if their summed potential is strong enough at the start of the axon (called the hillock).

"communicating" with each other. This is shown in Figure 2.2. It is important to note that each postsynaptic neuron sums together many synaptic potentials, which are generated at many different and distant dendritic sites (in contrast to a simple chain reaction between one neuron and the next). Passive conduction tends to be short range because the electrical signal is impeded by the resistance of the surrounding matter. Active conduction enables long-range signaling between neurons by the propagation of action potentials.

Electrical signaling and the action potential

Each neuron is surrounded by a cell membrane that acts as a barrier to the passage of certain chemicals. Within the membrane, certain protein molecules act as gatekeepers and allow particular chemicals in and out under certain conditions. These chemicals consist, among others, of charged sodium (Na^+) and potassium (K^+) ions. The balance between these ions on the inside and outside of the membrane is such that there is normally a resting potential of −70 mV across the membrane (the inside being negative relative to the outside).

Voltage-gated ion channels are of particular importance in the generation of an action potential. They are found only in axons, which is why only the axon is capable of producing action potentials. The sequence of events is as follows (see also Figure 2.3):

1. If a passive current of sufficient strength flows across the axon membrane, this begins to open the voltage-gated Na^+ channels.
2. When the channel is opened, then Na^+ may enter the cell and the negative potential normally found on the inside is reduced (the

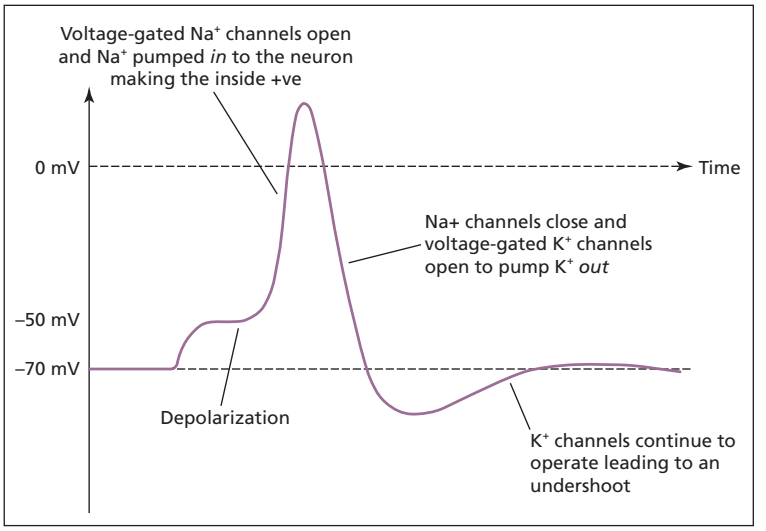

FIGURE 2.3: The action potential consists of a number of phases.

cell is said to *depolarize*). At about −50 mV, the cell membrane becomes completely permeable, and the charge on the inside of the cell momentarily reverses. This sudden depolarization and subsequent repolarization in electrical charge across the membrane is the action potential.

3. The negative potential of the cell is restored via the *outward* flow of K^+ through voltage-gated K^+ channels and closing of the voltage-gated Na^+ channels.
4. There is a brief period in which hyperpolarization occurs (the inside is more negative than at rest). This makes it more difficult for the axon to depolarize straight away and prevents the action potential from traveling backwards.

An action potential in one part of the axon opens adjacent voltage-sensitive Na^+ channels, and so the action potential moves progressively down the length of the axon, starting from the cell body and ending at the axon terminal. The conduction of the action potential along the axon may be speeded up if the axon is myelinated. **Myelin** is a fatty substance that is deposited around the axon of some cells (especially those that carry motor signals). It blocks the normal Na^+/K^+ transfer, and so the action potential jumps, via passive conduction, down the length of the axon at the points at which the myelin is absent (called *nodes of Ranvier*). Destruction of myelin is found in a number of pathologies, notably *multiple sclerosis*.

KEY TERM

Myelin
A fatty substance that is deposited around the axon of some neurons that speeds conduction.

Chemical signaling and the postsynaptic neuron

When the action potential reaches the axon terminal, the electrical signal initiates a sequence of events leading to the release of

neurotransmitters into the synaptic cleft. Protein *receptors* in the membrane of the postsynaptic neurons bind to the neurotransmitters. Many of the receptors are transmitter-gated ion channels (not to be confused with voltage-gated ion channels found in the axon). This sets up a localized flow of charged Na^+, K^+, or chloride (Cl^-), which creates the synaptic potential. Some neurotransmitters (e.g., GABA) have an inhibitory effect on the postsynaptic neuron (i.e., by making it less likely to fire). This can be achieved by making the inside of the neuron more negative than normal and hence harder to depolarize (e.g., by opening transmitter-gated Cl^- channels). Other neurotransmitters (e.g., glutamate) have excitatory effects on the postsynaptic neuron (i.e., by making it more likely to fire). These synaptic potentials are then passively conducted as already described.

Glutamate and GABA are the workhorse neurotransmitters of the brain in that nearly every neuron produces one or other of these. Note that it is not the chemicals themselves that make them excitatory and inhibitory. Rather it is the effect that they have on ion channels in the membrane which either pump positive or negative ions, thus making an action potential more or less likely. Other common neurotransmitters are serotonin, dopamine, acetylcholine, and noradrenaline. These are often considered to have modulatory functions. Rather than being distributed throughout the brain, as is the case with GABA and glutamate, the cell bodies of the neurons that release these neurotransmitters tend to be localized to specific brain areas, but their axonal projections spread diffusely throughout the brain.

How do neurons code information?

The amplitude of an action potential does not vary, but the number of action potentials propagated per second varies along a continuum. This rate of responding (also called the spiking rate) relates to the informational "code" carried by that neuron. For example, some neurons may have a high spiking rate in some situations (e.g., during speech) but not others (e.g., during vision), whereas other neurons would have a complementary profile. Neurons responding to similar types of information tend to be grouped together. This gives rise to the functional specialization of brain regions that was introduced in Chapter 1.

If information is carried in the response rate of a neuron, what determines the *type* of information that the neuron responds to? The type of information that a neuron carries is related to the input it receives and the output it sends to other neurons. For example, the reason neurons in the primary auditory cortex can be considered to carry information about sound is because they receive input from a pathway originating in the cochlea and they send information to other neurons involved in more advanced stages of auditory processing (e.g., speech perception). However, imagine that one were to rewire the brain such that the primary auditory cortex was

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to receive inputs from the retinal pathway, originating in the eyes, rather than the auditory pathway (Sur & Leamey, 2001). In this case, the function of the primary "auditory" cortex would have changed (as would the type of information it carries) even though the region itself was not directly modified (only the inputs to it were modified). This general point is worth bearing in mind when one considers what the function of a given region is. The function of a region is determined by its inputs and outputs. As such, the extent to which a function can be strictly localized is a moot point.

THE GROSS ORGANIZATION OF THE BRAIN

Gray matter, white matter, and cerebrospinal fluid

Neurons are organized within the brain to form white matter and gray matter. **Gray matter** consists of neuronal cell bodies. **White matter** consists of axons and support cells (**glia**). The brain consists of a highly convoluted folded sheet of gray matter (the cerebral cortex), beneath which lies the white matter. In the center of the brain, beneath the bulk of the white matter fibers, lies another collection of gray matter structures (the subcortex), which includes the basal ganglia, the limbic system, and the diencephalon.

White matter tracts may project between different cortical regions within the same hemisphere (called *association tracts*), or project between different cortical regions in different hemispheres (called *commissures*; the most important commissure being the **corpus callosum**) or may project between cortical and subcortical structures (called *projection tracts*) – see Figure 2.4.

The brain also contains a number of hollow chambers termed **ventricles**, shown in Figure 2.5. These were incorrectly revered for 1,500 years as being the seat of mental life. The ventricles are filled with *cerebrospinal fluid* (CSF), which does serve some useful functions, albeit non-cognitive. The CSF carries waste metabolites, transfers some messenger signals, and provides a protective cushion for the brain.

KEY TERMS

Gray matter
Matter consisting primarily of neuronal cell bodies.

White matter
Tissue of the nervous system consisting primarily of axons and support cells.

Glia
Support cells of the nervous system involved in tissue repair and in the formation of myelin (among other functions).

Corpus callosum
A large white matter tract that connects the two hemispheres.

Ventricles
The hollow chambers of the brain that contain cerebrospinal fluid.

A hierarchical view of the central nervous system

Brain evolution can be thought of as adding additional structures onto older ones, rather than replacing older structures with newer ones. For example, the main visual pathway in humans travels from the retina to the occipital lobe, but a number of older visual pathways also exist and contribute to vision (see Chapter 7). These older pathways constitute the dominant form of seeing for other species such as birds and reptiles. Figure 2.6 illustrates the major structures of the brain, showing a hierarchical arrangement (older structures toward the bottom of the diagram).

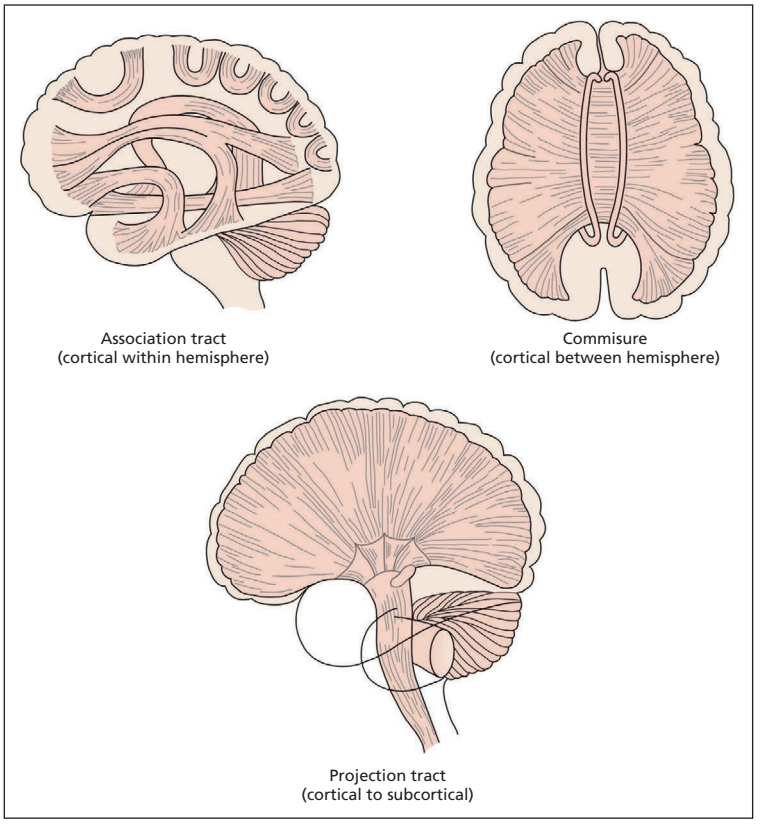

FIGURE 2.4: There are three different kinds of white matter tract, depending on the nature of the regions that are connected.

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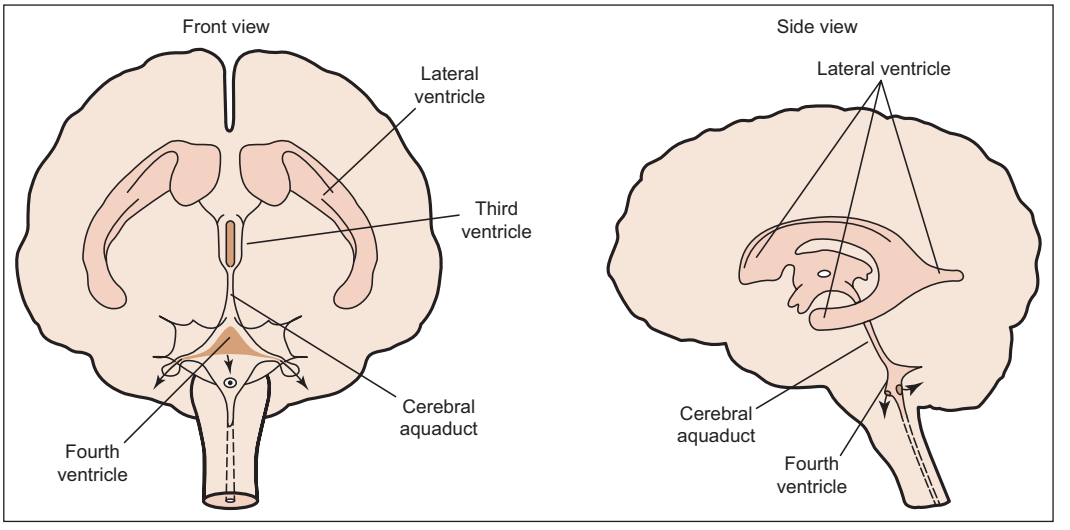

FIGURE 2.5: The brain consists of four ventricles filled with cerebrospinal fluid (CSF): the lateral ventricles are found in each hemisphere, the third ventricle lies centrally around the subcortical structures, and the fourth ventricle lies in the brainstem (hindbrain).

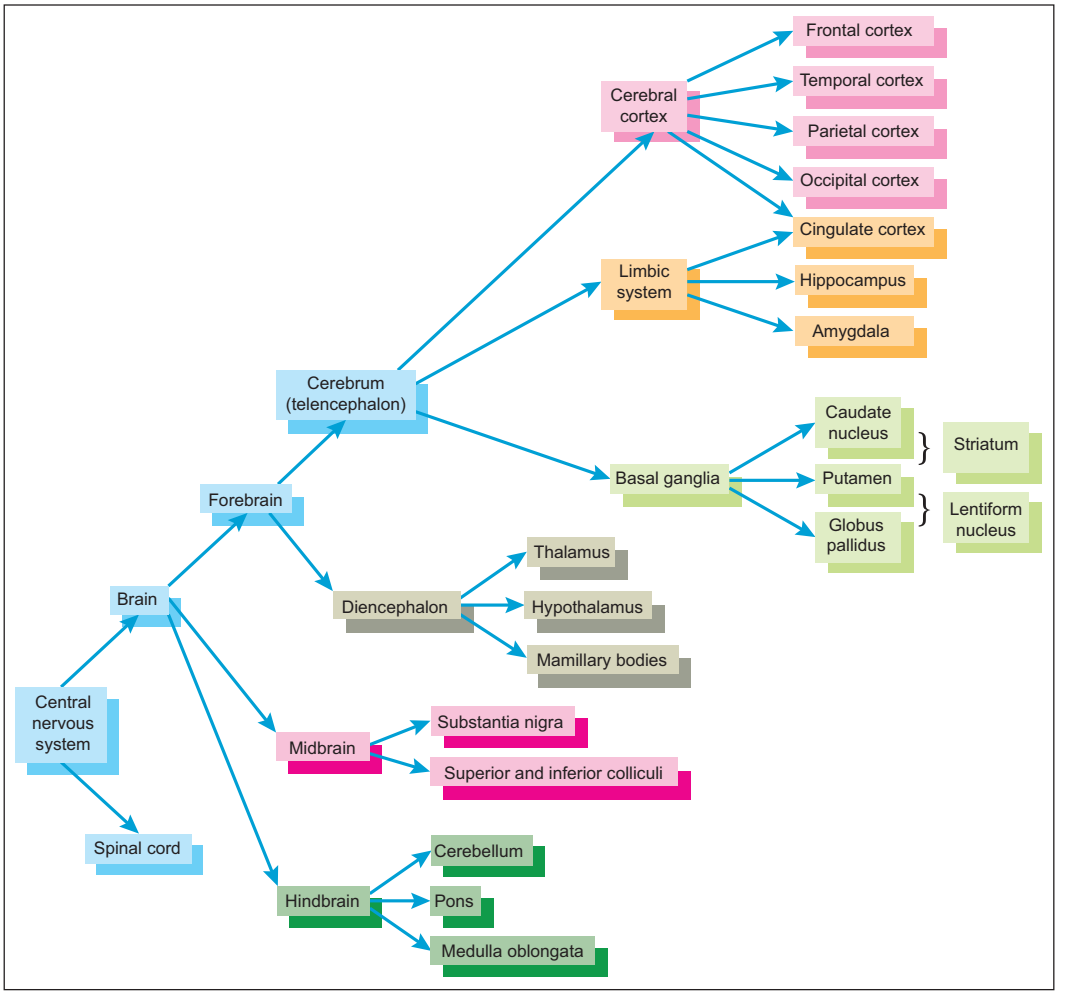

FIGURE 2.6: The central nervous system (CNS) is organized hierarchically. The upper levels of the hierarchy, corresponding to the upper branches of this diagram, are the newest structures from an evolutionary perspective.

Terms of reference and section

There are conventional directions for navigating around the brain, just as there is a north, south, east, and west for navigating around maps. **Anterior** and **posterior** refer to directions toward the front and back of the brain, respectively. These are also called *rostral* and *caudal*, respectively, particularly in other species that have a tail (caudal refers to the tail end). Directions toward the top and bottom are referred to as **superior** and **inferior**, respectively; they are also known as **dorsal** and **ventral**, respectively. The terms anterior, posterior, superior, and inferior (or rostral, caudal, dorsal, and ventral) enable navigation in two dimensions: front–back and top–bottom (see Figure 2.7). Needless to say, the brain is

KEY TERMS

Anterior
Toward the front.

Posterior
Toward the back.

Superior
Toward the top.

Inferior
Toward the bottom.

Dorsal
Toward the top.

Ventral
Toward the bottom.

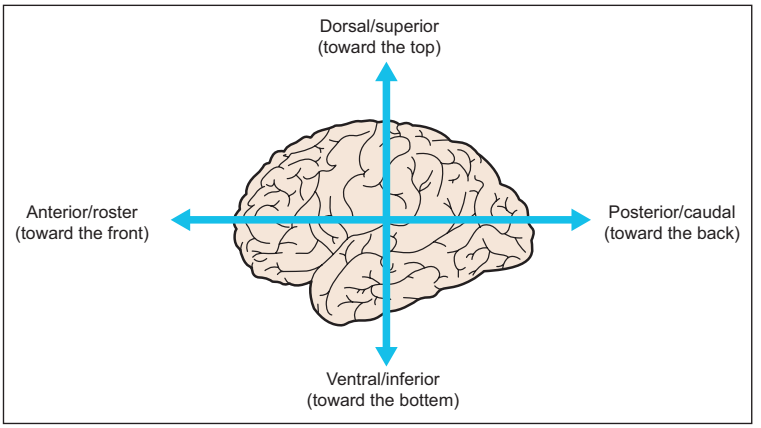

FIGURE 2.7: Terms of reference in the brain. Note also the terms *lateral* (referring to the outer surface of the brain) and *medial* (referring to the central regions).

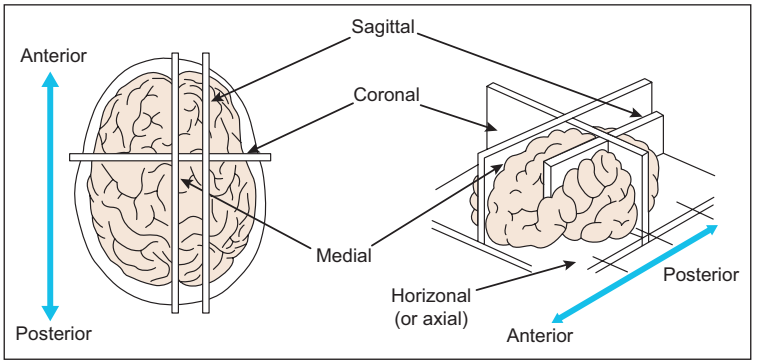

FIGURE 2.8: Terms of sections of the brain.

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KEY TERMS

Lateral
The outer part (cf. medial).

Medial
In or toward the middle.

three-dimensional and so a further dimension is required. The terms **lateral** and **medial** are used to refer to directions toward the outer surface and the center of the brain, respectively, although "medial" is ambiguous, because it is also used to refer to the middle of structures more generally. For example, the medial temporal gyrus lies on the lateral surface of the brain (not the medial surface). It is labeled medial because it lies midway between the superior and inferior temporal gyri.

The brain can be sectioned into two-dimensional slices in a number of ways, as shown in Figure 2.8. A *coronal* cross-section refers to a slice in the vertical plane through both hemispheres (the brain appears roundish in this section). A *sagittal* section refers to a slice in the vertical plane going through one of the hemispheres. When the sagittal section lies between the hemispheres, it is called a *midline* or medial section. An *axial* (or horizontal) section is taken in the horizontal plane.

THE CEREBRAL CORTEX

The cerebral cortex consists of two folded sheets of gray matter organized into two hemispheres (left and right). The surface

of the cortex has become increasingly more convoluted with evolutionary development. Having a folded structure permits a high surface area to volume ratio and thereby permits efficient packaging. The raised surfaces of the cortex are termed **gyri** (or gyrus in the singular). The dips or folds are called **sulci** (or sulcus in the singular).

The cortex is only around 3 mm thick and is organized into different layers that can be seen when viewed in cross-section. The different layers reflect the grouping of different cell types. Different parts of the cortex have different densities in each of the layers. Most of the cortex contains six main cortical layers, termed the *neocortex* (meaning "new cortex"). Other cortical regions are the mesocortex (including the cingulate gyrus and insula) and the allocortex (including the primary olfactory cortex and hippocampus).

The lateral surface of the cortex of each hemisphere is divided into four lobes: the frontal, parietal, temporal, and occipital lobes (Figure 2.9). The dividing line between the lobes is sometimes prominent, as is the case between the frontal and temporal lobes (divided by the lateral or *sylvian fissure*), but in other cases, the boundary cannot readily be observed (e.g., between temporal and occipital lobes). Other regions of the cortex are observable only in a medial section, for example, the cingulate cortex. Finally, an island of cortex lies buried underneath the temporal lobe; this is called the *insula* (which literally means "island" in Latin).

There are four different ways in which regions of cerebral cortex may be divided and, hence, labeled:

(1) *Regions divided by the pattern of gyri and sulci*. The same pattern of gyri and sulci is found in everyone (although the precise shape and size vary greatly). As such, it is possible to label different regions of the brain accordingly.

(2) *Regions divided by cytoarchitecture*. One of the most influential ways of dividing up the cerebral cortex is in terms of **Brodmann's areas**. Brodmann divided the cortex up into approximately 52 areas (labeled from BA1 to BA52), based on the relative distribution of cell types across cortical layers. Areas are labeled in a circular spiral starting from the middle, like the numbering system of Parisian suburbs. This is shown in Figure 2.10. Over the years, the map has been modified.

KEY TERMS

Gyri (gyrus = singular)
The raised folds of the cortex.

Sulci (sulcus = singular)
The buried grooves of the cortex.

Brodmann's areas
Regions of cortex defined by the relative distribution of cell types across cortical layers (cytoarchitecture).

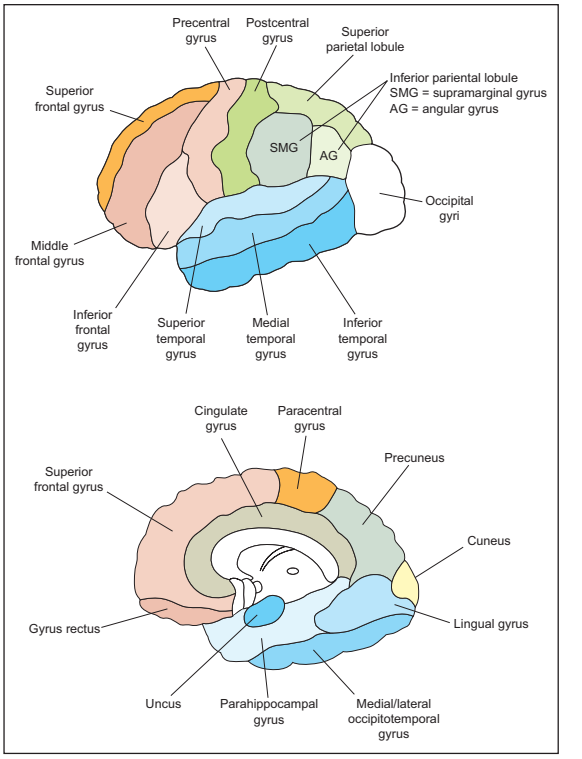

FIGURE 2.9: The main gyri of the lateral (top) and medial (bottom) surface of the brain. The cortical sulci tend to be labeled according to terms of reference. For example, the superior temporal sulcus lies between the superior and medial temporal gyri.

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(3) *Regions divided by function*. This method tends only to be used for primary sensory and motor areas. For example, Brodmann areas 17 and 6 are also termed the primary visual cortex and the primary motor cortex, respectively. Higher cortical regions are harder (if not impossible) to ascribe unique functions to.

(4) *Regions divided by connectivity*. Different brain regions have a different connectivity profile (i.e., they connect to some regions strongly and others weakly) and MRI techniques can be used to segment individual human brains using this kind of information (Glasser et al., 2016).

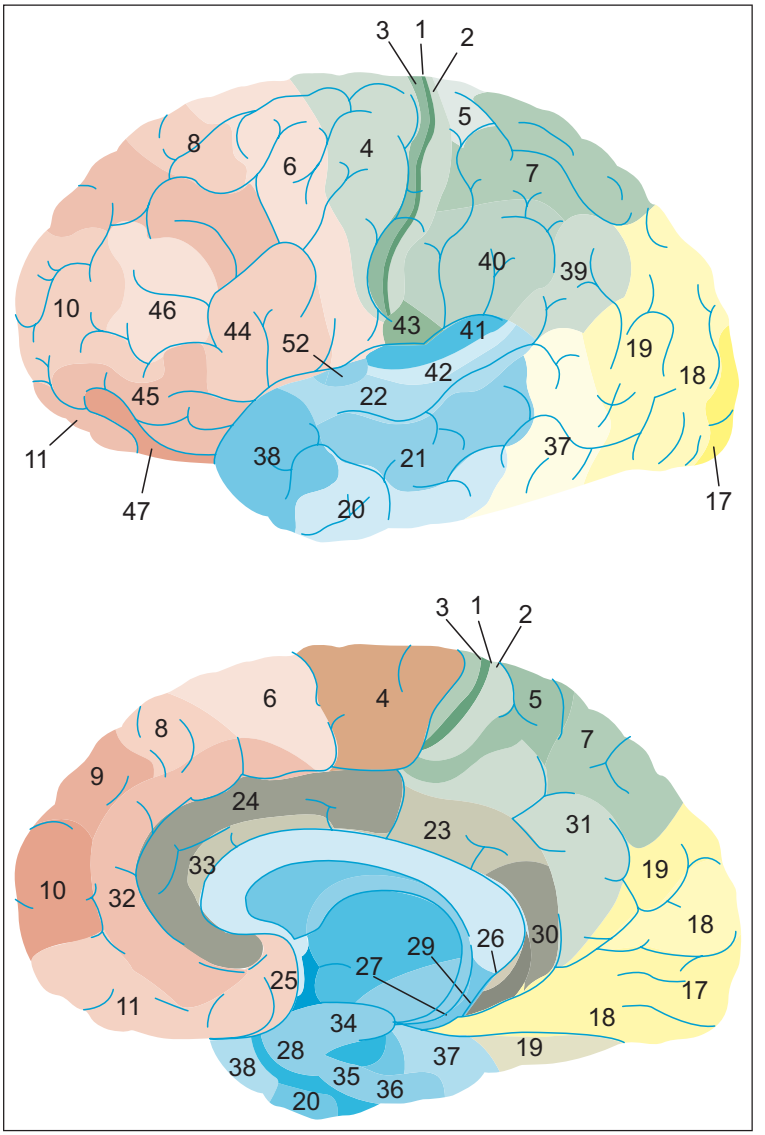

FIGURE 2.10: The Brodmann areas of the brain on the lateral (top) and medial (bottom) surface.

The subcortex

Beneath the cortical surface and the intervening white matter lies another collection of gray matter nuclei termed the subcortex. The subcortex is typically divided into a number of different systems with different evolutionary and functional histories.

The basal ganglia

The **basal ganglia** are large rounded masses that lie in each hemisphere and are illustrated in Figure 2.11. They surround and overhang the thalamus in the center of the brain. They are involved in regulating motor activity, and the programming and termination of action (see Chapter 10). Disorders of the basal ganglia can be characterized as hypokinetic (poverty of movement) or hyperkinetic (excess of movement). Examples of these include Parkinson's and Huntington's disease, respectively (see Chapter 10). The basal ganglia are also implicated in the learning of rewards, skills, and habits (see Chapters 11 and 16). The main structures comprising the basal ganglia are the *caudate nucleus* (an elongated tail-like structure), the *putamen* (lying more laterally), and the *globus pallidus* (lying more medially). The caudate and putamen funnel cortical inputs into the globus pallidus, from which fibers reach into the thalamus. Different circuits passing through these regions either increase or decrease the probability and intensity of certain behaviors (e.g., voluntary movements).

KEY TERMS

Basal ganglia
Regions of subcortical gray matter involved in aspects of motor control, skill learning, and reward learning; they consist of structures such as the caudate nucleus, putamen, and globus pallidus.

Limbic system
A region of subcortex involved in relating the organism to its present and past environment; limbic structures include the amygdala, hippocampus, cingulate cortex, and mamillary bodies.

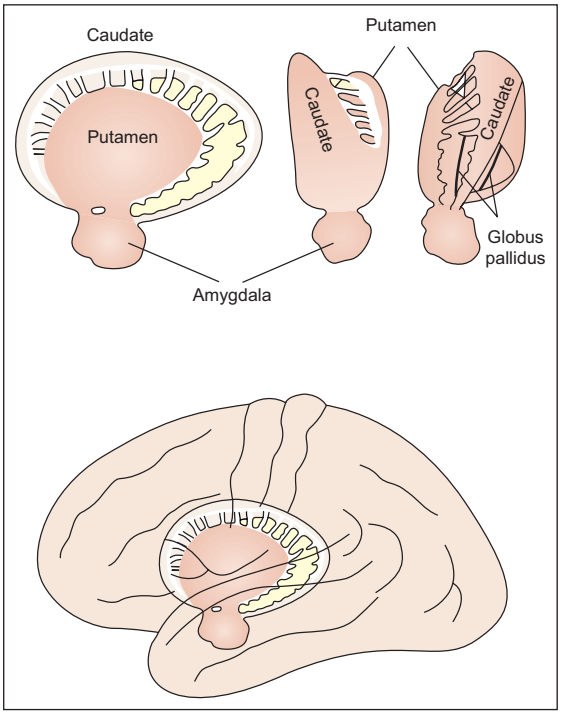

FIGURE 2.11: The basal ganglia are involved in motor programming, skill learning, and reward learning.

The limbic system

The structures of the **limbic system** are shown in Figure 2.12. The limbic system is important for relating the organism to its environment based on current context and previous experience. It is involved in the detection and expression of emotional responses. For example, the *amygdala* has been implicated in the detection of fearful or threatening stimuli (see Chapter 16), and parts of the *cingulate gyrus* have been implicated in the detection of emotional and cognitive conflicts (see Chapter 15). The *hippocampus* is particularly important for learning and memory (see Chapter 11). Both the amygdala and hippocampus lie buried in the temporal lobes of each hemisphere. Other limbic structures are clearly visible on the underside (ventral surface) of the

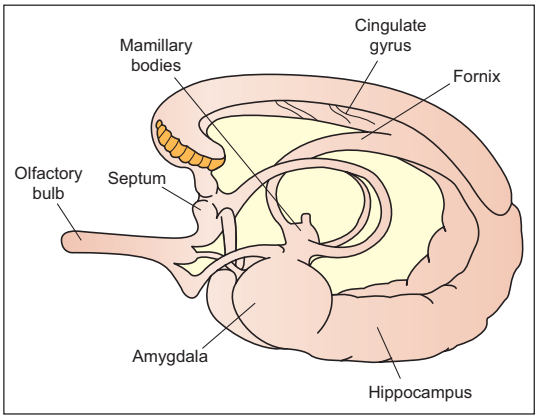

FIGURE 2.12: The limbic system.

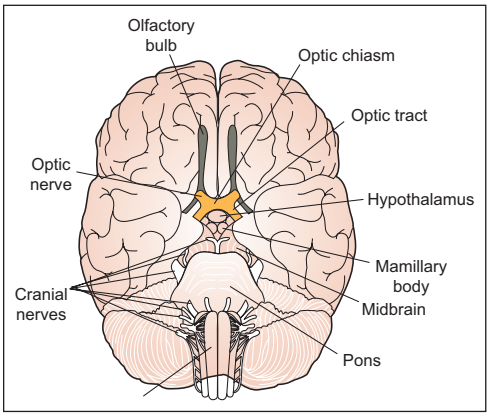

FIGURE 2.13: The ventral surface of the brain shows the limbic structures of the olfactory bulbs and mamillary bodies. Other visible structures include the hypothalamus, optic nerves, pons, and medulla.

brain, as shown in Figure 2.13. The *mamillary bodies* are two small round protrusions that have traditionally been implicated in memory (Dusoir et al., 1990). The *olfactory bulbs* lie on the under-surface of the frontal lobes. Their connections to the limbic system underscore the importance of smell for detecting environmentally salient stimuli (e.g., food, other animals) and its influence on mood and memory.

The diencephalon

The two main structures that make up the diencephalon are the thalamus and the hypothalamus. Their locations are shown in Figure 2.14.

KEY TERMS

Thalamus
A major subcortical relay center; for instance, it is a processing station between all sensory organs (except smell) and the cortex.

Hypothalamus
Consists of a variety of nuclei that are specialized for different functions that are primarily concerned with the body and its regulation.

The **thalamus** consists of two interconnected egg-shaped masses that lie in the center of the brain and appear prominent in a medial section. The thalamus is the main sensory relay for all senses (except smell) between the sense organs (eyes, ears, etc.) and the cortex. At the posterior end of the thalamus lie the *lateral geniculate nucleus* and the *medial geniculate nucleus*. These are the main sensory relays to the primary visual and primary auditory cortices, respectively. In addition to connecting the periphery to the cortex, there are also multiple pathways between cortical regions that pass via the thalamus giving it a gatekeeper role in intercortical connectivity (Sherman, 2007).

The **hypothalamus** lies beneath the thalamus and consists of a variety of nuclei that are specialized for different functions primarily concerned with the body. These include body temperature, hunger and thirst, sexual activity, and regulation of endocrine

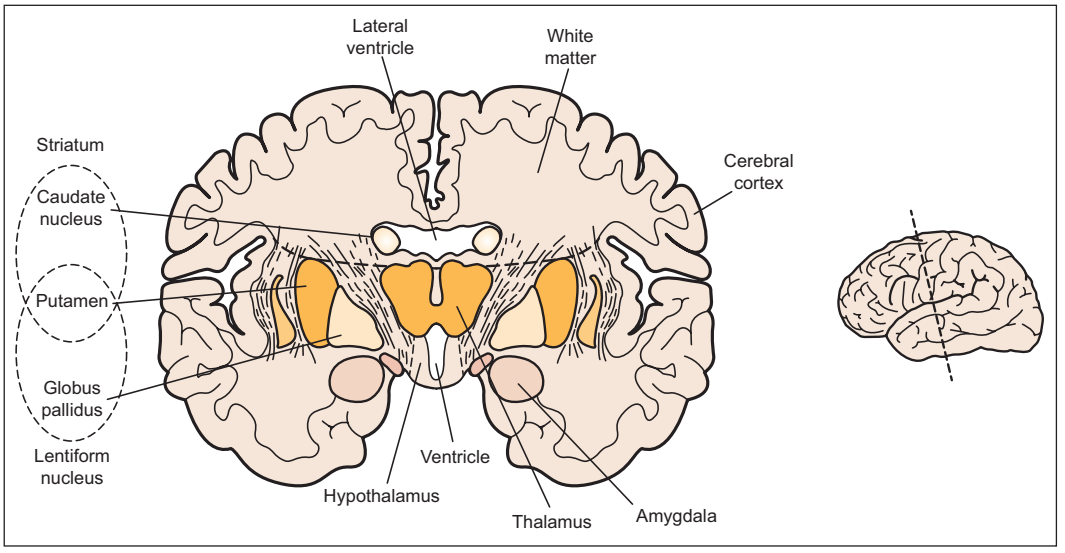

FIGURE 2.14: A coronal section through the amygdala and basal ganglia shows the thalamus and hypothalamus as prominent in the midline.

functions (e.g., regulating body growth). Tumors in this region can lead to eating and drinking disorders, precocious puberty, dwarfism, and gigantism.

THE MIDBRAIN AND HINDBRAIN

The midbrain region consists of a number of structures (see Figure 2.15), only a few of which will be considered here. The **superior colliculi** and **inferior colliculi** (or colliculus in singular) are gray matter nuclei. The superior colliculi integrate information from several senses (vision, hearing, and touch), whereas the inferior colliculi are specialized for auditory processing. These pathways are different from the main cortical sensory pathways and are evolutionarily older. They may provide a fast route that enables rapid orienting to sensory stimuli (flashes or bangs) before the stimulus is consciously seen or heard (Sparks, 1999). The midbrain also contains a region called the *substantia nigra*, which is connected to the basal ganglia. Cell loss in this region is associated with the symptoms of Parkinson's disease.

The **cerebellum** (literally "little brain") is attached to the posterior of the hindbrain via the cerebellar peduncles. It consists of highly convoluted folds of gray matter. It is organized into two interconnected lobes. The cerebellum is important for dexterity and smooth execution of movement. This function may be achieved by integrating motor commands with online sensory feedback about the current state of the action (see Chapter 10). Unilateral lesions to the cerebellum result in poor coordination

KEY TERMS

Superior colliculi
A midbrain nucleus that forms part of a subcortical sensory pathway involved in programming fast eye movements.

Inferior colliculi
A midbrain nucleus that forms part of a subcortical auditory pathway.

Cerebellum
Structure attached to the hindbrain; important for dexterity and smooth execution of movement.

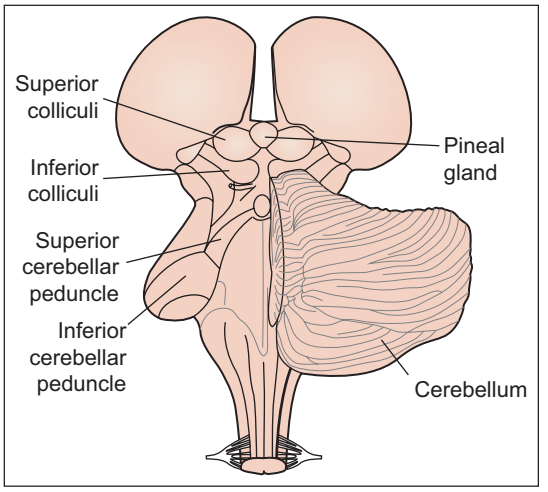

FIGURE 2.15: A posterior view of the midbrain and hindbrain. Visible structures include the thalamus (the two egg-shaped masses at the top), pineal gland, superior colliculi, inferior colliculi, cerebellum, cerebellar peduncle, and medulla oblongata (the pons is not visible but lies on the other side of the cerebellum).

KEY TERMS

Pons
Part of the hindbrain; a key link between the cerebellum and the cerebrum.

Medulla oblongata
Part of the hindbrain; it regulates vital functions such as breathing, swallowing, heart rate, and the wake–sleep cycle.

on the same side of the body as the lesion (i.e., ipsilesional side). Bilateral lesions result in a wide and staggering gait, slurred speech (dysarthria), and eyes moving in a to-and-fro motion (nystagmus). The **pons** is a key link between the cerebellum and the cerebrum. It receives information from visual areas to control eye and body movements. The **medulla oblongata** protrudes from the pons and merges with the spinal cord. It regulates vital functions such as breathing, swallowing, heart rate, and the wake–sleep cycle.

SUMMARY AND KEY POINTS OF THE CHAPTER

- The neuron is the basic cell type that supports cognition. Neurons form a densely interconnected network of connections. Axons send signals to other cells and dendrites receive signals.
- Neurons code information in terms of a response rate. They only respond in certain situations (determined by the input they receive from elsewhere).
- Neurons are grouped together to form gray matter (cell bodies) and white matter (axons and other cells). The cortical surface consists of a folded sheet of gray matter organized into two hemispheres.
- There is another set of gray matter in the subcortex that includes the basal ganglia (important in regulating movement), the limbic system (important for emotion and memory functions), and the diencephalon (the thalamus is a sensory relay center and the hypothalamus is concerned with homeostatic functions).

EXAMPLE ESSAY QUESTIONS

- How do neurons communicate with each other?
- Describe how electrical and chemical signals are generated by neurons.
- Compare and contrast the different functions of the forebrain, midbrain, and hindbrain.

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CHAPTER 3

The electrophysiological brain

CONTENTS

How is it possible that the world "out there" comes to be perceived, comprehended, and acted upon by a set of neurons operating "in here"? Chapter 2 introduced some of the basic properties of the neuron, including the fact that the rate of responding of a neuron (in terms of the number of action potentials or spikes) is a continuous variable that reflects the informational content of that neuron. Some neurons may respond, say, when an animal is looking at an object but not when listening to a sound. Other neurons may respond when an animal is listening to a sound but not looking at an object, and still others may respond when both a sound and an object are present. As such, there is a sense in which the world out there is reflected by properties of the system in here. Cognitive and neural systems are sometimes said to create **representations** of the world. Representations need not only concern physical properties of the world (e.g., sounds, colors) but may also relate to more abstract forms of knowledge (e.g., knowledge of the beliefs of other people, factual knowledge).

DOI: 10.4324/9781003429975-3

KEY TERMS

Representations
Properties of the world that are manifested in cognitive systems (mental representation) and neural systems (neural representation).

Single-cell recordings (or single-unit recordings)
Measure the responsiveness of a neuron to a given stimulus (in terms of action potentials per second).

Electroencephalography (EEG)
Measurements of electrical signals generated by the brain through electrodes placed on different points on the scalp.

Event-related potential (ERP)
The average amount of change in voltage at the scalp that is linked to the timing of particular cognitive events (e.g., stimulus, response).

Reaction time
The time taken between the onset of a stimulus/event and the production of a behavioral response (e.g., a button press). Also referred to as **response time**.

Cognitive psychologists may refer to a *mental representation* of, say, your grandmother being accessed in an information-processing model of face processing. However, it is important to distinguish this from its *neural representation*. There is unlikely to be a one-to-one relationship between a hypothetical mental representation and the response properties of single neurons. The outside world is not copied inside the head, neither literally nor metaphorically; rather, the response properties of neurons (and brain regions) correlate with certain real-world features. As such, the relationship between a mental representation and a neural one is unlikely to be straightforward. The electrophysiological method of **single-cell recordings** has been used to investigate questions related to neural representations, and this method will be considered first in this chapter.

The other electrophysiological method that will be considered in this chapter is **electroencephalography** (**EEG**). This is based on measurements of electrical signals generated by the brain through electrodes placed on different points on the scalp. Changes in the electrical signal are conducted instantaneously to the scalp, and this method is therefore particularly useful for measuring the relative *timing* of cognitive events and neural activity. The method of **event-related potentials** (**ERPs**) links the *amount* of change in voltage at the scalp with particular cognitive events (e.g., stimulus, response). It has also become increasingly common to link the *rate* of change of the EEG signal to cognitive processes (oscillation-based measures) that also depend on the good temporal resolution of EEG.

ERP measurements have much in common with the main method of cognitive psychology, namely the **reaction time** (also called response time) measure. It is important to note that the absolute time to perform a task is not normally the thing of interest in cognitive psychology. It is of little theoretical interest to know that one reads the word "HOUSE" within 500 ms (ms = milliseconds). However, relative differences in timing can be used to make inferences about the cognitive system. For example, knowing that people are slower at reading "HoUsE" when printed in mIxEd CaSe could be used to infer that, perhaps, our mental representations of visual words are case-specific (e.g., Mayall et al., 1997). The extra processing time for "HoUsE" relative to "HOUSE" may reflect the need to transform this representation into a more standard one. Other methods in cognitive neuroscience are sensitive to measures other than timing. For example, functional imaging methods (such as fMRI) have a better spatial resolution than temporal resolution (see Chapter 4). Lesion methods tend to rely on measuring error rates rather than time-based processes (see Chapter 5). Methods such as transcranial magnetic stimulation (TMS) have both good spatial and temporal resolution (see Chapter 5). It is important to stress that all these methods converge on the question of *how*

cognitive processes are carried out by the brain. Just because one method is sensitive to timing differences and another is sensitive to spatial differences does not mean that the methods just tell us *when* and *where*. The "when" and "where" constitute the data and the "how" is the theory that accounts for them.

IN SEARCH OF NEURAL REPRESENTATIONS: SINGLE-CELL RECORDINGS

How are single-cell recordings obtained?

By measuring changes in the responsiveness of a neuron to changes in a stimulus or changes in a task, it is possible to make inferences about the building blocks of cognitive processing. The action potential is directly measured in the method of single-cell (and multi-unit) recordings. Single-cell recordings can be obtained by implanting a very small electrode either into the neuron itself (intracellular recording) or outside the membrane (extracellular recording). Extracellular recordings are the norm in the mammalian brain because of the small size of neurons. The number of times that an action potential is produced in response to a given stimulus (e.g., a face) is counted, and the dependent measure is often referred to as spikes per second, firing rate, or spiking rate. This is an invasive method. As such, the procedure is normally conducted on experimental animals only. The method is occasionally conducted on humans undergoing brain surgery (see Fried et al., 2014). The electrodes are implanted during full anesthesia, and the recordings do not cause pain. After being implanted, the waking subject can be presented with stimuli as part of the experiment (see Figure 3.1) or simply as a result of going about its routine behavior. It is impossible to measure action potentials from a single neuron noninvasively (i.e., from the scalp) because the signal is too weak and the noise from other neurons is too high.

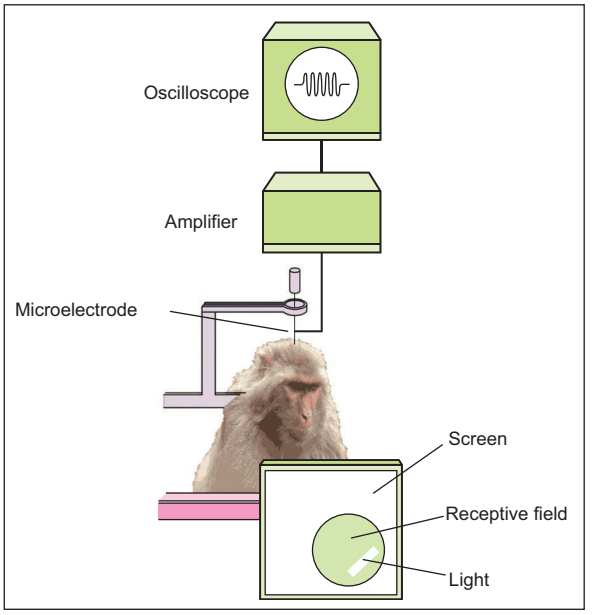

FIGURE 3.1: A typical experimental setup for single-cell recording.

An electrode may pick up on activity from multiple nearby neurons and, when used in this way, is referred to as a **multi-cell (or multi-unit) recording**. Special algorithms can then be applied to separate the combined signal into individual contributions from different neurons. Technology has now advanced such that it is possible to simultaneously record from 100 neurons in multi-electrode arrays.

KEY TERM

Multi-cell recordings (or multi-unit recordings) The electrical activity (in terms of action potentials per second) of many individually recorded neurons recorded at one or more electrodes.

Distributed versus sparse coding

Hubel and Wiesel (1959) conducted pioneering studies of the early visual cortical areas (see Chapter 7 for a detailed discussion). They argued that visual perception is hierarchical in that it starts from the most basic visual elements (e.g., small patches of light and dark) that combine into more complex elements (e.g., lines and edges) that combine into yet more complex elements (e.g., shapes). But what is the highest level of the hierarchy? Is there a neuron that responds to one particular stimulus? A hypothetical neuron such as this has been termed a **grandmother cell** because it may respond, for example, just to one's own grandmother (Bowers, 2009). The term was originally conceived to be multimodal, in that the neuron may respond to her voice, and the thought of her, as well as the sight of her (including from any viewpoint).

KEY TERM

Grandmother cell
A hypothetical neuron that just responds to one particular stimulus (e.g., the sight of one's grandmother).

Rolls and Deco (2002) distinguish between three different types of representation that may be found at the neural level:

1. *Local representation*. All the information about a stimulus/event is carried in one of the neurons (as in a grandmother cell).
2. *Fully distributed representation*. All the information about a stimulus/event is carried in all the neurons of a given population.
3. *Sparse distributed representation*. A distributed representation in which a small proportion of the neurons carry information about a stimulus/event.

Several studies have attempted to distinguish between these accounts. Bayliss et al. (1985) found that neurons in the temporal cortex of monkeys responded to several different faces (from a set of five), albeit to different degrees. This is illustrated in Figure 3.3. Similar results have been found with much larger sets of faces in

FIGURE 3.2: Could there be a single neuron in our brain that responds to only one stimulus, such as our grandmother? These hypothetical cells are called "grandmother cells."
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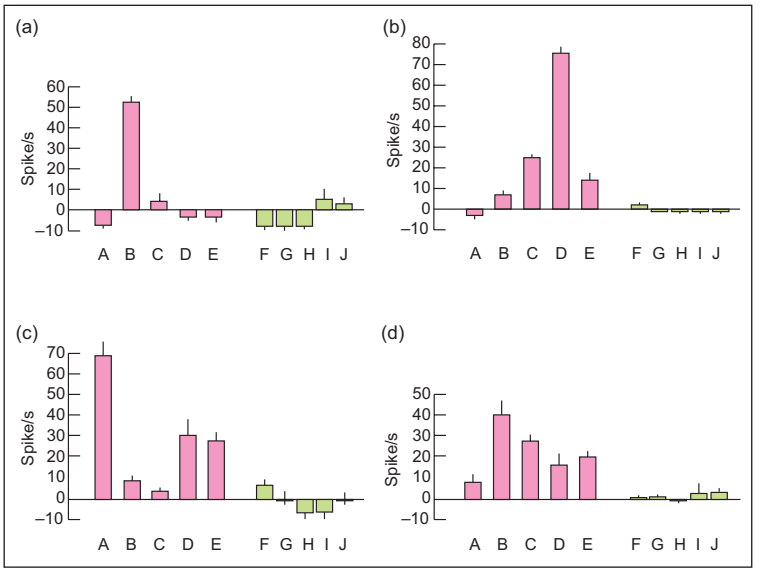

FIGURE 3.3: Four neurons (a, b, c, d) respond to different faces (A–E), but not different objects (F–J). They typically respond to several faces, albeit in a graded fashion.

Reprinted from Bayliss et al. (1985). © 1985, with permission from Elsevier.

both monkeys (Rolls & Tovee, 1995) and in humans undergoing surgery for epilepsy (Quiroga et al., 2005). The neurons typically respond to several different stimuli from within the same category (e.g., responding to several faces but no objects). This is inconsistent with a strict definition of a grandmother cell but does suggest a relatively sparse coding. Chang and Tsao (2017) argue, based on data of primate single-cell recordings to faces, that the identity of a face can be decoded from as few as 200 neurons. In their model, neurons are not tuned to particular people but rather to visuo-spatial features of faces that vary continuously from face to face.

In a study on humans, Quiroga et al. (2005) recorded from neurons in parts of the brain traditionally implicated in memory rather than perception (i.e., medial temporal lobes), further up the visual hierarchy. The neurons showed a surprising specificity. They found some neurons that responded maximally to celebrities such as Jennifer Aniston or Halle Berry, irrespective of the particular image used, clothes worn, etc. The "Halle Berry neuron" even responded to the sight of her name and to her dressed up as Catwoman, but not to other actresses dressed up as Catwoman (see Figure 3.4). For these neurons, the response is determined by how familiar a face is rather than its appearance, suggesting it is coding features that are relevant to memory (Viskontas et al., 2009). So are these neurons grandmother cells? They certainly have a very sparse coding. Quiroga (2016) argues that they are not grandmother cells because they respond to multiple stimuli albeit on the basis of prior association: for instance, the "Jennifer Aniston neuron" responded to the sight of Lisa Kudrow, her co-star on *Friends*, and experimentally pairing a person with a place (e.g., Jennifer Aniston at the Eiffel Tower) can activate the neuron when presented with an image of the place.

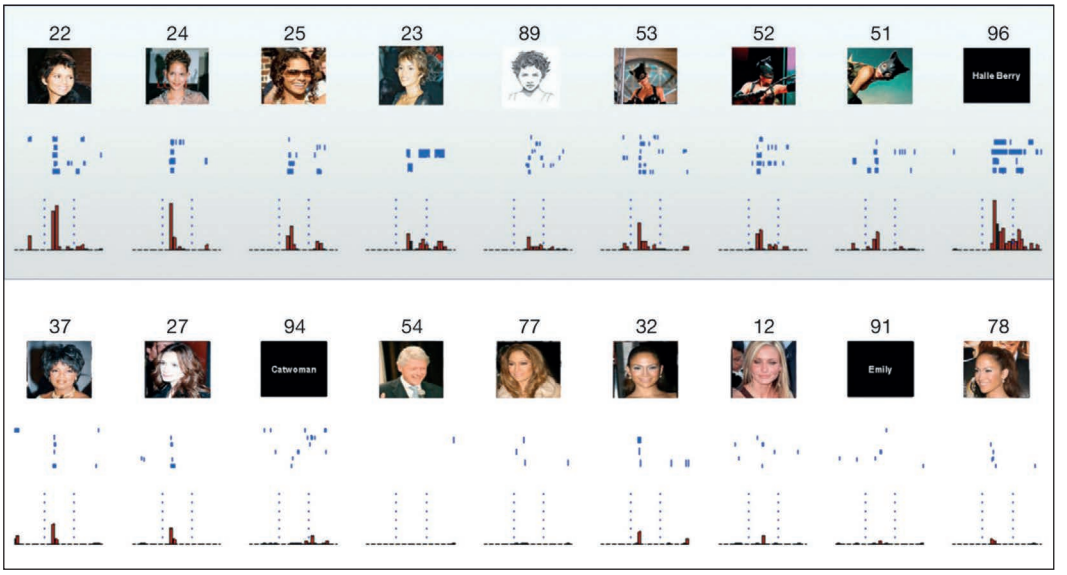

FIGURE 3.4: This neuron, recorded in the human medial temporal lobe, responds to Halle Berry (top panel) more than comparable stimuli (bottom panel). The response of the neuron is depicted in two ways. A raster plot (blue) depicts the firing of the neuron over time (represented left to right horizontally) by shading when the neuron fires. Each row is a different recording with that stimulus. The histogram (red) sums together the number of times that the neuron fired at each time point.

From Quiroga et al. (2005). Reproduced with permission from Springer Nature.

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ONLINE RESOURCES

To watch an interview with Professor Horace Barlow, who conducted seminal work on how neurons code visual information and who introduced the concept of grandmother cells, and to learn more about the discovery of the Jennifer Aniston Neuron and its implications, visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience).

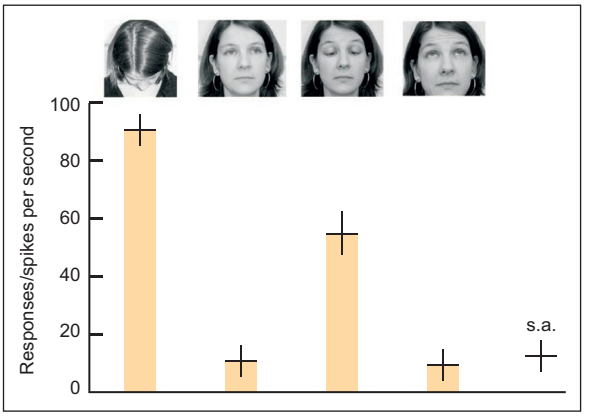

FIGURE 3.5: This neuron responds when gaze is oriented downwards. The activity of the neuron (spikes per second) is shown when presented with four faces and during spontaneous activity (s.a.).

Adapted from Perrett et al. (1992).

Some neurons code for other aspects of a stimulus than facial identity. For example, consider the pattern of responding of a particular neuron taken from the superior temporal sulcus (STS) of an alert macaque monkey shown in Figure 3.5 (Perrett et al., 1992). The activity of the neuron when shown four different

views of faces is compared with spontaneous activity in which no face is shown. The neuron responds strongly to a downward gaze, both with the eyes and the whole head, but not an upward or straight-ahead gaze. In this instance, the two stimuli that elicit the strongest response (head down and head forward with eyes down) do not resemble each other physically, although they are related conceptually. Coding of gaze direction may be important for cognitive processes involved in interpreting social cues (eye contact is perceived as a threat by many species), or for orienting attention and preparing action systems. Perhaps there is something interesting down there that would warrant our attention.

The studies described previously can all be classified as **rate coding** of information by neurons in that a given stimulus/event is associated with a change (typically increase) in the rate of neural firing. An alternative way for neurons to represent information about stimuli/events is in terms of **temporal coding**, in that a given stimulus/event is associated with greater synchronization of firing across different neurons. Engel et al. (1991) obtained multi-cell recordings from neurons in the primary visual cortex of cats. This region contains a spatial map of the retinal image (see Chapter 7). If two brain regions were stimulated with a single bar of light presented to the eyes (-----), then the two regions synchronized their neural firing. But if the two regions were stimulated by two different bars of light (-- --), there was no synchronization even though both regions showed a response in terms of increased rate of firing. Temporal coding may be one mechanism for integrating information across spatially separated populations of neurons. If many neurons are synchronized in their firing, then it may also be possible to record this noninvasively from the scalp, using the method of EEG. Indeed, there are comparable studies to that of Engel et al. (1991) in humans using the noninvasive method of EEG. Visual stimuli, comprising multiple parts, elicit more synchronized activity in a frequency range called gamma when they are perceived as belonging together (Tallon-Baudry et al., 1996).

KEY TERMS

Rate coding
The informational content of a neuron may be related to the number of action potentials per second.

Temporal coding
The synchrony of firing may be used by a population of neurons to code the same stimulus or event.

Evaluation

Information is represented in neurons by the response rates to a given stimulus or event and, in some circumstances, by the synchronization of their firing. This can be experimentally measured by the methods of single-cell and multi-cell recordings. Both ways of representing information may depend on sparse distributed coding such that activity in several neurons is required to represent a stimulus (e.g., a particular face). The sparseness of coding conserves energy and may enable the brain to have a high memory capacity. Distributed representations protect against information loss if synapses or neurons are lost. It may also allow the cognitive system to generalize and categorize: a novel stimulus that resembles a stored representation would partially activate this representation.

ONLINE RESOURCES

Check out the Cognitive Neuroscience Bitesize Video on EEG Electrical Brainwaves by Jamie Ward by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

ELECTROENCEPHALOGRAPHY AND EVENT-RELATED POTENTIALS

This section considers the basic principles behind the electrophysiological method known as electroencephalography (EEG). The following sections go on to consider some concrete examples of how EEG is used in contemporary cognitive neuroscience and contrast it with other methods used in cognitive psychology and cognitive neuroscience (principally the reaction-time measure).

How does EEG work?

The physiological basis of the EEG signal originates in the postsynaptic dendritic currents rather than the axonal currents associated with the action potential (Nunez, 1981). These were described as passive and active currents, respectively, in Chapter 2. EEG records electrical signals generated by the brain through electrodes placed on different points on the scalp as shown in Figure 3.6. As the procedure is non-invasive and involves recording (not stimulation), it is completely harmless as a method. For an electrical signal to be detectable at the scalp, a number of basic requirements need to be met in terms of underlying neural firing. First, a whole population of neurons must be active in synchrony to generate a large enough electrical field. Second, this population of neurons must be aligned in a parallel orientation so that they summate together rather than cancel out. Fortunately, neurons are arranged in this way in the cerebral cortex. However, the same cannot necessarily be said about all regions of the brain. For example, the orientation of neurons in the thalamus renders its activity invisible to this recording method.

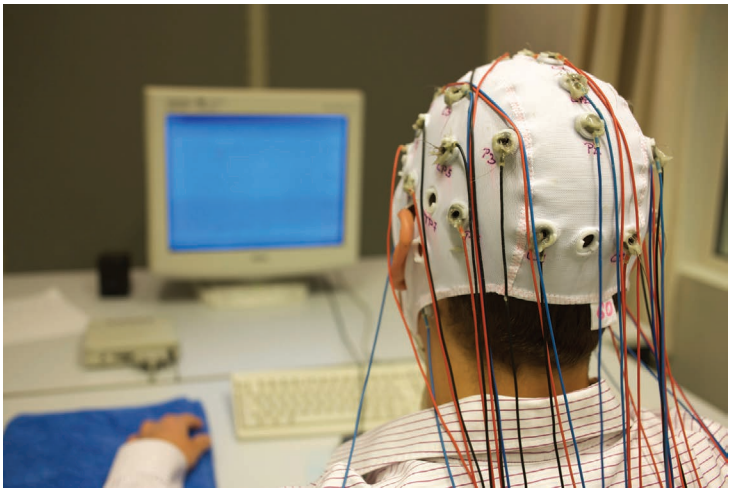

FIGURE 3.6: A participant in an EEG experiment. The hair and electrode cap is normally wet with saline solution to enable good electrical contact.

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In the previous section, the notion of rate coding (how much a neuron fires) and temporal coding (how synchronous the firing of neurons is) was introduced to describe properties of individual neurons. Analogous phenomena can be found in EEG data, although here they are measuring the summed electrical activity over millions of neurons. The method of event-

related potentials measures the amount of electrical activity (in terms of voltage change at the scalp) as a result of a stimulus or other event. This is akin to rate coding: the greater the electrical activity of neurons, the greater the change at the scalp. Alternatively, one can measure how synchronous the EEG signal is in terms of the extent to which it exhibits undulating wave-like properties as opposed to a random structure. This is akin to temporal coding. It is possible to have two sets of neurons that have similar levels of electrical activity (i.e., matched in terms of rate coding) but differ in terms of whether they respond in synch – as shown in Figure 3.7. Neurons that respond in synch are generally believed to be communicating with each other as opposed to responding in isolation (e.g., Fries, 2005). In this way, the neural description of cognitive processing moves from considering highly specialized response properties to considering the wider neural network in which it is situated.

To gain an EEG measure one needs to compare the voltage between two or more different sites. A reference site is often chosen that is likely to be relatively uninfluenced by the variable under investigation. One common reference point is the mastoid bone behind the ears or a nasal reference; another alternative is to reference to the average of all electrodes. The experimental electrodes themselves are arranged at various locations on the scalp and often described with reference to the so-called 10–20 system of Jasper (1958) and shown, in simplified form, in Figure 3.8. The electrodes are labeled according to their location (F = frontal, P = parietal, O = occipital, T = temporal, C = central) and the hemisphere involved (odd numbers for left, even numbers for right and "z" for the midline). For example, the O2 electrode is located over the right occipital lobe, and the Fz electrode is located over the midline of the frontal lobes. It is important to stress that the activity recorded at each location cannot necessarily be attributed to neural activity near to that region. Electrical activity in one location can be detected at distant locations. In general, EEG/ERP is not

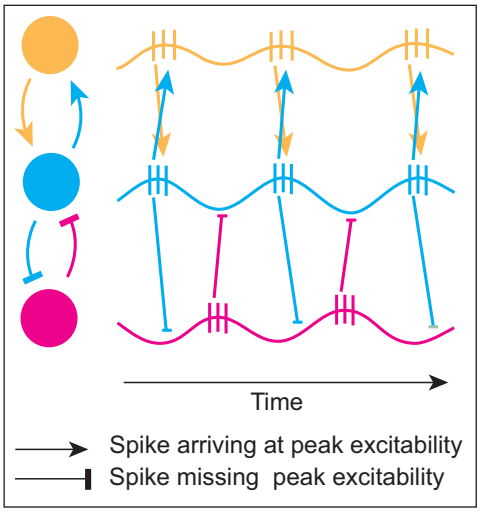

FIGURE 3.7: These three neurons (orange, blue, pink) are all firing at a similar rate: the firing is shown by the vertical lines. But whereas the orange and blue neurons fire at the same time, the pink neuron does not. This enables the orange and blue neurons to mutually influence each others excitability and, thus, to communicate. If there are enough synchronous neurons that repeatedly fire, then this wave-like structure can be detected in the EEG signal at a particular frequency range determined by the distance in time between the peaks of activity.

From Fries (2005).

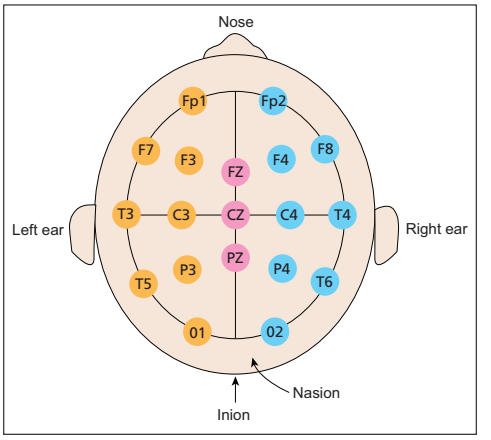

FIGURE 3.8: The 10–20 system of electrodes used in a typical EEG/ERP experiment.

best equipped for detecting the location of neural activity (see later for further discussion).

Rhythmic oscillations in the EEG signal

The EEG signal, when observed over a sufficiently long time scale, has a wave-like structure. The EEG signal tends to oscillate at different rates (also called frequency bands) that are named after letters of the Greek alphabet: thus alpha waves reflect oscillations in the 7 to 14 Hz range, beta in the 15 to 30 Hz range, and gamma in the 30 Hz and above range (and so on). These oscillations arise because large groups of neurons tend to be in temporal synchrony with each other in terms of their firing (action potentials) and in terms of their slower dendritic potentials (which form the basis of the EEG signal). It has long been established that different rates of oscillation characterize different phases of the sleep–wake cycle (for the detailed mechanisms see McCormick & Bal, 1997). In recent decades, attempts have been made to link the relative amount of oscillations (the "power") in different bands to different kinds of cognitive function during normal wakefulness (Ward, 2003). This section will provide only a few examples from the literature to illustrate the general principle.

Increases in the alpha band have been linked to increased attention. More specifically, they have been linked to filtering out of irrelevant information. If participants are asked to ignore a region of space in which an irrelevant stimulus will later appear (a so-called distractor), then increases in the alpha band are found over electrode sites that process that region of space (Worden et al., 2000). Alpha is also greater when attending to an internally generated image which involves ignoring the external visual input (Cooper et al., 2003). An "increase in the alpha band" means that neurons become more synchronized in their electrical activity specifically in the 7 to 14 Hz range. What is less clear is why this particular neural coding should be linked to this kind of cognitive mechanism rather than changes in any other frequency band.

By contrast, increases in the gamma band have been linked to perceptual integration of parts into wholes. This kind of mechanism is important for object recognition (e.g., deciding that a handle and hollowed cylinder is a single object – a mug), and the general process is referred to as binding or grouping. Rodriguez et al. (1999) presented participants with an ambiguous visual stimulus that could be perceived either as a face (parts bound into a whole) or a meaningless visual pattern (collection of separate parts). They found that increased gamma synchronization was linked to the face percept (Rodriguez et al., 1999).

Although gamma and alpha have been linked to rather different functions (similarly for other frequency bands), it is inconceivable that there will be a one-to-one mapping between particular frequency bands and particular cognitive functions or particular brain regions. Synchronization (or desynchronization) of alpha, gamma, and so on are linked to a wide range of cognitive functions, and each brain region is capable of producing different kinds of oscillations. However, they provide another tool with which to understand the different mechanisms that comprise cognition. Perhaps, most importantly, they suggest that there is more to cognition than the *amount* of brain "activity" (the standard interpretation of fMRI data) and suggest that the *synchronization* of brain activity (measurable in EEG because of its fast temporal resolution) has particular roles to play in cognition.

Event-related potentials (ERPs)

The most common use of EEG in cognitive neuroscience is the method known as ERP or event-related potentials. The EEG waveform reflects neural activity from all parts of the brain. Some of this activity may specifically relate to the ongoing task (e.g., reading, listening, calculating), but most of it will relate to spontaneous activity of other neurons that do not directly contribute to the task. As such, the *signal-to-noise ratio* in a single trial of EEG is very low (the signal being the electrical response to the event and the noise being the background level of electrical activity). The ratio can be increased by averaging the EEG signal over many presentations of the stimulus (e.g., 50–100 trials), relative to the onset of a stimulus, as shown in Figure 3.9. In general, the background rhythmic oscillatory activity (alpha, beta, etc.) will not be synchronized with the onset of events, and so these fluctuations are averaged out during the ERP method.

The results are represented graphically by plotting time (milliseconds) on the *x*-axis and electrode potential (microvolts) on the *y*-axis. The graph consists of a series of positive and negative peaks, with an asymptote at 0 μV. This is done for each electrode,

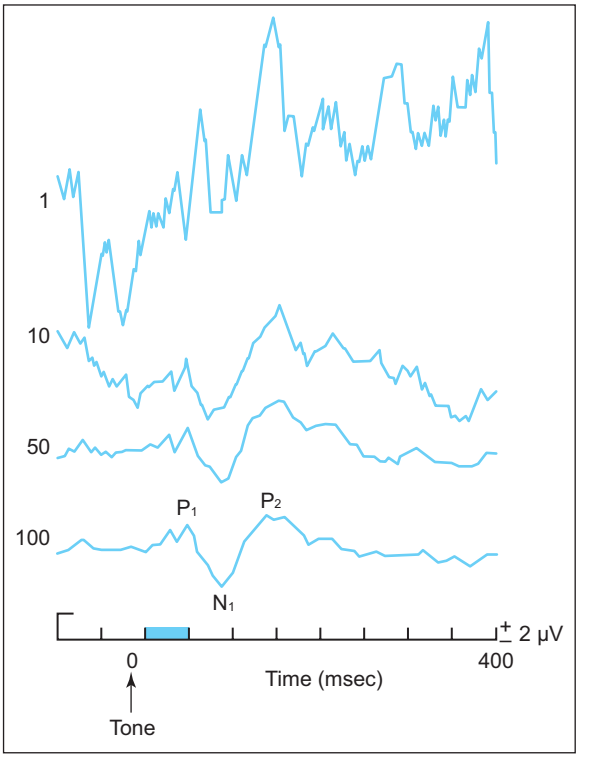

FIGURE 3.9: When different EEG waves are averaged relative to presentation of a stimulus (e.g., a tone), the signal-to-noise ratio is enhanced, and an event-related potential is observed. The figure shows the mean EEG signal to 1, 10, 50, and 100 trials.

From Kolb and Whishaw (2002). © 2002 by Worth Publishers. Used with permission.

and each will have a slightly different profile. The positive and negative peaks are labelled with "P" or "N" and their corresponding number. Thus, P1, P2, and P3 refer to the first, second and third positive peaks, respectively. Alternatively, they can be labeled with "P" or "N" and the approximate timing of the peak. Thus, P300 and N400 refer to a positive peak at 300 ms and a negative peak at 400 ms (*not* the 300th positive and 400th negative peak!).

Whether a peak is positive or negative (its *polarity*) has no real significance in cognitive terms, nor does a positive peak reflect excitation and a negative peak inhibition. The polarity depends on the spatial arrangement of the neurons that are giving rise to the signal at that particular moment in time. This is illustrated in Figure 3.10. Positive ions flow into the dendrites when an excitatory

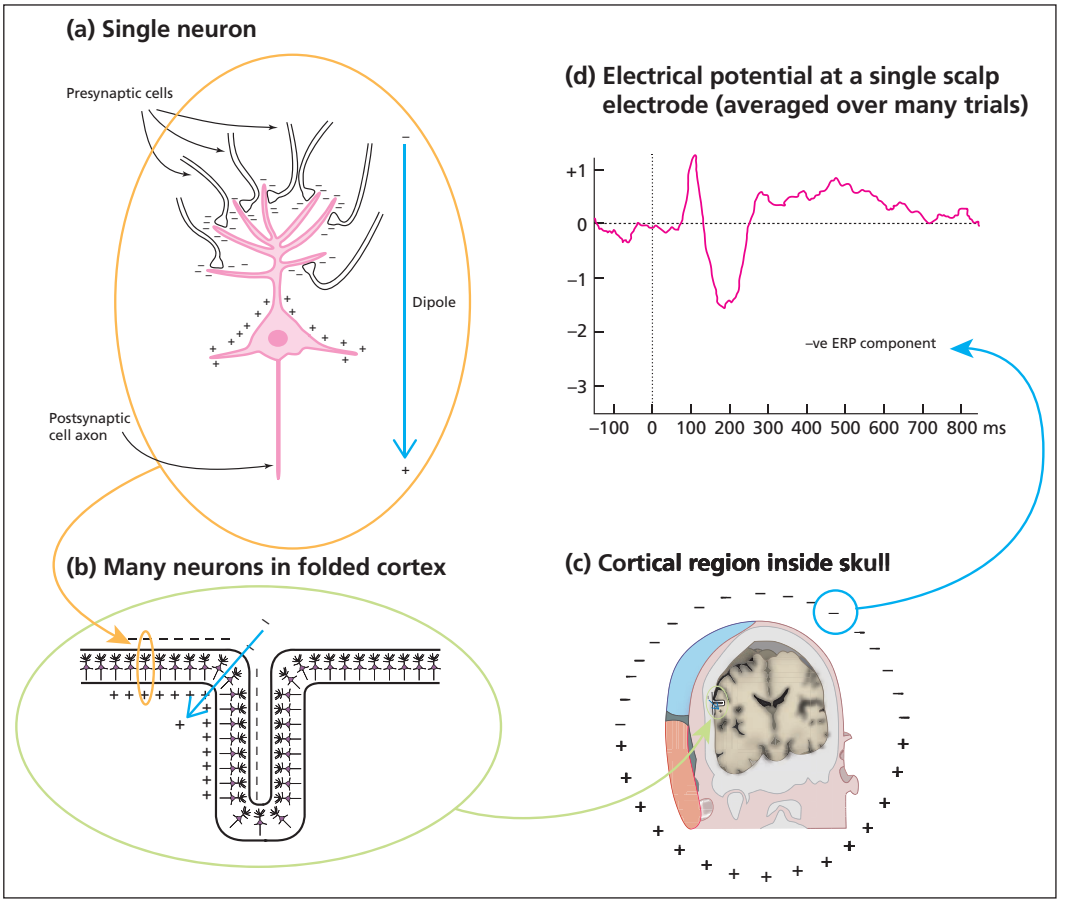

FIGURE 3.10: From electrical activity of neurons to a scalp-recorded event-related potential. (a) Release of an excitatory neurotransmitter results in positively charged ions flowing into the postsynaptic neuron (and a net negativity in the extracellular region). (b) This sets up a dipole that may sum together with dipoles from surrounding neurons (which tend to be aligned in the same way). (c) This conducts to the scalp as a distribution of positive and negative charges. (d) Changes in the negative or positive potential at a given site over time are the neural basis for the ERP signal.

neurotransmitter is released, leaving a net negative voltage in the extracellular space. This creates what is called a **dipole** (a separation of electrical charges that creates an electromagnetic field rather like the ones drawn around bar magnets in high school physics). Dipoles from different neurons and different regions summate and conduct to the skull, and these give rise to the characteristic peaks and troughs of the ERP waveform. What is of interest in the ERP waveform, in terms of linking it to cognition, is the timing and amplitude of those peaks. This is considered later.

KEY TERM

Dipole
A pair of positive and negative electrical charges separated by a small distance.

ONLINE RESOURCES

Find information for early career researchers working with EEG event-related potentials (erpinfo.org) and visit the Instructor & Student Resources website for further links (routledgelearning.com/wardcognitiveneuroscience).

SOME PRACTICAL ISSUES TO CONSIDER WHEN CONDUCTING EEG/ERP RESEARCH

Where can a set of guidelines for conducting and reporting EEG experiments be found?
A detailed set of guidelines is provided by Keil et al. (2014) and is based on recommendations by a working group set up by the Society for Psychophysiological Research. This is recommended reading for all new researchers in the field.

What behavioral measures should be obtained?
In almost all ERP experiments, participants are required to perform a task in which an overt behavioral response is required (e.g., a button press), and this can be analyzed independently (e.g., in terms of reaction times and/or error rates). One exception to this is ERP responses to unattended stimuli (e.g., ignored stimuli, stimuli presented subliminally). It is not possible to record vocal responses (e.g., picture naming) because jaw movements disrupt the EEG signal. It is important that the initial hypothesis places constraints on the ERP component of interest (e.g., "the experimental manipulation will affect the latency of the P300 component") rather than predicting nonspecific ERP changes (e.g., "the experimental manipulation will affect the ERP in some way"). This is because the dataset generated from a typical ERP experiment is large, and the chance of finding a "significant" result that is not justified by theory or reliable on replication is high.

How can interference from eye movement be avoided?
Not all of the electrical activity measured at the scalp reflects neural processes. One major source of interference comes from movement of the eyes and eyelids. These movements occur at the same frequencies as important components in the EEG signal. There are a number of ways of reducing or eliminating these effects. One can instruct the

participant not to blink or to blink only at specified times in the experiment (e.g., after making their response). The problem with this method is that it imposes a secondary task on the participant (the task of not moving their eyes) that may affect the main task of interest. It is also possible to discard or filter out the effect of eye movements in trials in which they have occurred (Luck, 2014), and so it is important to have a large number of trials in the first place to ensure enough "clean" data are obtained.

MENTAL CHRONOMETRY IN ELECTROPHYSIOLOGY AND COGNITIVE PSYCHOLOGY

KEY TERMS

Mental chronometry
The study of the time-course of information processing in the human nervous system.

Additive factors method
A general method for dividing reaction times into different stages.

Mental chronometry can be defined as the study of the time-course of information processing in the human nervous system (Posner, 1978). The basic idea is that changes in the nature or efficiency of information processing will manifest themselves in the time it takes to complete a task. For example, participants are faster at verifying that 4 + 2 = 6 than they are to verify that 4 + 3 = 7, and this is faster than verifying that 5 + 3 = 8 (Parkman & Groen, 1971). What can be concluded from this? First of all, it suggests that mathematical sums such as these are not just stored as a set of facts. If this were so, then all the reaction times would be expected to be the same because all statements are equally true. It suggests, instead, that the task involves a stage in processing that encodes numerical size together with the further assumption that larger sums place more limits on the efficiency of information processing (manifested as a slower verification time). This provides one example of how it is possible to make inferences about the nature of cognitive processes from timing measures.

A task such as verification of sums is likely to involve a series of stages, including visual recognition of the digits, computing the sum, and producing a response. The reaction-time measure is the end product of all these stages. Sternberg (1969) developed a general method for dividing reaction times into different stages termed the **additive factors method**. His experiment involved a working memory task in which participants were given an array of one, two, or four digits to hold in mind (e.g., 5, 9, 3, 2). They were then shown a single probe digit (e.g., 9) and asked to press one of two buttons (labeled "yes" and "no") to indicate whether this item had been in the previous array. Sternberg proposed that the task could be divided into a number of separate stages, including:

1 *Encoding* the probe digit.
2 *Comparing* the probe digit with the items held in memory.

3 *Deciding* which response to make.
4 *Responding* by executing the button press.

He further postulated that each of these stages could be independently influenced by different factors affecting the task. For instance, the encoding stage may be affected by the perceptibility of the probe digit (e.g., presenting it on a patterned background). The comparison stage may be affected by the number of items in the array (the more items in the array, the slower the task). He reasoned that if different factors affect different stages of processing, then the effects should have additive effects on the overall reaction time, whereas if they affect the same processing stage, they should have interactive effects. The strength of this method is that one could then take an unknown factor (e.g., sleep deprivation, Parkinson's disease, reading ability) and determine whether this has an interactive effect on stimulus perceptibility (implying that the new factor affects perceptual encoding) or whether it has an interactive effect with the number of items in the array (implying the new factor affects the comparison stage) or both (implying the new factor has effects at multiple levels) – see Figure 3.11.

The additive factors approach has been very influential in cognitive psychology research, although it is to be noted that the assumptions do not always apply. For example, the model assumes that the stages are strictly sequential (i.e., later stages do not occur until earlier ones are complete), but this assumption is not always valid.

At this juncture, it is useful to consider how the mental chronometry approach applies to the analysis and interpretation of ERP data. Whereas a reaction time consists of a *single* measure that is assumed to reflect different stages/components, an ERP waveform consists of a series of peaks and troughs that vary continuously over time. These peaks and troughs are likely to have some degree of correspondence with different cognitive stages of processing. For example, in the task described previously, earlier peaks may reflect perceptual encoding and later peaks may reflect the comparison stage. One could then observe how the

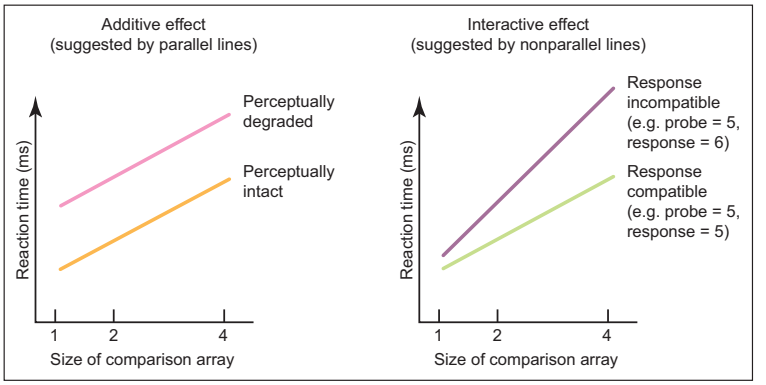

FIGURE 3.11: Sternberg's additive factors method assumes that if two variables affect different stages of processing, then they should have an additive effect on the overall reaction time (left), but if two variables affect the same stage of processing, then the factors should have an interactive effect (right). His task involved comparing a probe digit (e.g., 5) with an array of one, two, or four digits held in mind.

amplitude of those peaks varied, say, with the number of items to be compared. One could also observe whether a new variable (e.g., sleep deprivation) affected earlier or later peaks. The different peaks and troughs of the ERP signal have been referred to as *ERP components* (Donchin, 1981). There may not be a simple mapping between an ERP component and a cognitive component of a task. For example, a single cognitive component may reflect the action of several spatially separate neural populations (i.e., one cognitive component could affect several ERP components) or several cognitive components may be active at once and sum together, or cancel each other out, in the ERP waveform (i.e., several cognitive components affect a single ERP component). This is illustrated in Figure 3.12. As such, some researchers prefer to use the more neutral term ERP *deflection* rather than ERP *component*.

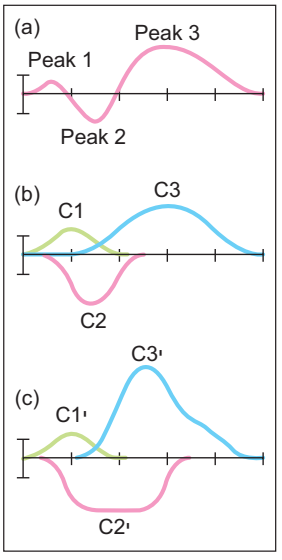

FIGURE 3.12: Graph (a) shows an observed ERP waveform, and graphs (b) and (c) show two different sets of hidden components that could have given rise to it. Although different peaks and troughs can be linked to different cognitive processes, we should not necessarily assume that a single peak/trough is linked to ***one*** single cognitive process (or reflects the activity of one single dipole in the brain).

From Luck, S.J in Handy, Todd C., ed., Event-Related Potentials, Figure 2.1 (p. 18), © 2004 Massachusetts Institute of Technology, by permission of The MIT Press.

Investigating face processing with ERPs and reaction times

This chapter has already considered the neural representation of faces as measured by single-cell recordings. ERP studies have also investigated the way that faces are processed. A full model of face processing is discussed in Chapter 7, but a consideration of a few basic stages will suffice for the present needs. An initial stage consists of perceptual coding of the facial image (e.g., location of eyes, mouth), followed by a stage in which the facial identity is computed. This stage is assumed to map the perceptual code onto a store of known faces and represents the face irrespective of viewing conditions (e.g., lighting, viewing angle). (Note that this doesn't assume grandmother cells because facial identity could be computed by a population of neurons.) Finally, there may be a representation of the identity of the person that is not tied to any modality (e.g., responds to faces and names) and may enable retrieval of other types of knowledge (e.g., their occupation).

As with the single-cell results, there is evidence for an ERP component that is relatively selective to the processing of faces compared with other classes of visual objects. This has been termed the **N170** (a negative peak at 170 ms) and is strongest over right posterior temporal electrode sites (Bentin et al., 1996). This is shown in Figure 3.13. This component is uninfluenced by whether the face is famous or not (Bentin & Deouell, 2000) and is also found for cartoon "smiley" faces (Sagiv & Bentin, 2001). It is, however, reduced if the face is perceptually degraded (Schweinberger, 1996). The N250, by contrast, is larger for famous and personally familiar faces relative to unfamiliar faces (Herzmann et al., 2004) and responds to the presentation of different images of the same person (Schweinberger et al., 2002b). This suggests that it codes properties of the specific face rather than the specific image. Later, positive-going components (from 300 ms onwards) are also sensitive to the repetition and familiarity of specific person identities, and the effects generalize to names as well as faces (Schweinberger et al., 2002a).

KEY TERM

N170
An ERP component (negative potential at 170 ms) linked to perceiving facial structure.

Having sketched out a plausible relationship between different components of the ERP waveform and different cognitive processes (see Figure 3.14), it is possible to use these electrophysiological markers to adjudicate between different theories of face processing. One debate in the cognitive psychology literature concerns the locus of associative priming. **Associative priming** refers to the fact that reaction times are faster to a stimulus if that stimulus is preceded by a stimulus that tends to co-occur with it in the environment. For example, judging that the face of Mikhail Gorbachev (the last President of the Soviet Union) is familiar is performed faster if it immediately follows Boris Yeltsin's face (former President of Russia) or even Yeltsin's name (Young et al., 1988). The fact that associative priming is found between names and faces might imply that the effect arises at a late stage of processing. However, there is evidence inconsistent with this. Using Sternberg's (1969) method, it has been found that associative priming interacts with stimulus degradation (Bruce & Valentine, 1986) and that associative priming interacts with how perceptually distinctive a face is (Rhodes & Tremewan, 1993). This would imply that associative priming has a perceptual locus such that perceiving Gorbachev's face also activates the perceptual face representation of Yeltsin. Schweinberger (1996) used ERP measures to determine the locus of associative priming of faces and names. ERP was suitable for addressing this question because it enables early and late time points to be measured separately. He found that associative priming has a late effect (after 300 ms) on the ERP waveform that is more consistent with a post-perceptual locus. Effects of stimulus degradation were found under 150 ms. Schweinberger (1996) suggests that, in this instance, the Sternberg method may have led to an invalid conclusion because it assumes discrete stages.

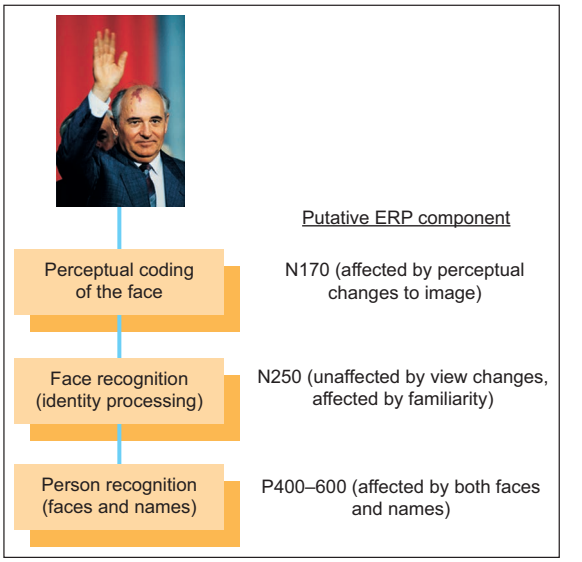

FIGURE 3.13: A simple model of several hypothetical stages involved in face processing together with their putative ERP manifestations.

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KEY TERM

Associative priming
Reaction times are faster to stimulus X after being presented to stimulus Y if X and Y have previously been associated together (e.g., if they tend to co-occur).

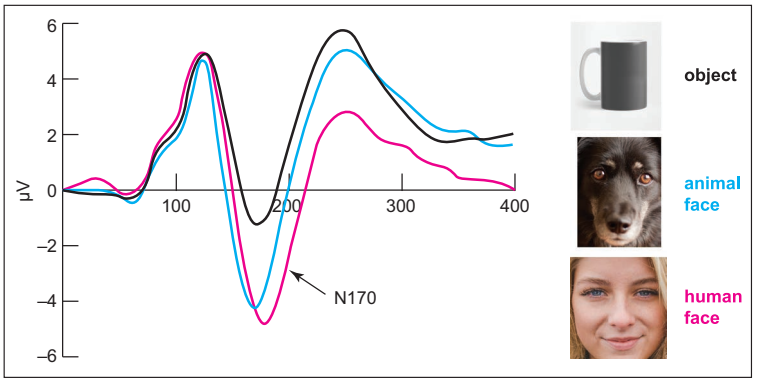

FIGURE 3.14: The N170 is observed for both human faces (purple) and animal faces (blue), but not other objects (green).

From Rousselet et al. (2004). With permission of ARVO.

KEY TERMS

Exogenous
Related to properties of the stimulus.

Endogenous
Related to properties of the task.

Inverse problem
The difficulty of locating the sources of electrical activity from measurements taken at the scalp (in ERP research).

Dipole modeling
An attempt to solve the inverse problem in ERP research that involves assuming how many dipoles (regions of electrical activity) contribute to the signal recorded at the scalp.

ENDOGENOUS AND EXOGENOUS ERP COMPONENTS

Traditionally, ERP components have been classified as belonging to one of two categories. **Exogenous** components are those that appear to depend on the physical properties of a stimulus (e.g., sensory modality, size, intensity). These have also been called *evoked potentials*. **Endogenous** components, in contrast, appear to depend on properties of the task (e.g., what the participant is required to do with the stimulus). These can even occur in the absence of an external stimulus (e.g., if an expected stimulus does not occur; Sutton et al., 1967). Exogenous components tend to be earlier than endogenous components.

Although the exogenous–endogenous classification is useful, it should be considered as a dimension rather than a true categorical distinction. To remain with the current example of face processing, consider the nature of the ERP waveform when viewing two repeated symbols that are horizontally spaced (e.g., + +). Typically, such symbols do not evoke the N170 response characteristic of face processing (Bentin et al., 2002). However, if the symbols have previously been shown embedded in a face context (as eyes), then the pair of symbols do elicit the N170 response, but they don't if they were shown in a flower context (Bentin et al., 2002) – see Figure 3.15. Is this an endogenous or exogenous component? It is impossible to say. Although the N170 is normally taken as indicative of perceptual processing (an exogenous component), in this instance it is entirely dependent on the interpretive bias given.

THE SPATIAL RESOLUTION OF ERPS

The discussion so far has emphasized the importance of ERPs in the timing of cognition. The reason why the spatial resolution of this method is poor is given by the so-called **inverse problem**. If one had, say, three sources of electrical activity in the brain during a given task, and the magnitude and location of the activity were known, then it would be possible to calculate the electrical potential that we would expect to observe some distance away at the scalp. However, this is not the situation that is encountered in an ERP study; it is the inverse. In an ERP study, the electrical potential at the scalp is known (because it is measured), but the number, location, and magnitude of the electrical sources in the brain are unknown. Mathematically, there are an infinite number of solutions to the problem.

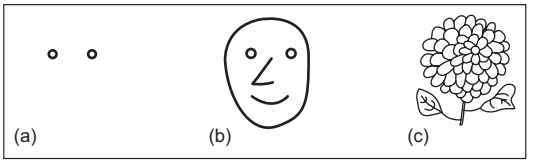

FIGURE 3.15: Two horizontally spaced symbols (the dots in (a)) do not elicit an N170 unless they have previously been presented in the context of a face (b). The participant's task was merely to count flowers (e.g., (c)), and so both the faces and "eyes" were irrelevant to the task.

From Bentin et al. (2002). Reprinted by permission of Blackwell Publishing.

The most common way of attempting to solve the inverse problem involves a procedure called **dipole modeling**. This

requires assumptions to be made about how many regions of the brain are critical for generating the observed pattern of scalp potentials. Attempts at dipole modeling with the N250 and N170 evoked by face processing (see previously) revealed probable loci in the fusiform gyrus and the posterior occipital region, respectively (Schweinberger et al., 2002b). However, the most common way of obtaining good spatial resolution is to use a different method altogether, such as fMRI (see Chapter 4) or magnetoencephalography (MEG). It is also possible to collect data from fMRI and EEG at the same time. Using this approach, Sadeh et al. (2010) found evidence that the N170 correlated with fMRI activity in the fusiform face area and the superior temporal sulcus.

WHY ARE CARICATURES EASY TO RECOGNIZE?

Caricatures of faces are typically considered humorous and are often used for deliberate mockery or propaganda (Figure 3.16). As Richard Nixon's unpopularity grew during the Watergate scandal, so did his nose and jowls in published caricatures (see Rhodes, 1996). The paradox of caricatures is that the face is instantly recognizable despite being perceptibly wrong. In fact, people can sometimes be twice as fast at recognizing a caricature of a face as the same face undistorted (Rhodes et al., 1987); the caricature appears to be more like the face than the face itself. What does this reveal about the way that faces are processed and represented?

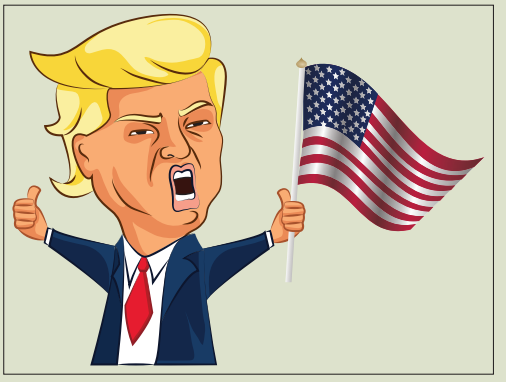

FIGURE 3.16: This caricature is instantly recognizable despite significant distortions. We are sometimes faster at recognizing caricatures than actual depictions. Why might this be?

First of all, it is important to clarify how caricatures are created. Caricatures exaggerate the distinctive features of an individual. Computer routines now exist that compare, for example, the size of an individual's nose with the average nose size. If the person has a larger than average nose, then this will be enlarged further in the caricature. If someone has a smaller than average nose, it will be shrunk in the caricature. It is also possible to morph a face to make it look more average (a so-called anti-caricature), and such faces are typically rated as more attractive than the real or caricatured face. One explanation for the effect of caricatures is to assume that our memory representations of faces are caricatured themselves; that is, we store the distinctive properties of a face rather than the face as it is. However, explanations such as these must assume that a "norm" or prototype face exists from which to infer what constitutes a distinctive feature. Another hypothesis is that it is the distinctiveness of caricatures per se that aids their recognition because there are fewer similar-looking competitor faces

(Valentine, 1991). This account does not need to assume the existence of a face prototype or that the stored representations themselves are caricatured. Research using ERPs is consistent with this view. Photographic caricatures of unfamiliar people lead, initially, to an enhancement of the N170 component relative to undistorted images or anti-caricatures (Kaufmann & Schweinberger, 2008). As this component is normally associated with perceptual coding of faces rather than memory of faces, it suggests that the effect is more likely to be due to perceptual distinctiveness rather than the way faces are coded in memory.

Evaluation

Investigating the time-course of cognitive processes is an important method in cognitive psychology and cognitive neuroscience. Event-related potentials have an excellent temporal resolution. This method has a number of benefits over and above reaction-time measurements: it provides a continuous measurement of changes over time (rather than a single timing measure), and it is possible to link this to neural processes in the brain. ERP also enables electrophysiological changes associated with unattended stimuli (that are not responded to) to be measured, whereas a reaction-time measure always requires an overt behavioral response.

MAGNETOENCEPHALOGRAPHY

KEY TERM

Magnetoencephalography (MEG)
A noninvasive method for recording magnetic fields generated by the brain at the scalp.

All electric currents, including those generated by the brain, have an associated magnetic field that is potentially measurable. As such, **magnetoencephalography (MEG)** can be regarded as a parallel method to EEG that is similar in many regards. For instance, one can examine either rhythmic neural oscillations or stimulus-evoked changes. There are some key differences too. The biggest potential advantage of MEG over EEG is that it permits a much better spatial resolution in addition to the excellent temporal resolution (e.g., Hari et al., 2010). For example, it is possible to detect an MEG equivalent to the N170 linked, in ERP research, to structural encoding of faces (MEG components tend to be prefaced by an "m/M"). One MEG study showed that the M170 is sensitive both to facial expressions (angry, happy, neutral) and to head posture that may indicate status (aloof or downcast) (Arviv et al., 2015). However, the authors were able to demonstrate that different brain regions were influencing this process rather than reflecting a single localized mechanism. This conclusion rested on the enhanced spatial resolution of MEG relative to EEG. Gross et al. (2013) provide guidelines on current best practice for researchers who are using this method.

In terms of practicalities, MEG is a more challenging and costly enterprise than EEG. The size of the magnetic field

generated by the brain is very small relative to the ambient magnetic field of the Earth. As such, the development of MEG had to wait for suitable technological advances to become a viable enterprise. This technological advance came in the form of superconducting devices termed SQUIDs (an acronym of superconducting quantum interference devices). A whole-head MEG contains 200–300 of these devices, and the participant typically sits upright with their head in the bore (Figure 3.17). The apparatus used requires extreme cooling, using liquid helium, and isolation of the system in a magnetically shielded room. More recently, MEG systems have become available with room-temperature sensors called OPMs (optically-pumped magnetometers) that also operate as a wearable system for the participant (Boto et al., 2018).

FIGURE 3.17: A MEG scanner. This extremely powerful machine measures the magnetic fields produced by electrical activity in the brain.

PJF Military Collection/Alamy Stock Photo

MEG	EEG
· Signal unaffected by skull, meninges, etc.	· Signal affected by skull, meninges, etc.
· Poor at detecting deep dipoles	· Detects deep and shallow dipoles
· More sensitive to activity at sulci	· Sensitive to gyri and sulci activity
· Millisecond temporal resolution	· Millisecond temporal resolution
· Potentially good spatial resolution (2–3 mm)	· Poor spatial resolution
· Expensive and limited availability	· Cheaper and widely available

SUMMARY AND KEY POINTS OF THE CHAPTER

- Neuronal activity generates electrical and magnetic fields that can be measured either invasively (e.g., single-cell recording) or noninvasively (e.g., EEG).
- Studies of single-cell recordings are based on measuring the number of action potentials generated and provide clues about how neurons code information, by measuring the specificity of their responses to external stimuli.
- When populations of neurons are active in synchrony, they produce an electric field that can be detected at the scalp (EEG). When many such waves are averaged

together and linked to the onset of a stimulus (or response), an ERP is obtained.
- An ERP waveform is an electrical signature of all the different cognitive components that contribute to the processing of that stimulus. Systematically varying certain aspects of the stimulus or task may lead to systematic variations in particular aspects of the ERP waveform. This enables inferences to be drawn about the timing and independence of cognitive processes.
- EEG has a wave-like structure, that reflects the rhythmic, synchronized neural activity of many neurons. Changes in this measure reflect changes in the coordinated activity across sets of neurons and are correlated with cognitive processes such as attention and perceptual grouping.

EXAMPLE ESSAY QUESTIONS

- How does the brain generate electrical signals, and how are these used in electrophysiological techniques?
- How do neurons code information?
- What is an event-related potential (or ERP), and how can it be used to inform theories of cognition?
- What have electrophysiological studies contributed to our understanding of how faces are represented and processed by the brain?

FREE INSTRUCTOR & STUDENT RESOURCES

ONLINE RESOURCES

Visit the Instructor & Student Resources website at routledgelearning.com/wardcognitiveneuroscience for:

- Videos on key topics covered in this chapter and a lecture by author Jamie Ward on *The Electrophysiological Brain*
- Multiple-choice questions and interactive flashcards to test your knowledge

CHAPTER 4

The imaged brain

CONTENTS

If George Orwell had written *Nineteen Eighty-Four* during our times, would he have put an MRI scanner in the Ministry of Truth? Could we ever really know the content of someone else's thoughts using functional imaging technology? Already, there have been attempts to introduce fMRI-based lie detection into US courts (Farah et al., 2014). There have even been successful attempts at decoding the visual contents of dreams – normally an entirely private experience – using fMRI (Horikawa et al., 2013).

This chapter will consider how functional imaging methods work, focusing in particular on fMRI (functional magnetic resonance imaging). This chapter is broadly divided into three parts. The first part considers how structural and functional brain imaging works, with particular reference to underlying neurophysiology. The second part considers methodological

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factors that are important in ensuring that the results obtained can indeed be meaningfully linked to cognitive theory. The third part covers how functional imaging data are analyzed to find regions of activation and considers some of the pitfalls in their interpretation. Finally, the chapter returns to the question of whether functional imaging could be used as an Orwellian-like mind reader.

STRUCTURAL IMAGING

KEY TERMS

Structural imaging
Measures of the spatial configuration of different types of tissue in the brain (principally CT and MRI).

Functional imaging
Measures temporary changes in brain physiology associated with cognitive processing; the most common method is fMRI and is based on a hemodynamic measure.

One key distinction is the difference between **structural imaging** methods and **functional imaging** methods. Structural imaging is based on the fact that different types of tissue (e.g., skull, gray matter, white matter, cerebrospinal fluid) have different physical properties. These different properties can be used to construct detailed *static* maps of the physical structure of the brain (Figure 4.1). The most common structural imaging methods are computerized tomography (CT) and magnetic resonance imaging (MRI). Functional imaging is based on the assumption that neural activity produces local physiological changes in that region of the brain. This can be used to produce *dynamic* maps of the moment-to-moment activity of the brain when engaged in cognitive tasks.

Computerized tomography

Computerized tomography (CT) scans are constructed according to the amount of X-ray absorption in different types of tissue. The amount of absorption is related to tissue density: bone absorbs the most (and so the skull appears white), cerebrospinal fluid absorbs the least (so the ventricles appear black), and the brain matter is intermediate (and appears gray). Given that CT uses X-rays, the person being scanned is exposed to a small amount of radiation.

CT scans are typically used only in clinical settings, for example to diagnose tumors or to identify hemorrhaging or other

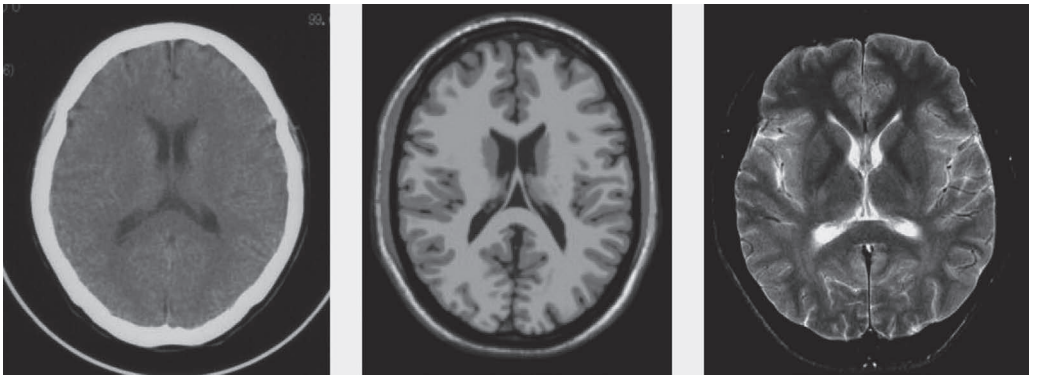

FIGURE 4.1: An example of CT (left), T1-weighted MRI (center), and T2-weighted MRI (right) scans of the brain. Note how the MRI scans are able to distinguish between gray matter and white matter. On the T1-weighted scan (normally used for structural images), gray matter appears gray and white matter appears lighter.

gross brain anomalies. CT cannot distinguish between gray matter and white matter in the same way as MRI, and it cannot be adapted for functional imaging purposes.

Magnetic resonance imaging

Magnetic resonance imaging (MRI) was one of the most important advances in medicine made during the twentieth century. Its importance was recognized by the awarding of the 2003 Nobel Prize to its inventors – Sir Peter Mansfield and Paul Lauterbur. There are a number of advantages of this method over CT scanning, as summarized here:

- It does not use ionizing radiation and so is completely safe (people can be scanned many times).
- It provides a much better spatial resolution, which allows the folds of individual gyri to be discerned.
- It provides better discrimination between white matter and gray matter; this may enable early diagnosis of some pathologies, and can be used to explore how normal variation brain structure is linked to differences in cognitive ability.
- It can be adapted for use in detecting the changes in blood oxygenation associated with neural activity and in this context is called functional MRI (fMRI).

MRI physics for non-physicists

MRI is used to create images of soft tissue of the body, which X-rays pass through largely undistorted. Most human tissue is water-based and the amount of water in each type of tissue varies. Different types of tissue will thus behave in slightly different ways when stimulated, and this can be used to construct a three-dimensional image of the layout of these tissues (for an accessible but more detailed description, see Savoy, 2002).

The sequence of events for acquiring an MRI scan is illustrated in Figure 4.2. First, a strong magnetic field is applied across the part of the body being scanned (e.g., the brain). The single protons that are found in water molecules in the body (the hydrogen nuclei in H_2O) have weak magnetic fields. (Other atoms and nuclei also have magnetic properties, but in MRI it is the hydrogen nuclei in water that form the source of the signal.) Initially, these fields will be

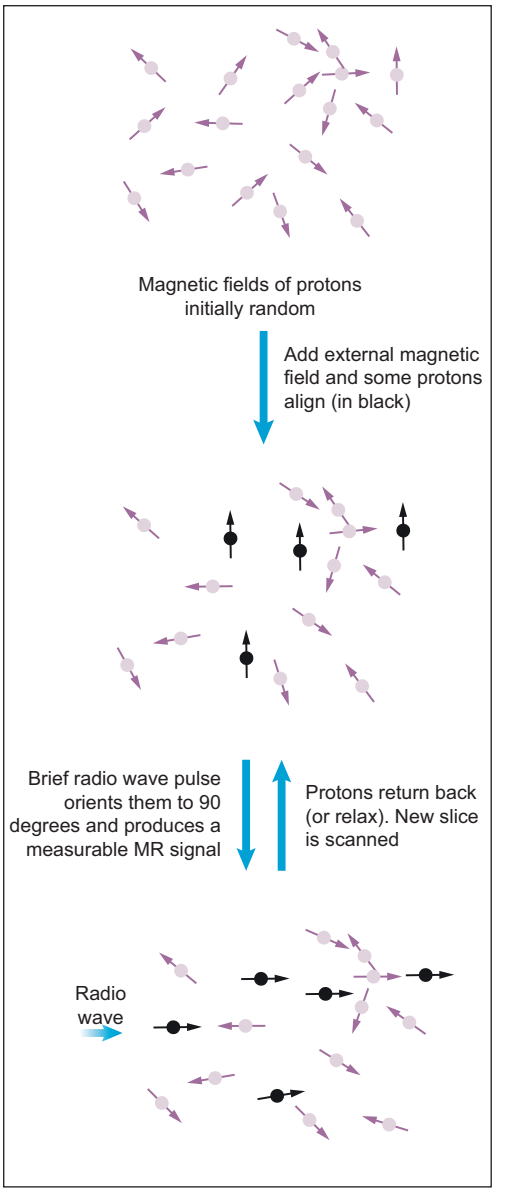

FIGURE 4.2: The sequence of events in the acquisition of an MRI scan involves applying a constant magnetic field and an intermittent radio frequency pulse.

oriented randomly, but when the strong external field is applied, a small fraction of them will align themselves with this. The external field is applied constantly during the scanning process. The strength of the magnetic field is measured in units called tesla (T). Typical scanners have field strengths between 1.5 and 3 T, although 7 T is becoming more common; the Earth's magnetic field is of the order of 0.0001 T.

When the protons are in the aligned state a brief radio frequency pulse is applied that knocks the orientation of the aligned protons by 90 degrees to their original orientation. As the protons spin (or *precess*) in this new state, they produce a detectable change in the magnetic field, and this is what forms the basis of the MR signal. The protons will eventually be pulled back into their original alignment with the magnetic field (they "*relax*"). The scanner repeats this process serially by sending the radio wave to excite different slices of the brain in turn. With the advent of acquisition methods such as echo planar imaging, a whole brain can typically be scanned in about 2 s with slices of around 3 mm.

Different types of image can be created from different components of the MR signal. Variations in the rate at which the protons return back to the aligned state following the radio frequency pulse (called the T1 relaxation time) can be used to distinguish between different types of tissue. These T1-weighted images are typically used for structural images of the brain. In a T1-weighted image, gray matter looks gray and white matter looks white. When in the misaligned state, at 90 degrees to the magnetic field, the MR signal also decays because of local interactions with nearby molecules. This is termed the T2 component. Deoxyhemoglobin produces distortions in this component and this forms the basis of the image created in functional MRI experiments (called a T2* image, "tee-two-star") (Figure 4.2).

WHY ARE MRI SCANNERS SO NOISY?

Very strong magnetic fields are created by passing electric currents through coils and switching them on and off rapidly. When the current is switched on, it causes the coil to expand very slightly, but suddenly, and this generates a loud banging noise. Most MR scanners generate noise in excess of 100 dB.

FUNCTIONAL IMAGING

Whereas structural imaging measures the static characteristics of the brain, functional imaging is designed to measure the moment-to-moment variable characteristics of the brain that may be associated with changes in cognitive processing.

Basic physiology underpinning functional imaging

The brain consumes 20 percent of the body's oxygen uptake; it does not store oxygen, and it stores little glucose. Most of the brain's oxygen and energy needs are supplied from the local blood supply. When the metabolic activity of neurons increases, the blood supply to that region increases to meet the demand (for a review, see Raichle, 1987; but see Attwell & Iadecola, 2002). Techniques such as PET (positron emission tomography) measure the change in blood flow to a region directly, whereas fMRI and the emerging method of fNIRS (functional near-infrared spectroscopy) are sensitive to the concentration of oxygen in the blood. All of these techniques are referred to as hemodynamic methods. PET requires administration of a radioactive tracer, whereas fMRI uses a naturally occurring signal in the bloodstream. The use of PET in cognitive neuroscience has effectively been replaced by fMRI, although it can still be useful for selectively targeting certain neurotransmitter pathways (through specialist tracers). Figure 4.5 shows a typical MRI scanner used for neuroimaging.

LINKING STRUCTURE TO FUNCTION BY IMAGING WHITE MATTER AND GRAY MATTER

Small-scale differences (at the millimeter level) in the organization and concentration of white matter and gray matter can now be analyzed noninvasively using MRI. This is providing important clues about how individual differences in brain structure are linked to individual differences in cognition. Two important methods are **voxel-based morphometry**, or VBM, and **diffusion tensor imaging**, or DTI (Figure 4.3).

Voxel-based morphometry (VBM) capitalizes on the ability of structural MRI to detect differences between gray matter and white matter (Ashburner & Friston, 2000). VBM divides the brain into tens of thousands of small regions, several cubic millimeters in size (called **voxels**), and the concentration of white/gray matter in each voxel is estimated. It is then possible to use this measure to compare across individuals by asking questions such as these: If a new skill is learned, such as a second language, will gray matter density increase in some brain regions? Will it decrease in other regions? How does a particular genetic variant affect brain development? Which brain regions are larger, or smaller, in people with good social skills versus

KEY TERMS

Voxel-based morphometry (VBM)
A technique for segregating and measuring differences in white matter and gray matter concentration.

Diffusion tensor imaging (DTI)
Uses MRI to measure white matter connectivity between brain regions.

Voxel
A volume-based unit (cf. pixels, which are 2D); in imaging research the brain is divided into many thousands of these.

those who are less socially competent? Kanai and Rees (2011) provide a review of this method in relation to cognitive differences.

Diffusion tensor imaging (DTI) is different from VBM in that it measures the white matter connectivity (Le Bihan et al., 2001). (Note: VBM measures the *amount* of white matter without any consideration of how it is connected.) It is able to do this because water molecules trapped in axons tend to diffuse in some directions but not others. Specifically, a water molecule is free to travel down the length of the axon but is prevented from traveling out of the axon by the fatty membrane. When many such axons are arranged together, it is possible to quantify this effect with MRI (using a measure called **fractional anisotropy**). This is illustrated in Figure 4.4. As an example of a cognitive study using DTI, Bengtsson et al. (2005) found that learning to play the piano affects the development of certain white matter fibers. However, different fibers were implicated depending on whether the piano was learned during childhood, adolescence, or adulthood.

KEY TERM

Fractional anisotropy (FA)
A measure of the extent to which diffusion takes place in some directions more than others.

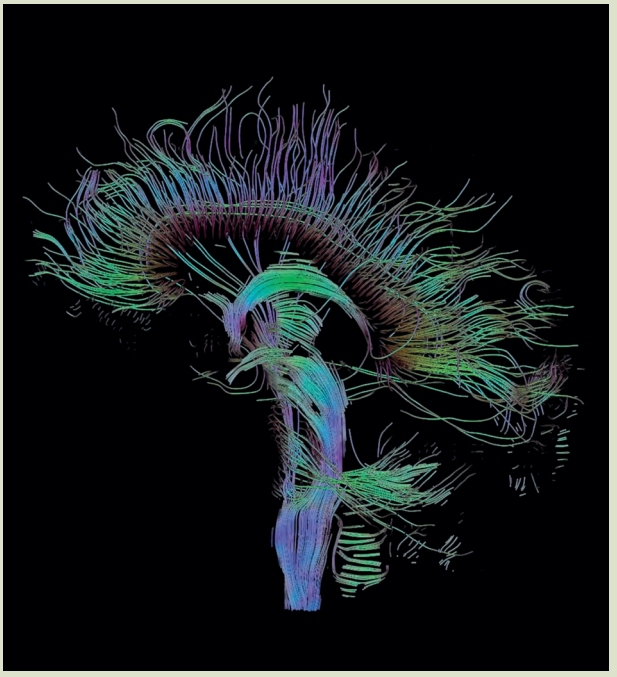

FIGURE 4.3: Visualization of a DTI measurement of a human brain. Depicted are reconstructed fiber tracts that run through the midsagittal plane.
Image by Thomas Schultz via Wikimedia commons

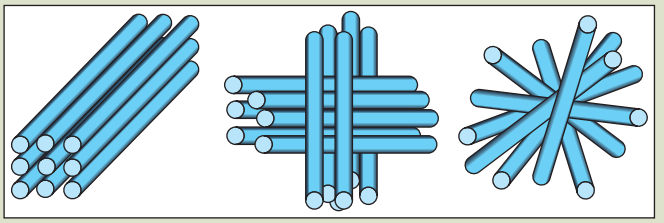

FIGURE 4.4: Diffusion tensor imaging (DTI) measures the degree of organization of white matter tracts using a measure called fractional anisotropy (FA). The image on the left has an FA close to 1, the image on the right has an FA close to 0, and the image in the middle is intermediate in FA.

FIGURE 4.5: A typical MRI scanner used in functional imaging research. Testing of a single participant can normally be completed in under an hour, allowing 30–40 min to complete the experiment and 10 min for a high-resolution structural MRI scan to be obtained.

Sputnik/Science Photo Library

The brain is always physiologically active. Neurons would die if they were starved of oxygen for more than a few minutes. This has important consequences for using physiological markers as the basis of neural "activity" in functional imaging experiments. It would be meaningless to place someone in a scanner, with a view to understanding cognition, and simply observe which regions were receiving blood and using oxygen because this is a basic requirement of all neurons, all of the time. As such, when functional imaging researchers refer to a region being "active," what they mean is that the physiological response in one task is greater *relative* to some other condition. There is a basic requirement in all functional imaging studies involving cognitive tasks that the physiological response must be compared with one or more baseline responses. Good experimental practice is needed to ensure that the baseline task is appropriately matched to the experimental task, otherwise the results will be very hard to interpret.

It is also worth pointing out that hemodynamic methods are not measuring the activity of neurons directly but, rather, are measuring a downstream consequence of neural activity (i.e., changes in blood flow/oxygen to meet metabolic needs). This is to be contrasted with methods such as EEG (electroencephalography) and MEG (magnetoencephalography) that measure the electrical/magnetic fields generated by the activity of neurons themselves.

Functional magnetic resonance imaging

The component of the MR signal that is used in fMRI is sensitive to the amount of deoxyhemoglobin in the blood. When neurons consume oxygen they convert oxyhemoglobin to deoxyhemoglobin. Deoxyhemoglobin has strong paramagnetic properties, and this introduces distortions in the local magnetic field. (Note: a paramagnetic material isn't magnetic in its own right but acts like a magnet when put in a magnetic field, e.g., a paper clip becomes magnetic when next to a magnet.) This distortion can itself be measured to give an indication of the concentration of deoxyhemoglobin present in the blood. This technique has therefore been termed **BOLD** (for blood oxygen-level-dependent contrast; Ogawa et al., 1990). The way that the BOLD signal evolves over time in response to an increase in neural activity is called the **hemodynamic response function (HRF)**. The hemodynamic response function has three phases, as shown in Figure 4.6 (see also Hoge & Pike, 2001):

1. *Initial dip*. As neurons consume oxygen there is a small rise in the amount of deoxyhemoglobin, which results in a reduction of the BOLD signal.
2. *Overcompensation*. In response to the increased consumption of oxygen, the blood flow to the region increases. The increase in blood flow is greater than the increased consumption, which means that the BOLD signal increases significantly. This is the component that is normally measured in fMRI, and the size of this peak is taken as indicative of the extent to which this region is active in the task.
3. *Undershoot*. Finally, the blood flow and oxygen consumption dip before returning to their original levels. This may reflect a relaxation of the venous system, causing a temporary increase in deoxyhemoglobin again.

The hemodynamic signal changes are small – approximately 1–3 percent with moderately sized magnets (1.5 T). The hemodynamic response function is relatively stable across sessions with the same participant in the same region but is more variable across different regions within the same individual and more variable between individuals (Aguirre et al., 1998).

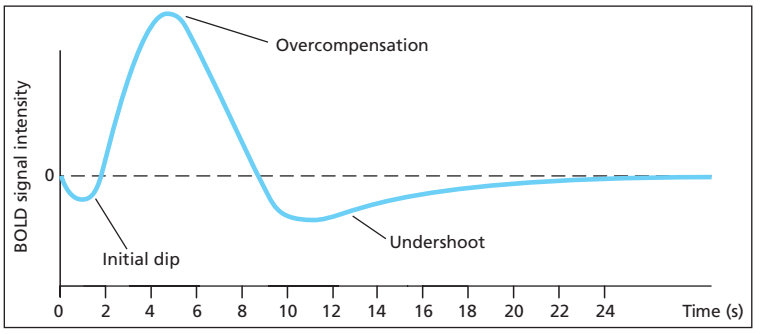

FIGURE 4.6: The HRF has a number of distinct phases.

ONLINE RESOURCES

Check out the Cognitive Neuroscience Bitesize, by Jamie Ward, on the basics of fMRI by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.
For a deeper dive, there are videos of lectures given by Professor Geoffrey Aguirre on the physics and biology of fMRI, as well as various other issues such as study design and analysis.

KEY TERMS

BOLD
Blood oxygen-level-dependent contrast; the signal measured in fMRI that relates to the concentration of deoxyhemoglobin in the blood.

Hemodynamic response function (HRF)
Changes in the BOLD signal over time.

The spatial resolution of fMRI is up to around 1 mm depending on the size of the voxel. The temporal resolution of fMRI is several seconds and related to the rather sluggish hemodynamic response. This is very slow compared with the speed at which cognitive processes take place. The sluggishness of the hemodynamic response to peak and then return to baseline does place some constraints on the way that stimuli are presented in the scanning environment that differ from equivalent tasks done outside the scanner. However, it is not the case that one has to wait for the BOLD response to return to baseline before presenting another trial, as different hemodynamic response functions can be superimposed on each other (Dale & Buckner, 1997), as illustrated in Figure 4.7. In general, during fMRI, there may be fewer trials that are more spaced out in time than standard cognitive testing, and it is common to have "null events" (e.g., a blank screen). These null events allow the BOLD signal to dip toward baseline, essentially providing the necessary variability in the signal needed for the analysis. In standard cognitive psychology experiments (e.g., using response time measures), the amount of data is effectively the same as the number of *trials and responses*. In the equivalent fMRI experiment, the amount of data is related to the number of *brain volumes* acquired rather than the number of trials or responses.

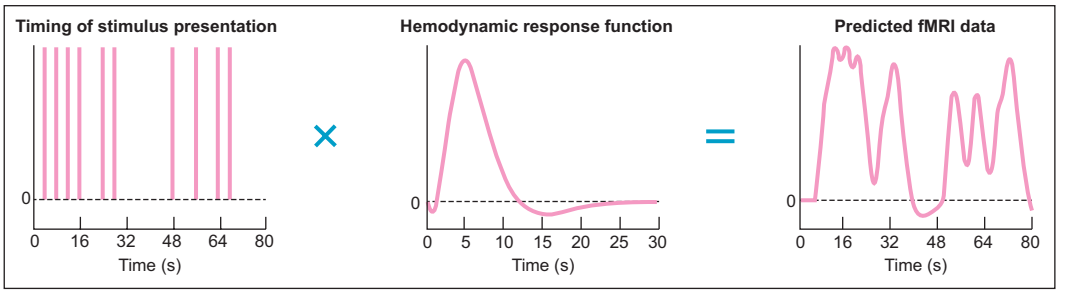

FIGURE 4.7: Unless the stimuli are presented far apart in time (e.g., every 16 sec), the predicted change in BOLD response will not resemble a single HRF but will resemble many superimposed HRFs. Statistically, the analysis is trying to find out which voxels in the brain show the predicted changes in the BOLD response over time, given the known design of the experiment and the estimated shape of the HRF. To achieve this there has to be sufficient variability in the predicted BOLD response (big peaks and troughs).

Functional near infrared spectroscopy

The newer method of fNIRS measures the same BOLD signal as fMRI although it does so in a completely different way (Ferrari & Quaresima, 2012). It does not require the use of magnetic fields, but instead, it sends "light" of a particular wavelength to the brain; specifically, in the near infrared range, about 800 nanometers (i.e., not visible light). This signal passes relatively freely through bone and skin but is more strongly scattered by oxy- and deoxyhemoglobin, each of which is sensitive to slightly different wavelengths in the near infrared range. The extent to which the signal is scattered by these different wavelengths is then used to compute the BOLD

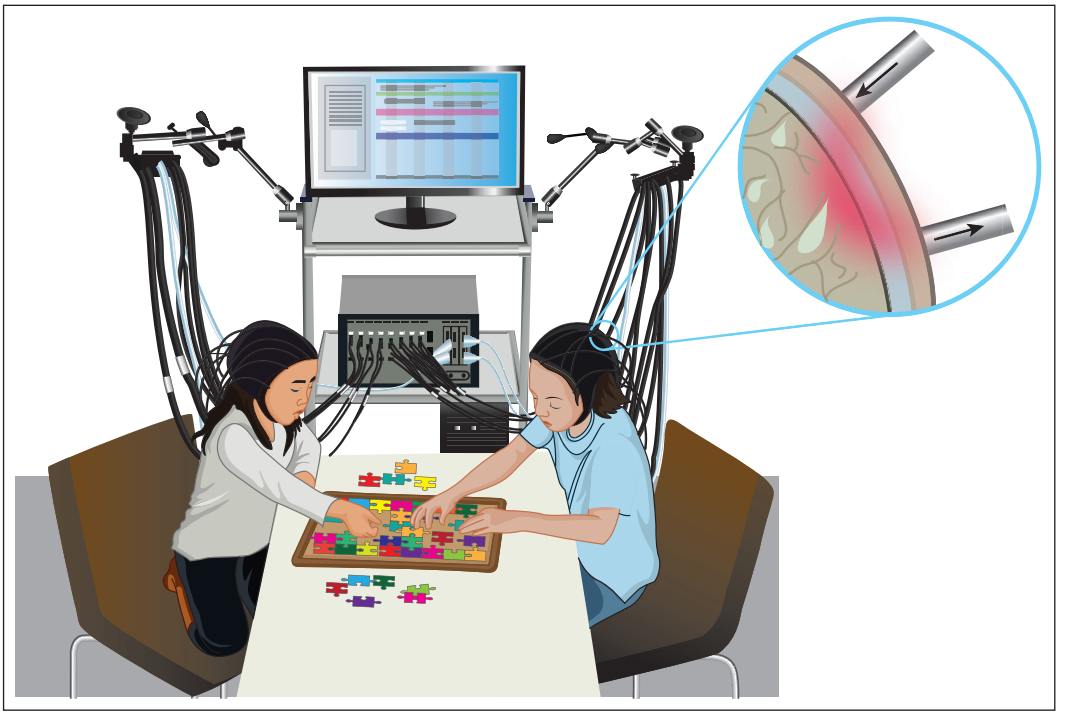

FIGURE 4.8: fNIRS involves an optical signal that is absorbed differently by oxy- and deoxyhemoglobin. The equipment can be fixed on a cap, allowing more naturalistic behavior during scanning.

response. As with fMRI, a larger BOLD response is interpreted as reflecting more cognitive and neural activity.

fNIRS is more portable and more tolerant of movement than fMRI, and for these reasons, it has become popular in developmental research (Lloyd-Fox et al., 2010). It is also far cheaper. However, it can only be used to image shallow neural activity that is close to the scalp (Figure 4.8).

FROM IMAGE TO COGNITIVE THEORY: EXPERIMENTAL DESIGN

An example of cognitive subtraction methodology

One of the groundbreaking studies for establishing the use of functional imaging of cognition was that by Petersen et al. (1988), which was designed to look for brain regions specialized for the processing of written and spoken words. A consideration of this study provides a good introduction to the principle of **cognitive subtraction**. The idea behind cognitive subtraction is that, by comparing the activity of the brain in a task that utilizes a particular cognitive component (e.g., a store of visual words, or visual lexicon) to the activity of the brain in a baseline task that does not, it is possible to infer which regions are specialized for this

KEY TERM

Cognitive subtraction
A type of experimental design in functional imaging in which activity in a control task is subtracted from activity in an experimental task.

particular cognitive component. As has been noted, the brain is always active in the physiological sense, and so it is not possible to infer from a single task which regions are dedicated to specific aspects of the task; a comparison between two or more tasks or conditions is always needed.

Let's consider the different processes involved with reading and understanding isolated written words. A simple model of written word recognition is given in Figure 4.9, which forms the motivation for the imaging study to be described. The study by Petersen et al. (1988) was concerned with identifying brain regions involved with (1) recognizing written words, (2) saying the words, and (3) retrieving the meaning of the words. To do this, the researchers performed a number of cognitive subtractions.

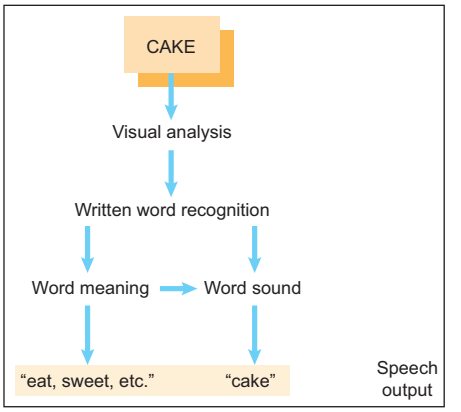

FIGURE 4.9: Basic cognitive stages involved in reading written words aloud and producing spoken semantic associates to written words.

To work out which regions are involved with recognizing written words, Petersen *et al.* compared brain activity when passively viewing words (e.g., CAKE) with passively viewing a cross (+) (see Figure 4.10). The logic is that both experimental and baseline tasks involve visual processing (and so a subtraction

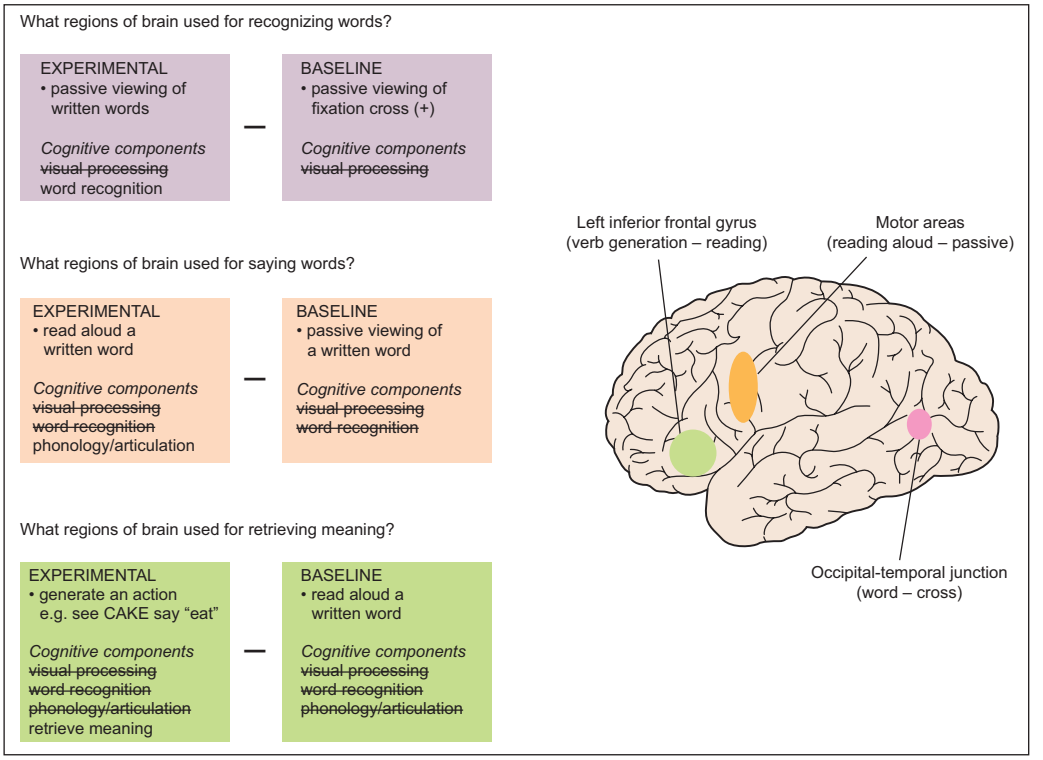

FIGURE 4.10: Cognitive subtraction is founded on the assumption that it is possible to find two tasks (an experimental and baseline task) that differ in terms of a small number of cognitive components. The results show several regions of activity, but only the main results on the left lateral surface are depicted here.

should cancel this out), but only the experimental task involves visual word recognition (so this should remain after subtraction).

To work out which regions are involved with producing spoken words, they compared reading aloud the word (see CAKE, say "cake") with passive viewing of written words (see CAKE). In this instance, both experimental and baseline tasks involve visual processing of the word and word recognition (so subtracting should cancel these out), but only the experimental task involves spoken output (so activity associated with this should remain after subtraction).

To work out which regions are involved with retrieving the meaning of written words, they compared a verb-generation task (e.g., see CAKE, say "eat") with reading aloud (e.g., see CAKE, say "cake"). In this instance, both experimental and baseline tasks involve visual processing, word recognition, and spoken output (so subtracting should cancel out the activity associated with these processes), but only the experimental task involves generating a semantic associate (so activity associated with this should remain after subtraction).

The results of these subtractions show activity in a number of different sites. Only the principal sites on the left lateral hemisphere are depicted in the diagram. Recognizing written words activates bilateral sites in the visual (striate) cortex as well as a site on the left occipitotemporal junction. Producing speech output in the reading aloud condition activates the sensorimotor cortex bilaterally, whereas verb generation activates the left inferior frontal gyrus. This last result has provoked some controversy because of an apparent discrepancy from lesion data; this is discussed later.

Problems with cognitive subtraction

With the benefit of hindsight, there are a number of difficulties with this study, some of which are related to the particular choice of baseline tasks that were employed. However, there are also more general problems with the method of cognitive subtraction itself (Friston et al., 1996). Consider the subtraction aimed at identifying brain regions associated with written word recognition. The assumption here was that both tasks involve visual processing but that one has the added component of word recognition. That is, one assumes that adding an extra component does not affect the operation of earlier ones in the sequence. This is referred to as the assumption of **pure insertion** (or **pure deletion**). This idea was already encountered in Chapter 3 in the context of the additive factors method. However, it could be that the type or amount of visual processing that deals with written words is not the same as for non-linguistic vision. The fact that the visual information presented in the baseline task (viewing a cross, +) was simpler than in the experimental task makes this a real possibility. However, a more basic problem is common to all functional imaging

KEY TERM

Pure insertion (also pure deletion)
The assumption that adding a different component to a task does not change the operation of other components.

experiments that employ this methodology. The addition of an extra component in the task has the potential to change the operation of other components in the task. That is, **interactions** are possible that make the imaging data, at best, ambiguous. The next sections consider other types of design that allow one to eliminate or even directly study these interactions.

KEY TERM

Interactions
The effect of one variable upon another.

The choice of baseline is crucial in imaging experiments and can have substantial impacts on the data obtained. Ideally, the baseline should be as similar to the experimental task as possible. For example, to find brain regions involved with producing spoken words, Petersen et al. (1988) compared reading aloud with viewing of written words. This is likely to involve several stages of processing. It will involve retrieving the word from the brain's store of vocabulary (the mental lexicon), preparing and executing a motor command (to speak) and also listening to what was said. The pattern of activity observed is therefore ambiguous with regards to linking a precise cognitive function with brain structure. Another baseline that could be used is to get the participant to articulate generic verbal responses, such as saying the word "yes" whenever a word comes up (Price et al., 1996a). This would enable one to study the lexical retrieval component while factoring out the articulation and auditory feedback components.

In summary, functional imaging requires comparisons to be made between different conditions because the brain is always physiologically active. Regions of "activity" can only be meaningfully interpreted relative to a baseline, and the selection of an appropriate baseline requires a good cognitive theory of the elements that comprise the task. The simplest way of achieving this is the method of cognitive subtraction that compares activity in an experimental task with activity in a closely matched baseline task. However, the main problem with cognitive subtraction is that it assumes that a cognitive component can be added on to a task without changing the other components in the task (the problem of pure insertion). Adding a new component to a task may interact with existing components, and this interaction may show up as a region of activity. Other types of experimental design that reduce this particular problem have been developed and are discussed in the next section.

Cognitive conjunctions and factorial designs

The method of cognitive conjunction requires that one is able to identify a set of tasks that have a particular component in common. One can then look for regions of activation that are shared across several different subtractions rather than relying on a single subtraction. A baseline task (or tasks) is still required, but the problem of interactions can be reduced. This is because the interaction terms will be different for each pair of subtractions.

Let's consider one concrete example from the literature: why can't we tickle ourselves? Tactile sensations applied to the skin

are rated as less ticklish if produced by oneself relative to if they are elicited by another person. The key to explaining this lies in the fact that it is possible to predict the sensory consequences of our own actions. The motor commands that we generate specify where and when the touch will occur and the manner of the touch (e.g., a rough or gentle tickle). This information can then be used to predict what the action will feel like. Thus a representation of the motor command (a so-called **efference copy**) is sent to the relevant sensory area, touch in this example, so that the perceptual system knows what to expect. This may help the brain to prioritize incoming sensory information toward the most relevant stimuli in the environment. Being touched by someone or something else is arguably more important to the organism in terms of detecting potential threats than being touched by oneself.

KEY TERM

Efference copy
A motor signal used to predict sensory consequences of an action.

To investigate this, Blakemore et al. (1998) set up a factorial design with two factors. The first factor was whether a tactile stimulus was felt; the second factor was whether the participants moved their arm. The experiment involved moving a felt rod that tickled the palm. The rod could be moved either by the experimenter or the participant. It could either make contact with the palm or miss it altogether. In total, this produced four experimental conditions, which have been labeled A to D in Figure 4.11.

Before going on to consider the neural basis of the less tickly sensation associated with tickling one's self in condition

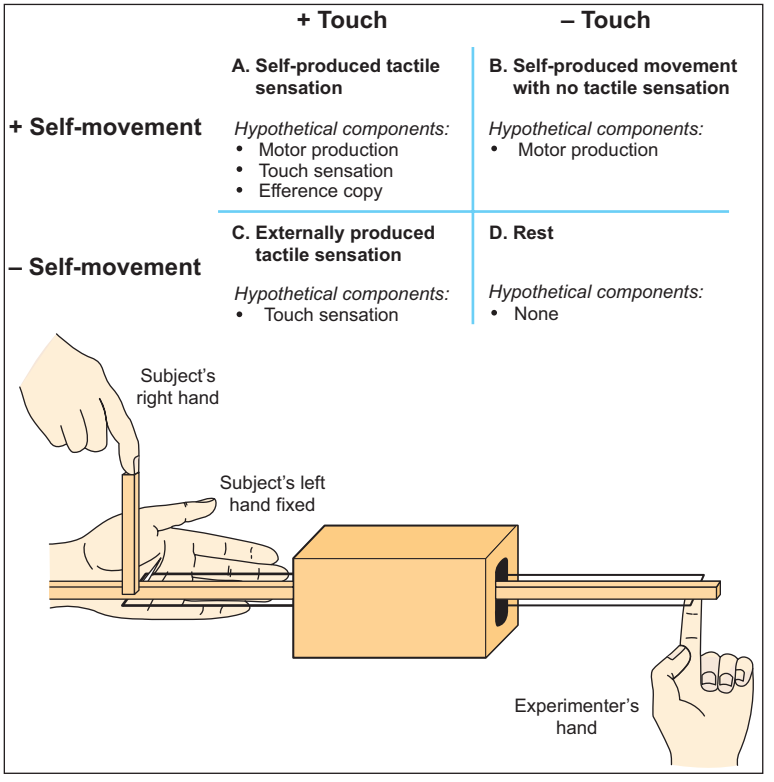

FIGURE 4.11: Why can't we tickle ourselves? Self-produced touches (condition A) are less tickly because we can predict their sensory consequences using an "efference copy" of the motor command. Bottom diagram adapted from Blakemore et al. (1998).

A (hypothetically due to an efference copy), one can perform two cognitive conjunctions to identify regions involved in motor production and the tactile sensation per se. Consider the two pairs of subtractions, A − B and C − D. If one asks the question, "What regions do these subtractions have in common [i.e., (A − B) and (C − D)]?", then this can isolate regions involved in tactile sensation. The experiment found activity in the primary and secondary somatosensory cortex in the hemisphere opposite the hand that was stimulated. Consider the two pairs of subtractions, A − C and B − D. If one asks the question, "What regions do these subtractions have in common [i.e., (A − C) and (B − D)]?", then this can isolate regions involved in motor production. In this analysis, the experiment found several active regions, including primary motor, premotor, and prefrontal regions. In terms of methodology, the key point to note is that both of these results are based on conjunctions between two different tasks and baselines, and this is sufficient to minimize the problem of pure insertion faced by using a single subtraction alone.

However, these conjunction analyses do not enable one to analyze the neural basis of the efference copy or the reduced ticklishness when self-produced. To find this out, one can examine the interaction directly by performing the following analysis: (A − B) − (C − D). This effectively asks the question: is the difference between A and B more (or less) than the difference between C and D (an interaction is simply a difference of differences)? In the present example, it would ask whether the effect of touch is greater in the presence of self-movement than in the presence of other-movement. Blakemore et al. (1998) report that there was decreased activity in the somatosensory cortex. This is likely to be the neural correlate of reduced ticklishness. There were also changes in cerebellum activity that were not found in any other condition and were interpreted as the neural correlate of the efference copy that links self-movement with touch.

Parametric designs

The main difference between a parametric design and a categorical design is that, in a parametric design, the variable of interest is treated as a continuous dimension rather than a categorical distinction (Friston, 1997). In intuitive terms, one is measuring *associations* between brain activity and changes in the variable of interest, rather than measuring *differences* in brain activity between two or more conditions. Thus, one is ultimately likely to use correlations (or similar) to analyze data collected using a parametric design.

Price et al. (1992) conducted an imaging study in which participants listened passively to lists of spoken words spoken at six different rates between 0 words per minute (i.e., silence or rest) and 90 words per minute. The change in activity in various regions could then be correlated with the rate of speech. Note that in a

parametric design such as this, a separate baseline condition is not necessary (the effects are evaluated globally across all levels of the factor). In terms of the results, a number of interesting findings were observed. In areas involved in auditory *perception* (e.g., the primary auditory cortex), the faster the speech rate, the greater the activity. However, in regions involved in non-acoustic processing of *language* (e.g., Wernicke's area), the activity was related to the presence of words irrespective of speech rate. In a region often associated with verbal *working memory* (the left dorsolateral prefrontal cortex), a more complex picture was found (Friston, 1997). Activity increased with speech rate but then decreased as the speech rate got faster (an inverted-U function). It suggests that the region has an optimal level at which it functions, beyond which it fails to keep up. This is consistent with the notion of working memory having a limited capacity. One interesting point to note is that, if the experimenters had compared 20 words per minute with 50 words per minute in a cognitive subtraction or a factorial design, this region would not have appeared to be implicated in the task (Figure 4.12).

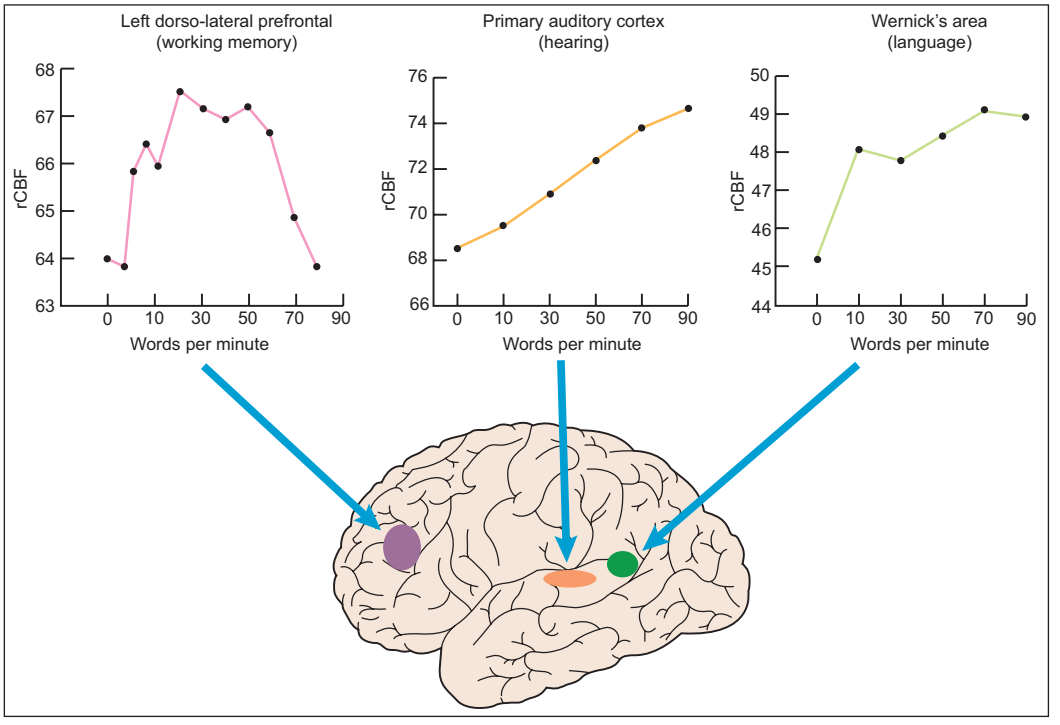

FIGURE 4.12: Different regions of the brain respond to changes in speech rate (words per minute, wpm) in different ways. Note that 0 wpm is equivalent to rest. rCBF = regional cerebral blood flow (from PET). Adapted from Price et al. (1992), and Friston (1997).

Functional integration: measuring networks in the brain

Most of the functional imaging studies described in this book could be labeled as studies of *functional specialization*. Functional specialization implies that a region responds to a limited range of stimuli/conditions and that this distinguishes it from the responsiveness of other neighboring regions. It is not strictly the same as *localization*, in that it is not necessary to assume that the region is solely responsible for performance on a given task or to assume that other regions may not also respond to the same stimuli/conditions (Phillips et al., 1984). **Functional integration**, on the other hand, refers to the way in which different regions communicate with each other. This is likely to be essential for a full understanding of how cognition is linked to the brain, and also for dismissing claims that functional imaging is a new phrenology (Friston, 2002; Horwitz et al., 1999).

The basic approach of functional integration is to model how activity in different regions is interdependent. This is used to infer the *effective connectivity* or *functional connectivity* between regions when performing a task (these methods use techniques such as structural equation modeling and principal components analysis, which are beyond the scope of the present discussion). If parametric designs correlate brain activity with some cognitive/behavioral measure, then designs employing functional integration correlate different regions of brain activity with each other. To give a concrete example, Friston and Frith (1995) conducted an imaging study with a 2 × 2 factorial design with task instruction as one factor (generate words beginning with "A" versus repeating letters) and subject group as the other factor (participants either had or had not been diagnosed as schizophrenic). Although both groups showed a number of similar frontal and temporal lobe activities, there was a strong correlation between activity in these regions in controls and a striking absence of correlation in the schizophrenics. Friston and Frith (1995) argued that schizophrenia is best characterized in terms of a failure of communication between distant brain regions (i.e., a functional disconnection).

One commonly used procedure for measuring functional integration does not use any task at all. These are known as **resting state paradigms**. Participants are merely asked to lie back and rest. In the absence of a task, the fluctuations in brain activity are little more than noise. However, in brain regions that are functionally connected, the noise levels tend to correlate together. This has enabled researchers to identify sets of networks in the brain, consisting of spatially separated regions, for which fluctuations in activity tend to be shared (Damoiseaux et al., 2006). For instance, one commonly studied network is called the **default mode network** of the brain and is implicated in internalized thoughts: it tends to be more active when *not*

KEY TERMS

Functional integration
The way in which different regions communicate with each other.

Resting state paradigm
A technique for measuring functional connectivity in which correlations between several regions (networks) are assessed while the participant is not performing any tasks.

Default mode network
A set of brain regions that is more hemodynamically active during rest than during tasks.

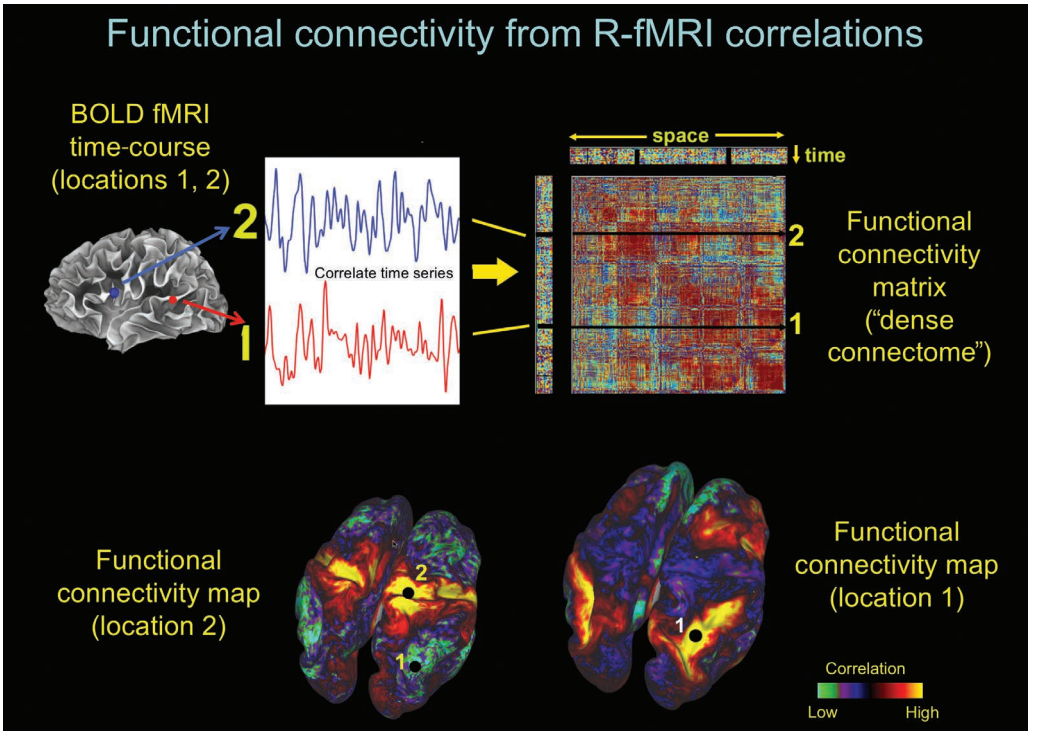

FIGURE 4.13: Every region of the brain shows fluctuations in the BOLD response over time (shown here in detail for two regions, 1 and 2). If different regions show a very similar profile of fluctuations, then this is likely to reflect the fact that they are communicating. In resting state paradigms, fluctuations in the BOLD response from all brain regions are entered into a correlation matrix and, from the pattern of correlations, sets of regions that habitually correlate together (i.e., networks) are identified.

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Check out the Cognitive Neuroscience Bitesize, by Jamie Ward, on Networks in the Brain.

To watch a TEDx talk by Professor David van Essen, visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience).

engaged in an experimental task (Raichle et al., 2001). Differences in the way that these networks operate and are constructed are found in various conditions such as schizophrenia and autism (Buckner et al., 2008).

The basic principles behind resting state approaches are illustrated in Figure 4.13. Each region of the brain shows spontaneous fluctuations in the BOLD response over time. In the figure, this is shown for two brain regions (1 and 2). The time-varying activity in each brain region is then correlated with every other brain region, producing a very large correlation matrix (as shown on the right-hand side, with different colors representing different magnitudes of correlation). Through a statistical analysis of the pattern of correlations, it is then possible to identify sets of regions that show a similar profile of correlations to each other, presumably because they are communicating. These sets of regions are inferred to constitute a network.

SAFETY AND ETHICAL ISSUES IN FUNCTIONAL IMAGING RESEARCH

It is essential to be aware of the local regulations that apply in your own institution but the following points generally apply:

What are the risks of taking part in functional imaging experiments?
fMRI does not use radiation and the same participants can take part in multiple experiments without any harm. Participants wear ear protectors, given that the scanner noise is very loud. Larger magnets (> 3 T) can be associated with dizziness and nausea (caused by stimulating the balance organs rather than the brain), and participants need to enter the field gradually to prevent this.

Are some people excluded from taking part in functional imaging experiments?
Before entering the scanner, all participants should be given a checklist that asks them about their current and past health. People with metal body parts, cochlear implants, embedded shrapnel or pacemakers will not be allowed to take part in fMRI experiments. In larger magnets, eye makeup should not be worn (it can heat up, causing symptoms similar to sunburn), and women wearing some types of contraceptive coil should not be tested. Before going into the scanner, both the researcher and participant should put to one side all metal objects such as keys, jewelry, and coins, as well as credit cards, which would be wiped by the magnet. Zips and metal buttons are generally okay, but metal spectacle frames should be avoided. It is important to check that participants do not suffer from claustrophobia as they will be in a confined space for some time. Participants have a rubber ball that can be squeezed to signal an alarm to the experimenter, who can terminate the experiment if necessary.

What happens if a brain abnormality is detected during scanning?
There is always a very small possibility that a brain tumor or some other unsuspected abnormality could be detected during the course of the study. In such instances, the researcher has a duty to double-check this by inviting the participant back for a subsequent scan. Potential abnormalities are followed up by a neurologist (or a clinically qualified member of staff), who would inform the participant and their doctor, if need be. Wolf et al. (2008) provide a set of ethics concerning the incidental discovery of abnormalities during nonclinical scanning.

How can I find up-to-date details about safety in fMRI experiments?
The standard safety reference is by Shellock (2020), and updates can be found at: www.MRIsafety.com.

ANALYZING DATA FROM FUNCTIONAL IMAGING

The images of brains with superimposed colored blobs are the outcome of several stages of data processing and statistical analysis. In fact, these images are not literal pictures of the workings of the brain at all. What these images depict are the regions of the brain that are computed to be statistically significant given the type of design used. Functional imaging is a statistical science and, as such, is susceptible to error. Although

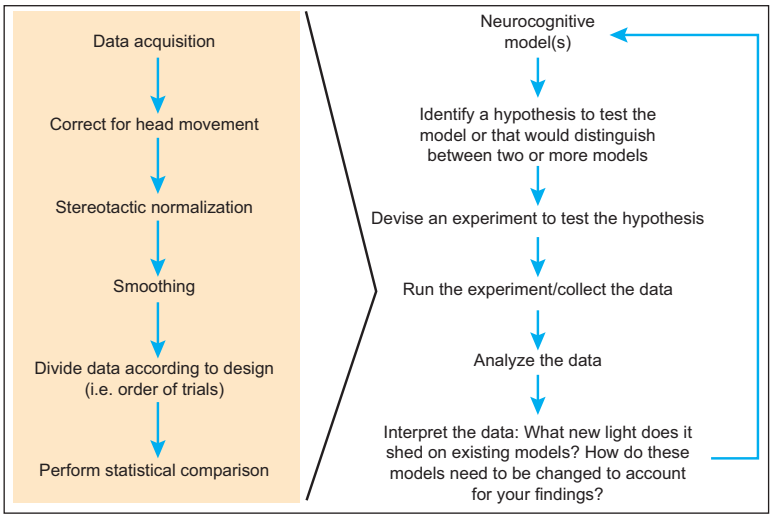

FIGURE 4.14: The main stages of analyzing data in a functional imaging experiment.

different laboratories use different packages to analyze their data, the challenges faced in analyzing and interpreting functional imaging data are common to them all (for a detailed discussion, see Petersson et al., 1999a, 1999b).

A central problem faced in the analysis of functional imaging data is how to deal with individual differences. Although the gross brain structure does not differ considerably from one person to the next, there are nevertheless significant individual differences in the size of gyri and the location of folds in the brain. For example, the location of sulci can vary between people by a centimeter or more (Thompson et al., 1996).

The most common way of dealing with individual differences is effectively to assume that they do not exist. Or more properly put, individual differences needn't get in the way of making claims about general brain function. Individual differences are minimized by averaging data over many participants, and one is left with regions of activity that are common to most of us. Before this averaging process can occur, the data from each individual need to be modified in a number of ways. First, each brain is mapped onto a standard reference brain (called **stereotactic normalization**). This is followed by a process called **smoothing**, which can enhance the signal-to-noise ratio and facilitates detection of common regions of activity across individuals. Figure 4.14 summarizes the sequence from initial hypothesis to data interpretation that typically occurs in a functional imaging experiment. These main stages will be considered in turn.

KEY TERMS

Stereotactic normalization
The mapping of individual differences in brain anatomy onto a standard template.

Smoothing
Redistributing brain activity from neighboring voxels to enhance the signal-to-noise ratio.

Correction for head movement

Perhaps the biggest advantage of the fMRI technique over others is its good spatial resolution. It is able to identify differences in activity over millimeter distances (although this resolution still entails

millions of neurons). However, there is a downside to this; namely, that small spatial differences can produce spurious results. One key problem that has already been noted is that every brain differs spatially in terms of size and shape. The process of stereotactic normalization attempts to correct for this. A different problem is that each person's head might be aligned slightly differently in the scanner over time. If a person wriggles or moves their head in the scanner, then the position of any active region will also move around. This could either result in the region being harder to detect (because the activity is being spread around) or a false-positive result could be obtained (if a particular head movement is correlated with experimental conditions). It is for this reason that the collected data are corrected for head movement (Brammer, 2001), which is minimized in the first place by physically restraining the head in position and instructing participants to keep as still as possible.

Stereotactic normalization

The process of stereotactic normalization involves mapping regions of each individual brain onto a standard brain. Each brain is divided up into thousands of small volumes, called voxels (volume elements). Each voxel can be given three-dimensional spatial coordinates (x = left/right, y = front/back, z = top/bottom). This enables every x, y, z coordinate on a brain to be mapped onto the corresponding x, y, z coordinate on any other brain. Basically, the template of each brain is squashed or stretched (by applying mathematical transformations that entail an optimal solution) to fit into the standard 3D space. Many contemporary studies use a standard based on an average of 305 brains provided by the Montreal Neurological Institute (Collins et al., 1994), termed MNI template, which was a significant advancement over the older atlas of Talairach and Tournoux (1988) that was based on anatomical data from a single post-mortem brain.

When it comes to a standard anatomical model of the cortex, one common approach is to treat this as a 2D surface rather than a 3D volume. This has the advantage of taking into account the wrinkled nature of the brain's surface. For example, imagine that the cortex folds itself into something resembling the letter U (as it often does). The two endpoints would be considered as next to each other in 3D space but would be represented as further apart in 2D surface space. The latter being more anatomically accurate. A commonly used 2D surface space is fsaverage, where fs refers to the FreeSurfer analysis package (Fischl, 2012). Points on the surface are referred to as vertices rather than voxels.

Smoothing

After each brain has been transformed into this standard space, further stages of preprocessing *may* take place before a statistical

analysis. The process of "smoothing" sounds like it could waste important information, but it is an important part of data manipulation. Smoothing spreads some of the raw activation level of a given voxel to neighboring voxels. The closer the neighbor is, the more activation it gets (the mathematically minded might be interested to know that the function used is a Gaussian or normal distribution centered on each voxel). In Figure 4.15, the darker the square, the more active it is. Consider voxel D4. Prior to smoothing, this voxel is inactive, but because it has many active neighbors the voxel gets "switched on" by the smoothing process. In contrast, consider voxel L8. This voxel is initially active but, because it has inactive neighbors, it gets "switched off" by the smoothing process. Smoothing thus enhances the signal-to-noise ratio. In this instance, one assumes that the signal (i.e., the thing of interest) corresponds to the larger cluster of activity, and the noise is the isolated voxel. Neighboring voxels that are active mutually reinforce each other, and the spatial extent (i.e., size) of the active region is increased. If the brain happened to implement cognition using a mosaic of non-adjacent voxels, then smoothing would work against detecting such a system. Indeed, there are some statistical techniques (such as multi-voxel pattern analysis, MVPA) that can be used to analyze this kind of mosaic-like neural representation that do not require smoothing (Norman et al., 2006). This is considered later.

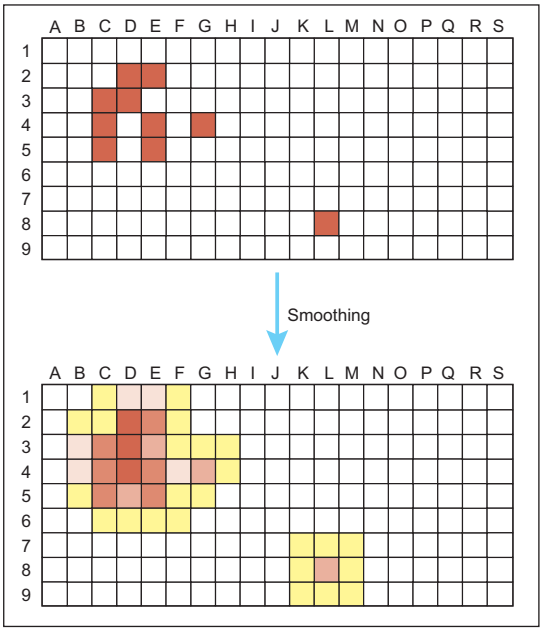

FIGURE 4.15: Smoothing spreads the activity across voxels – some voxels (e.g., D4) may be enhanced whereas others (e.g., L8) may be reduced.

As well as enhancing the signal-to-noise ratio, smoothing offers an additional advantage for analyzing groups of participants. Smoothing increases the spatial extent of active regions. As such, when averaging the activity across individuals, there is a greater chance of finding common regions of activity.

Statistical comparison

After the data have been stereotactically normalized, smoothed, and corrected for head movement, it is possible to perform a statistical analysis. The standard way to do this is to ask the question: "Is the mean activity at a particular voxel in the experimental condition greater than in the baseline condition?" The same types of statistical test as would be employed in any psychology experiment can be used in functional imaging (e.g., a *t*-test to compare means). But there are complications. In most psychology experiments one would typically have, at most, only a handful of means to compare. In functional imaging, each brain slice is divided up into tens of thousands of voxels and each one needs to be considered.

If one uses the standard psychology significance level of $P < 0.05$, then there would be thousands of brain voxels active just by chance. (Recall that the significance level represents the probability, P, at which one is willing to say that a result is more than just a chance occurrence. The value of 0.05 represents a 1 in 20 chance level.) How could one minimize the influence of lots of brain regions being active by chance? One could have a more conservative criteria (i.e., a lower significance level), but the danger is that this will not detect regions that are important (this is termed a type II error). For instance, in a Bonferroni correction one would divide the nominal P value (0.05) by the number of tests (i.e., voxels). A difficulty with this approach is that the activity at each voxel is not independent: neighboring voxels tend to have similar activity, particularly if smoothed. This has led to the development of sophisticated mathematical models of choosing a statistical threshold, based on spatial smoothness (so-called *random field theory*). This general method of correction is termed **Family Wise Error (FWE)**. Another common approach is to generate thousands of random brain images (e.g., by permuting the data) and select a threshold (e.g., $P < 0.05$) based on random datasets. This method of correction is termed the **False Discovery Rate (FDR)**. In this method a more conservative statistical threshold would be used for datasets in which lots of voxels are active than in a dataset in which only few voxels are active.

When reading papers that have used functional imaging methods, one sometimes observes that they report different significance levels that are "corrected" or "uncorrected." Why is this done and is it acceptable? A corrected level implies that a more conservative criterion has been used to prevent detecting lots of regions just by chance. However, if the interest is in *one* particular voxel, then it is possible to use an uncorrected significance level (e.g., the standard $P < 0.05$) because in this instance there are not multiple comparisons over lots of brain regions. Other procedures are used when investigating effects in a predetermined region covering several voxels (a so-called *small volume correction*).

KEY TERMS

Family Wise Error (FWE)
An approach for correcting for many statistical comparisons based on the number of tests being conducted.

False Discovery Rate (FDR)
An approach for correcting for many statistical comparisons based on the number of positive results obtained.

INTERPRETING DATA FROM FUNCTIONAL IMAGING

What does it mean to say that a brain region is active in a functional imaging experiment? Literally speaking, what this means is that the signal from that region (the BOLD signal in fMRI) is greater in one condition than in other conditions that are being compared (whether in a categorical design, parametric design, or whatever). There are several reasons why a region may be active, and not all of them are theoretically interesting. Importantly, it need not imply that the particular region is essential for the task. Alternative accounts include an increase in signal could reflect the strategy that the participants happen to adopt, it could reflect use of some general mechanism (e.g., increased attention) that is not specific to the task,

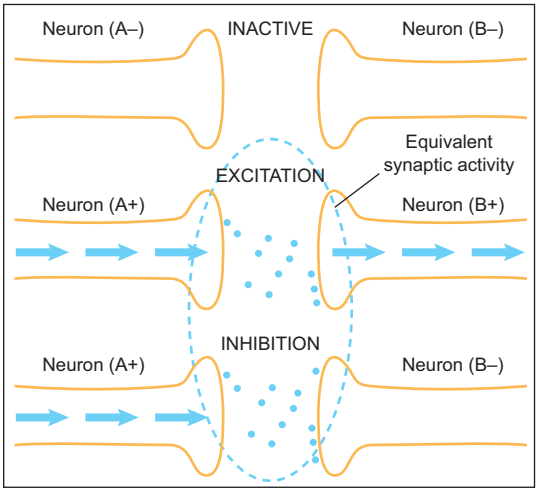

FIGURE 4.16: Excitatory and inhibitory synaptic connections both involve metabolic activity and thus an inhibited region could be mistakenly interpreted as a region of activity.

KEY TERMS

Inhibition
A reduction/suppression of the activity of a brain region (or a cognitive process), triggered by activity in another region/process.

Excitation
An increase of the activity of a brain region (or a cognitive process), triggered by activity in another region/process.

Activation
An increase in physiological processing in one condition relative to some other condition(s).

Deactivation
A decrease in physiological processing in one condition relative to some other condition(s).

or it could reflect the fact that a region is receiving input but is not responding to the input (i.e., **inhibition**). These competing scenarios can only be ruled out with more rigorous experimentation. Chance occurrences can be ruled out by replicating the results and the necessity of a region for a task can be determined using lesion methods. This is discussed in more detail in the next section.

Inhibition versus excitation

Functional imaging signals are assumed to be correlated with the metabolic activity of neurons, and synapses in particular (see Jueptner & Weiller, 1995). However, neurons can be metabolically active by virtue of both inhibitory interactions (when the presynaptic neurons are active, the postsynaptic neuron is switched off) and **excitations** (when the presynaptic neurons are active, the postsynaptic neuron is switched on) – see Figure 4.16. Most connections are excitatory in nature. Logothetis et al. (2001) demonstrated that the BOLD signal used in fMRI is more sensitive to the neuronal input into a region rather than the output from the region. Thus, regions that "listen" to other active regions but do not themselves respond to it could appear as areas of activation.

It is unclear whether functional imaging can distinguish between these two types of neural function since both are assumed to be associated with similar physiological changes.

Activation versus deactivation

Activation and deactivation simply refer to the sign (positive or negative) of the difference in signal between two conditions. This is not to be confused with excitation/inhibition which refers to the nature of the mechanism by which neurons communicate. If the subtraction (Task A) − (Task B) is performed, there could be a set of regions that show a significant positive effect (i.e., **activation**) because they are used more in Task A than in Task B, and there could also be a set of regions that show a significant negative effect (i.e., **deactivation**) because they are more active in Task B than in Task A. Of course, if one had done the subtraction (Task B) − (Task A), then the same regions would be identified, but the positive and negative signs would merely swap. Thus, the terms activation and deactivation merely refer to whether there is a difference in signal between conditions and the direction of that difference. The question of *why* there is a difference is open to theoretical interpretation. If the baseline task is very different from the

experimental conditions, the activations and deactivations may be very hard to interpret.

Necessity versus sufficiency

In an intriguingly titled paper, "If neuroimaging is the answer, what is the question?", Kosslyn (1999) sets out some of the reasons why functional imaging has its limitations. One particular point that will be picked up on here is the notion that some of the regions that appear active may indeed be used during performance of the task but might not be critical to the task. For example, a region may appear to be active because of a particular strategy that the participants adopted, even though other strategies might be available. It could also be the case that the tasks being compared differ in some other, more general, way. For example, if one task is harder than the other, it could demand more attention, and this demanding of attention would have its own neural correlate. Although paying more attention could certainly help with the performing of the task, it may not in and of itself be crucial for performing the task. As such, it has been claimed that functional imaging gives us a better idea of which regions may be sufficient for performing a particular task but not always which regions are crucial and necessary for performing a task.

The value of functional imaging data is likely to be enhanced when it is used in conjunction with other methods. One early benefit of functional imaging was mooted to be that it could replace lesion-based neuropsychology. However, this is unlikely to happen because the logic of inference is different in these two methods, as illustrated in Figure 4.17. In lesion-based neuropsychology, the location of the lesion is manipulated (or selected for in a patient sample), and the resulting behavior is observed. In doing this, a causal connection is assumed between the lesion and the ensuing behavior. In functional imaging the reverse is true. In this instance, the task given to participants in the scanner is manipulated, and changes in brain regions are observed. Although some of these changes are likely to be critically related to the performance of the task, other changes may be incidental to it. It is for this reason that functional imaging is unlikely to supplant the traditional lesion-based approach. The next section discusses in more detail how divergent results between imaging and neuropsychology could be reconciled.

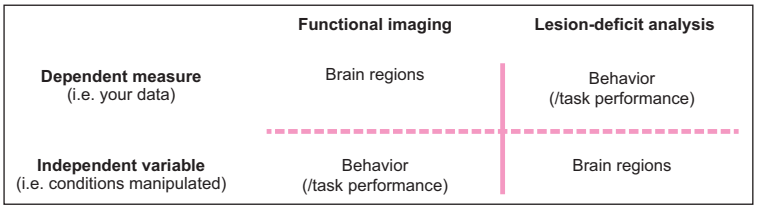

FIGURE 4.17: Functional brain imaging and lesion-deficit analysis of patients (or TMS, see Chapter 5) are logically different types of methodology. It is unlikely that one will supplant the other.

WHY DO FUNCTIONAL IMAGING DATA SOMETIMES DISAGREE WITH LESION DATA?

There are two broad scenarios in which functional imaging data and lesion-deficit data can disagree. These are listed next, together with possible ways of resolving the disagreement, as described in the following box.

Disagreement 1: Imaging data imply that a brain region is used in a given task, but lesion data suggest that this region is not essential to the task (imaging +, lesion –)
Possible reasons for disagreement:

- The activated region reflects a particular strategy adopted by the participants that is not essential to performing the task.
- The activated region reflects the recruitment of some general cognitive resource (e.g., due to increased task difficulty, attention or arousal) that is not specific to the task.
- The activated region is being inhibited (i.e., switched off) rather than excited (i.e., switched on).
- The lesion studies have not been powerful enough to detect the importance of the region (e.g., too few patients, lesion not in the correct location, tasks used with patients not the same as those used in imaging).

Disagreement 2: Imaging data imply that a brain region is not used in a given task, but lesion data suggest that this region is critical to the task (imaging –, lesion +)
Possible reasons for disagreement:

- If the experimental task and baseline task both depend critically on this region, then a comparison between them might produce an artifactual null result.
- It might be intrinsically hard to detect activity in this region of the brain (e.g., it is a very small region, it is in different places in different individuals or genuine activity produces a small signal change).
- The impaired performance after lesion reflects damage to tracts passing through the region rather than the synaptic activity in the gray matter of the region itself.

This box highlights the fact that disagreements between results from functional imaging and results from lesion data could lie with imaging results, with the lesion results, or with both. There is no magic solution for resolving the disagreements except through more rigorous experimentation. Each method has some relative merit. As such, disagreements should be viewed as something that is potentially of theoretical interest rather than dismissed as a failure of one or other method (Henson, 2005). To provide a feel for how this might be achieved, the next section considers a concrete example from the literature.

Having your cake and eating it

A small proportion of unfortunate people in later life start to lose the meanings of words and objects that they previously understood. This

deterioration can spare, at least in the early stages, memory for events, calculation abilities and syntax, among other things (e.g., Hodges et al., 1992). These patients would probably be given a diagnosis of **semantic dementia**, because their functional lesion is primarily in the **semantic memory** system that stores the meaning of words and objects. This has been reported for the *Die Hard* actor Bruce Willis. Where are the anatomical lesions in these patients? Lesion studies based on voxel-based morphometry (VBM) have shown that the degree of semantic memory impairment is correlated with the amount of atrophy in the left anterior temporal lobe (Mummery et al., 2000), as shown in Figure 4.18. (Semantic dementia is itself a form of frontotemporal dementia but where patients vary in where the atrophy lies and, hence, in the accompanying cognitive symptoms). Given this finding, it would be encouraging if functional imaging studies also activated this particular region when healthy (non-brain-damaged) people are given semantic memory tasks. However, this has not always been the case, and a number of studies have reliably shown activation in a different region – the left inferior frontal gyrus (also referred to as the ventrolateral prefrontal cortex). How can these divergent results be explained? It will be argued that a more careful comparison of the tasks used can account for this divergence and reveals, in turn, more about how the brain supports semantic memory.

KEY TERMS

Semantic dementia
A progressive loss of information from semantic memory, linked to frontotemporal dementia.

Semantic memory
Conceptually based knowledge about the world, including knowledge of people, places, the meaning of objects and words.

One of the first ever functional imaging studies of cognition tried to address the question of where semantic memories are stored. As already discussed, Petersen et al. (1988) compared brain activation in two tasks: verb generation (e.g., the participant sees CAKE and says "eat") and reading aloud (e.g., the participant sees CAKE and says "cake"). The verb-generation task is assumed to tap semantic memory more than the reading task. However, a comparison of the two tasks shows activity in regions of the left inferior frontal gyrus but not in the same regions that are associated with semantic memory loss. Is the imaging data or the lesion data to be believed?

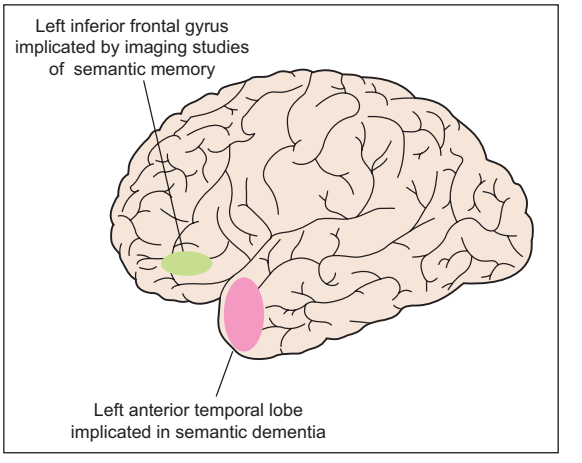

FIGURE 4.18: Studies of brain-damaged patients with semantic memory and imaging studies of semantic memory have not always highlighted the importance of the same regions.

Could it be the case that the left inferior frontal gyrus is really involved in semantic memory? To test this hypothesis, instead of taking a group of patients with semantic memory difficulties and asking where the lesion is, one would need to take a group of patients with selective lesions to the left inferior frontal gyrus and give them the same verb-generation task that the healthy people were given when they were scanned. As it turns out, such patients do have subtle but real difficulties with these tasks. Thompson-Schill et al. (1998) asked these patients to generate verbs that had either a low selection demand (e.g., scissors), in which most people agree upon a verb (i.e., cut), and words with a

high selection demand (e.g., cat), which do not suggest an obvious single answer. The patients are impaired on the latter but not the former. More extensive imaging data on controls show that the region is responsive to the difficulty of semantic memory retrieval (Thompson-Schill et al., 1997, 1999). Thus, this disagreement is perhaps more apparent than real. The reason why patients with damage to the left inferior frontal gyrus do not show clinical symptoms of semantic memory impairment is because the region is involved in strategic retrieval operations from semantic memory when no obvious answer comes to mind. By contrast, the temporal regions may be the *store* of semantic information, and lesions here can produce more devastating impairments of semantic knowledge. So why didn't these particular imaging studies activate regions that are putatively the store of semantic knowledge? One possibility could be the baseline that was used. Petersen et al. (1988) compared verb generation (their semantic task) with reading (their putatively non-semantic task). However, if word reading does depend on the semantic store, and there is, in fact, good evidence that it might (Woollams et al., 2007), then the two conditions would cancel each other out when subtracted away.

In this instance, an initial discrepancy between functional imaging and lesion data has resulted in a more complete understanding of how semantic memory is both stored and retrieved. This is a nice example of how the strengths of different methodologies can be combined in cognitive neuroscience.

BRAIN-READING: IS "BIG BROTHER" ROUND THE CORNER?

This chapter started with the specter of functional imaging being used to reveal one's innermost thoughts to the outside world. It therefore seems appropriate to return to this interesting theme in light of the various points raised so far. It should by now be clear that the process of analyzing and interpreting data produced by functional imaging is not straightforward. It entails a number of stages, each with its own assumptions, rather than a literal reading of the MR signal. Nonetheless, the technology is still relatively new, and the amount of progress that has already been made is substantial. Even at this early stage, there are serious studies exploring how functional imaging could be used as a lie detector and studies that try to predict the content of another person's thoughts at some basic level (for a review, see Haynes & Rees, 2006).

It is generally believed that different classes of objects (e.g., faces, places, words, tools) activate somewhat different regions of the brain. So is it possible to infer what someone is looking at from brain activity alone? A number of studies have attempted to guess, in a third-person way, what a person is observing (Haxby et al., 2001) or imagining (O'Craven & Kanwisher, 2000) on a particular trial using only the concomitant neural activity (see Figure 4.20).

To achieve this, each person requires pretesting on a whole range of objects to determine the average response to that class of objects relative to some baseline (e.g., all the other objects). Rather than locating the peak area of activity (as in regular fMRI analysis), one can examine the *pattern* of activation over a distributed set of voxels to enable a more fine-grained approach. This method is called MVPA or **multi-voxel pattern analysis** (for a review see Tong & Pratte, 2012). For example, Haxby et al. (2001) gave participants pictures from eight different types of category, including cats, houses, faces, and shoes. The neural activity from an individual trial was then compared to the previous known patterns of activity to determine the most probable category that was being viewed. This procedure could predict, given pairwise comparisons, what the person was seeing with 96 percent accuracy. The same regions of the brain are used, to some extent, when thinking about objects even when they are not physically seen. O'Craven and Kanwisher (2000) obtained comparable results on individual imagery trials. Other research has shown that activity in these regions can be used to accurately predict semantic categories when reading words (Mitchell et al., 2008) or when recalling previously seen images from memory (Polyn et al., 2005). Decoding the visual content of dreams involves essentially the same method as these studies (Horikawa et al., 2013). Participants were awoken during sleep and asked to report, in words, the content of their dreams. They were then shown sets of images, whilst awake, of the objects in their dreams (faces, places, etc.) and a machine learning algorithm (classifier) was trained to discriminate the *visual* images (as in similar previous studies). The classifier was then tested against the original dream episodes to predict the dream content at above chance levels.

KEY TERM

Multi-voxel pattern analysis (MVPA)
An fMRI analysis method in which distributed patterns of activity are linked to cognitive processes.

COULD FUNCTIONAL IMAGING BE USED AS A LIE DETECTOR?

Lying appears to be a normal component of human social interaction. It is likely to be composed of several cognitive components. For example, it requires an understanding that other people can have states of mind that are different from one's own (so-called theory of mind). Lying also requires an ability to inhibit a truthful response and generate a plausible alternative response. Given this complexity, there will probably be no single "deception module" in the brain dedicated specifically to lying (Figure 4.19). Nevertheless, there is every reason to believe that studying the brain during deception might lead to more reliable indices of lying than the traditional lie detector (or "polygraph"), given that the brain is the organ that produces the lie in the first place.

The traditional polygraph monitors a number of bodily responses, including sweating, respiration, and heart rate, which are considerably downstream from the thought process that creates the lie. As these measures are associated with increased arousal generally (e.g., anxiety), they cannot exclusively detect guilt and their usage is highly questionable. Also, if a liar does not feel guilty there may be no strong arousal response.

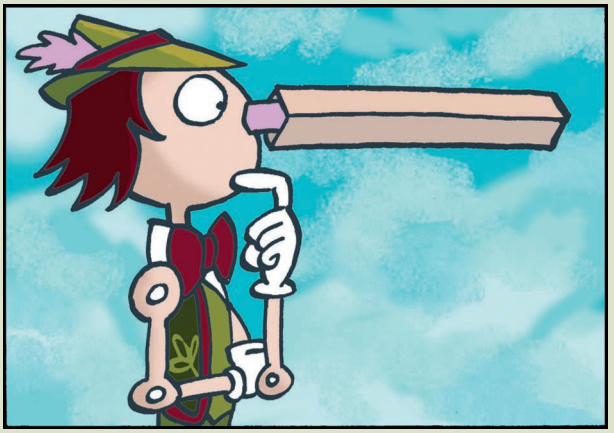

FIGURE 4.19: Not all lies are as easy to detect.

Many studies have used fMRI to measure the neural correlates of deception and, studies have reported accuracies between 69 percent and 100 percent in separating simple deceitful versus truthful responses (Farah et al., 2014). When participants are asked to generate a lie to a question (e.g., "Who did you visit during your vacation?", "Was that the card you were shown before?"), a number of regions are activated, including the anterior cingulate cortex. This region is of particular interest in this context, because it has been implicated in monitoring conflicts and errors (Carter et al., 1998) and also in generating the kinds of bodily response that form the basis of the traditional polygraph (Critchley et al., 2003). However, not all types of deception may recruit this region. Ganis et al. (2003) found that, if participants memorized a lie in advance of being interviewed in the scanner, then this region was not involved, but regions involved in memory retrieval were involved. Thus, to conclude, although fMRI might have some use in lie detection, it is unlikely to offer a simple solution to this complex and important real-world problem.

The studies described thus far are limited in that they generate answers from a closed set of options (e.g., cat compared with dog). However, other studies have used this approach to generate an open-ended set of responses. The primary visual cortex (also termed V1) has a particular functional layout such that it is a mosaic of small regions that are specialized for detecting lines of certain orientations and also for detecting light in particular locations. The grid of voxels used in fMRI may capture some of this patterning, and attempts have been made to reconstruct visual images (presented to a participant) based on the pattern of activity in this region. For instance, Miyawaki et al. (2008) used a 10 × 10 grid of pixels to train a classifier. Just as the classifier can search for voxels that "prefer" cats over dogs, one can do the same for voxels that prefer brightness in, say, the top

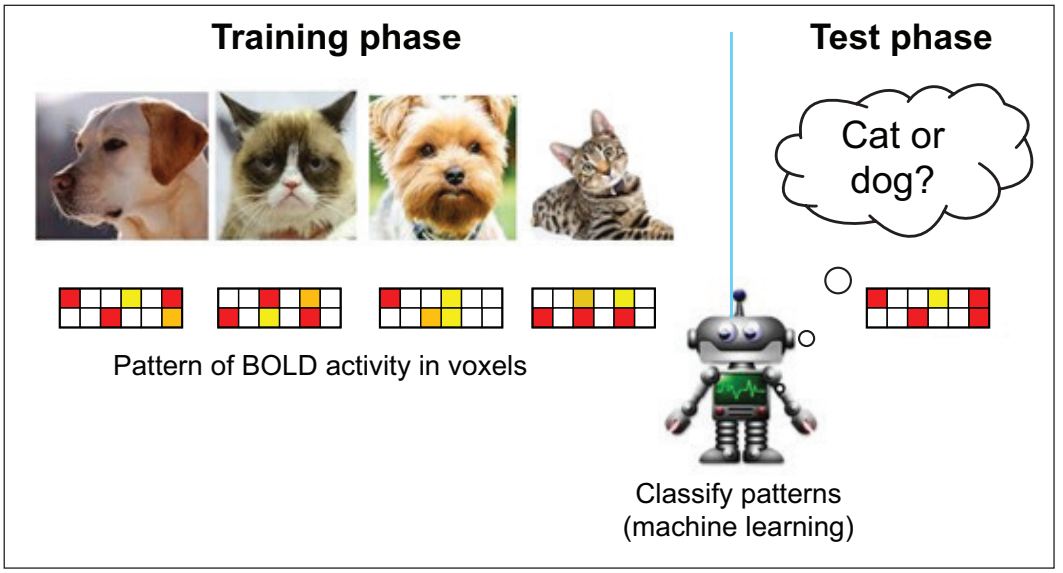

FIGURE 4.20: Multi-voxel pattern analysis (MVPA) has two main phases. In the training phase, participants are given certain tasks or stimuli – in this example seeing cats or dogs – and fMRI data are collected in the normal way. The pattern of BOLD activity across many voxels (hundreds, or thousands) is measured for each trial. A mathematical algorithm (a "classifier") is trained to optimally discriminate the categories. In the next phase (testing), the participant is then given more tasks or stimuli (e.g., *new* images of cats and dogs) and the algorithm must classify them. In this phase the participant's mind/brain is effectively being "read." In this simple example, we would predict DOG (because it's pattern of activity more closely resembles the two dog examples). Note that if we averaged activity across the voxels in this brain region, there would be little hope of being able to discriminate these categories.

left of the grid as opposed to bottom right or for voxels that prefer horizontal over vertical orientations. From this simple training, it was possible to reconstruct letters and words that were presented to the participants as shown in Figure 4.21 (top). Again, it is worth reiterating that the experimenter is not literally seeing words spelled out in a participant's brain in the scanner. Instead, a computer algorithm is taking fluctuations in brain activity and making a best guess about whether each voxel is being activated in response to a visual stimulus or not (and from that an image is reconstructed). Attempts at generating more complex images using this method have more limited success but are good at finding a close match to a novel image from within a large database, as shown in the bottom panel of Figure 4.21 (Naselaris et al., 2009).

Much of the discussion has focused on brain decoding of external inputs. What about intentions and decisions that are, by their nature, internally driven? Patterns of activity in the prefrontal cortex can be used to predict (even before the person made their response) which of two tasks will be performed – in this study the decision was whether to add or subtract digits (Haynes et al., 2007). Brain activity when shown a series of goods predicts, above chance, subsequent purchasing decisions in those same participants

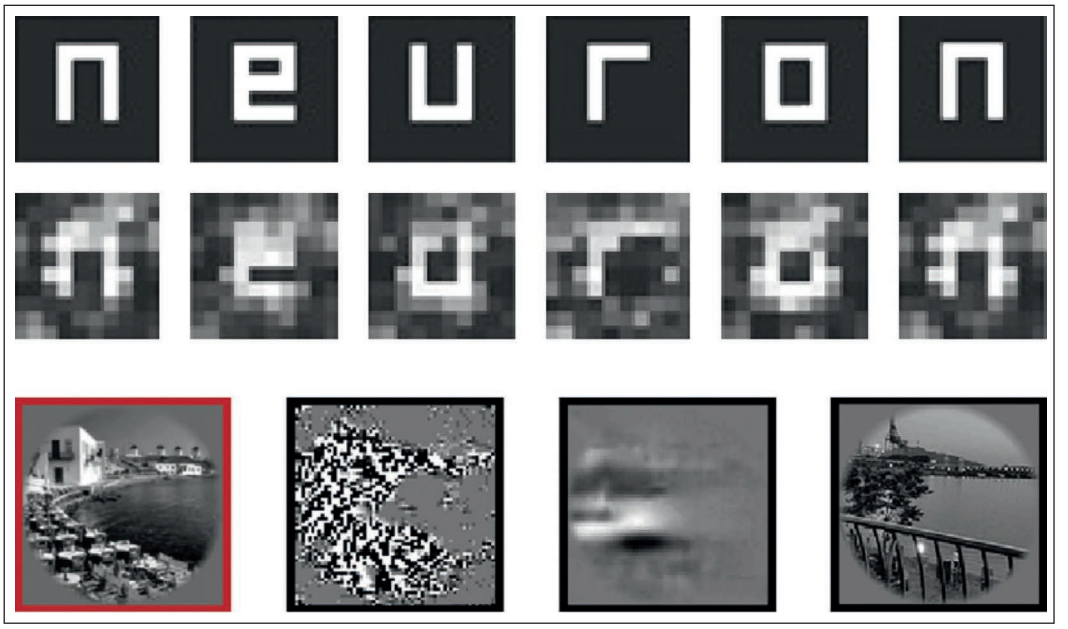

FIGURE 4.21: Can activity in the brain be used to reconstruct what image is being seen? In the top example, letters displayed in a 10 × 10 grid to the participants can clearly be read out from the pattern of brain activity. In the bottom example, the target image is shown on the left (red outline) and, to the right, are shown three attempts at image reconstruction from the pattern of activity (black outline). The first reconstruction uses an algorithm based on detecting local contrast. The second reconstruction uses the global (blurred) image characteristics. The final attempt involves finding a best match from a database of 6 million images (not including the target image). Top, from Miyawaki et al. (2008). Bottom, from Naselaris et al. (2009).

ONLINE RESOURCES

Watch a TEDx talk by Jack Gallant on brain decoding by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

(Knutson et al., 2007). These kinds of value predictions can, to some extent, also generalize to decision-making in larger real-world samples. Differences in activity in ventral striatum to unknown pop songs correlates with future commercial success of those songs over the following three years (Berns & Moore, 2012).

Brain-reading may ultimately have real clinical significance rather than being an instrument of a "Big Brother" state. For example, paralyzed patients may be able to control robot arms or vehicles by reading their brain activity in motor cortex (Bouton et al., 2016) and non-communicative patients may be able to communicate with others by having their inner speech read. Spoken language is tricky to decode with fMRI because of the rapidly changing acoustic signal and sluggish haemodynamic response. One study has got around this by extracting the gist (meaning) of language from fMRI rather than precise words, using technology similar to ChatGPT (Tang et al., 2023). In the training phase, participants listened to 16 hours of natural speech, and this was tested on new heard speech, imagined speech, and silent videos. As an example, when a participant was played the words "I don't have my driver's license yet," the decoder translated them as "She has not even started to learn to drive yet." Accurate decoding was also found to depend on participants willingness to cooperate, respecting their mental privacy.

Evaluation

In summary, brain imaging can be used to infer the *type* of stimulus that is being processed and simple cognitive decisions (e.g., add or subtract). However, it is unclear whether fMRI will ever be able to infer the *specific content* of thought. To infer, for example, whether someone in a scanner is thinking about his or her own cat or next-door's cat would require knowledge of how and where an individual stimulus is represented in the brain. We have all been exposed to different cats, houses, and so on during the course of our life. Moreover, all our brains differ in subtle ways. This presents a natural boundary on the imaging enterprise that technological developments alone are unlikely to resolve.

SUMMARY AND KEY POINTS OF THE CHAPTER

- Structural imaging reveals the static physical characteristics of the brain (useful in diagnosing disease), whereas functional imaging reveals dynamic changes in brain physiology (that might correlate with ongoing cognitive function).
- Neural activity consumes oxygen from the blood. This triggers an increase in blood flow to that region (measured by PET) and a change in the amount of deoxyhemoglobin in that region (measured by fMRI and fNIRS). As the brain is always physiologically active, functional imaging needs to measure relative changes in physiological activity.
- The most basic experimental design in functional imaging research is to subtract the activity in each part of the brain while doing one task away from the activity in the same parts of the brain while doing a slightly different task. This is called cognitive subtraction. Other methods, including parametric and factorial designs, can minimize many of the problems associated with cognitive subtraction.
- There is no foolproof way of mapping a point on one brain onto the putatively same point on another brain because of individual differences in structural and functional anatomy. Current imaging methods cope with this problem by mapping individual data onto a common standard brain (stereotactic normalization) and by diffusing regions of significance (smoothing).
- A region of "activity" refers to a local increase in metabolism in the experimental task compared

with the baseline, but it does not necessarily mean that the region is essential for performing the task. Lesion studies might provide evidence concerning the necessity of a region for a task.
- Functional imaging can be used to make crude discriminations about what someone is thinking and feeling and could potentially outperform traditional lie detectors. However, it is highly unlikely that they will ever be able to produce detailed accounts of another person's thoughts or memories.

EXAMPLE ESSAY QUESTIONS

- What are the physiological processes that underpin fMRI? What determines the temporal and spatial resolution of this method?
- What is meant by the method of "cognitive subtraction" in functional imaging research? What problems does this method face?
- Is functional imaging ever likely to completely replace lesion methods for informing theories of cognition?
- If a brain region is shown to be "active" in a given task, does it mean that this region is critical for performing the task? If not, why not?
- Could functional imaging be used in lie detection? Could it be used to read someone else's thoughts and feelings?

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CHAPTER 5

The lesioned brain and stimulated brain

CONTENTS

Studies of humans who have been unfortunate enough to acquire brain damage have provided a rich source of information for cognitive neuroscientists. The basic premise behind the approach is that, by studying the abnormal, it is possible to gain insights into normal function. This is a form of "reverse engineering," in which one attempts to infer the function of a component (or region) by observing what the rest of the cognitive system can and can't do when that component (or region) is removed. Following brain damage, it may be possible to write but not speak, or recognize objects but not faces. In this way, lesions "carve cognition at its seams" (McCarthy & Warrington, 1990).

From a contemporary perspective, studies of the effects of brain lesions on cognition can be regarded as one example of a wider class of approaches in which brain functioning is disrupted or stimulated in some way – either in humans or animals. This stands in contrast to other methods, such as EEG and fMRI, where some aspect of brain activity is recorded and for which the relationship between

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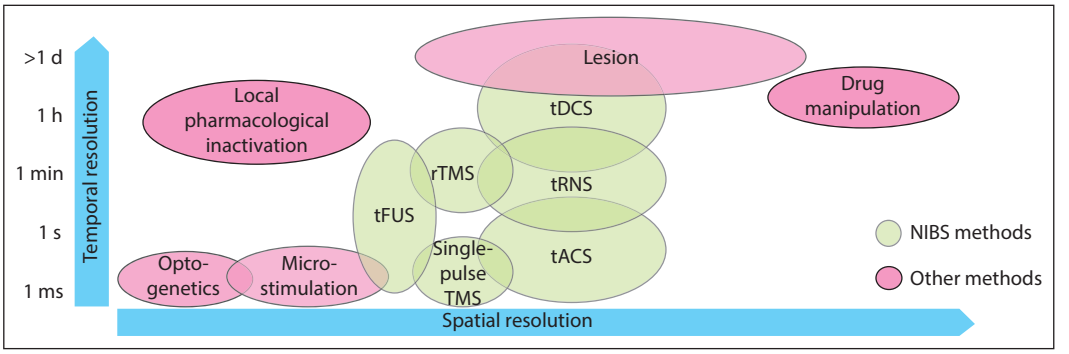


FIGURE 5.1: A taxonomy of current approaches that directly manipulate brain function either as a result of brain damage (lesions) or via short- or long-term brain stimulation. The latter can occur either invasively (shown in purple) or noninvasively (shown in green). Noninvasive brain stimulation methods (NIBS) include TMS (repetitive, rTMS, or single-pulse), electrical stimulation methods (tDCS, transcranial direct current stimulation; tACS, transcranial alternating current stimulation; tRNS, transcranial random noise stimulation), or even using ultrasound (tFUS, transcranial focal ultrasound stimulation). Adapted from Polania et al. (2018).

KEY TERMS

Noninvasive brain stimulation (NIBS)
A name for a variety of methods that stimulate the brain noninvasively (i.e., outside the skull) including by magnetic, electrical, and ultrasound methods.

Transcranial magnetic stimulation (TMS)
Noninvasive stimulation of the brain caused by magnetic induction from a rapidly changing electrical current in a coil held over the scalp.

Transcranial electrical stimulation (tES)
Noninvasive stimulation of the brain caused by passing a weak electrical current through it, either direct currents (tDCS) or alternating currents (tACS).

brain and behavior is correlational. Figure 5.1 gives an overview of these brain manipulation methods summarized according to their approximate temporal and spatial resolutions. It includes classical pharmacological manipulations on either the whole brain or local circuits; together with invasive electrical stimulation of neurons or – in genetically modified animals – by light stimulation of neurons that contain light-sensitive proteins that excite or inhibit neural activity (opto-genetics). Primarily used in humans, there are various **noninvasive brain stimulation (NIBS)** techniques of which **transcranial magnetic stimulation (TMS)** is the most famous. TMS involves magnetic stimulation of the intact brain to produce what has been described as "virtual lesions" or "reversible lesions" (e.g., Pascual-Leone et al., 1999). A set of newer methods (tDCS, tACS, tRNS) are based on the principle of electrical stimulation (Nitsche et al., 2008). Like TMS, **transcranial electrical stimulation (tES)** can be used to temporarily disrupt cognitive function (a virtual lesion approach). However, it can also be used to boost cognitive function which has important implications for rehabilitation as well as for exploring the brain basis of cognition.

WAYS OF ACQUIRING BRAIN DAMAGE

Brain damage can be acquired in a number of ways, as summarized here:

Neurosurgery
Operations are occasionally performed in cases of severe epilepsy in which the focus of the epileptic seizure is surgically

removed. One of the most famous cases in neuropsychology, HM, had dense amnesia after part of his medial temporal lobe was surgically removed (see Chapter 11). Another surgical procedure formerly used to reduce epileptic seizures spreading across the brain was to sever the fibers of the corpus callosum. This operation was referred to as the **split-brain** procedure. Patients who have undergone this intervention have only mild impairments in daily living, but the impairments can be observed in laboratory conditions in which stimuli are presented briefly to each hemisphere (for a review, see Gazzaniga, 2000). Surgical intervention was also previously common in psychiatric patients (see the discussion on the prefrontal lobotomy in Chapter 15). In general, surgical procedures are only carried out in the absence of suitable pharmacological treatments.

Strokes (or cerebrovascular accident; CVA)

Disruptions to the blood supply of the brain (called **strokes** or cerebrovascular accidents, CVA) can result in global or local death of neurons. They may be hemorrhagic or ischemic depending, respectively, on whether the blood vessel ruptures or not. If an artery ruptures, this leads to a hemorrhage and an increase in intracranial pressure (typically relieved by surgery). Blood vessels may also become blocked if, for example, a fatty clot gets pushed from a large vessel into a smaller one (an *embolism*) or a stationary clot becomes large enough to block the vessel (*thrombosis*). Other vascular disorders include *angiomas* (tangled and tortuous blood vessels liable to rupture), *arteriosclerosis* (hardening of the vessel walls), and *aneurysms* (over-elastic arteries susceptible to rupture).

Traumatic head injuries

Whereas vascular disorders tend to affect older people, traumatic head injuries are the most common form of brain damage in people of less than 40 years of age. They are particularly common in young men as a result of road traffic accidents. Traumatic head injuries are classified in two ways, "open" or "closed," depending on whether the skull is fractured. Open head injuries often have more localized injuries, whereas closed head injuries have more widespread effects (as the brain ricochets in the skull) and often produce loss of consciousness.

Tumors

The brain is the second most common site for tumors (after the

KEY TERMS

Split-brain
A surgical procedure in which fibers of the corpus callosum are severed.

Strokes
Disruption in the blood supply to the brain; also called cerebrovascular accidents (CVA).

uterus), and brain tumors are often spread from other parts of the body (these are called metastatic tumors). Tumors are caused when new cells are produced in a poorly regulated manner. Brain tumors are formed from supporting cells such as the meninges and glia (termed "meningioma" and "gliomas," respectively). Tumors adversely affect the functioning of the brain because the extra cellular material puts pressure on the neurons, disrupting functioning and possibly leading to cell death.

Viral infections

A number of viruses target specific cells in the brain. These include herpes simplex encephalitis (HSE), human immunodeficiency virus (HIV), and Creutzfeldt-Jakob disease (CJD).

Neurodegenerative disorders

Most Western societies have a large aging population that will, if anything, continue to get larger and older. In 1900, 4 percent of people were over the age of 65; in 2030, 20 percent of the population is estimated to be over 65. An increase in life expectancy is bringing about an increase in degenerative illnesses that affect the brain. By far the most common is dementia of the Alzheimer type (or DAT). This is associated with atrophy in a number of regions of the brain, with memory loss (amnesia) typically being the earliest noted symptom. Other neurodegenerative diseases include Parkinson's disease and Huntington's disease (see Chapter 10), frontotemporal dementia (affecting personality and/or language, as in semantic dementia), posterior cortical atrophy (dementia affecting vision), and multi-infarct dementia (caused by many small strokes that can be hard to distinguish from DAT).

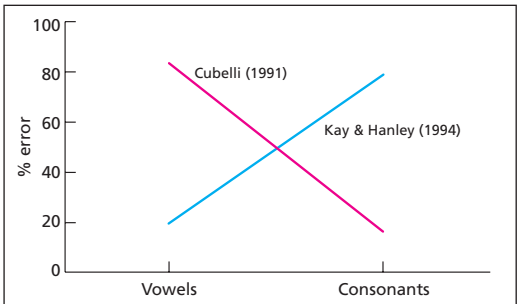
DISSOCIATIONS AND ASSOCIATIONS IN NEUROPSYCHOLOGY

In 1990, two very unusual brain-damaged patients came to the attention of Roberto Cubelli (Cubelli, 1991). One patient, CF, was unable to write any vowel letters and left gaps in their place ("Bologna" → B L GN). Another patient, CW, made spelling errors selectively on vowels (e.g., "dietro" → diatro); equivalent errors were not found in his spoken language. By contrast, Kay and Hanley (1994) report a different patient who made spelling errors selectively on consonants (e.g., "record" → recorg); see Figure 5.2. The basic logic behind the cognitive neuropsychological approach is that a difficulty in one domain relative to an absence of difficulty in another domain can be used to infer the independence of these domains. In the case of the patients just discussed, the implication was that the brain has separate neural

resources for the processing of written vowels relative to consonants. These neural resources need not lie in different locations of the brain (at least on a millimeter or centimeter scale), but might reflect two different populations of interspersed neurons. Note, also, that one cannot conclude that the *only* function of these neurons is the coding of consonants and/or vowels. The difference could be relative and, indeed, without testing a whole range of other stimuli (e.g., digits), it is unwise to conclude exclusivity of function. Nonetheless, it is reasonable to conclude that there are some neural resources predominantly implicated in written vowel processing relative to consonants and vice versa.

If a patient is impaired on a particular task (task A) but relatively spared on another task (task B), this is referred to as a **single dissociation**. If the patient performs entirely normally on task B compared with a control group, this has been termed a *classical* single dissociation, whereas if the patient is impaired on both tasks but is significantly more impaired on one task, this is referred to as a *strong* single dissociation, as shown in Figure 5.3 (Shallice, 1988). In either of these instances, one inference is that task A and task B utilize different cognitive processes with different neural resources. However, other inferences could also be made.

It could be the case that both task A and task B use exactly the same cognitive/neural resources as each other, but task B requires more of this resource than task A (i.e., task B is harder). If brain damage depletes this resource, then task B may be relatively or selectively impaired (Figure 5.4). This has been referred to as a **task-resource artifact** (Shallice, 1988). Another explanation of a single dissociation is in terms of a **task-demand artifact** (Shallice, 1988). A task-demand artifact is when a single dissociation occurs because a patient performs one of the tasks suboptimally. For example, the patient may have misunderstood the instructions or have adopted an unusual strategy for performing the task. Task-demand artifacts can be minimized by assessing the patient's general intellectual functioning, giving clearer instructions or training, using ecologically valid tests and repeating the same (or similar tests) on several occasions.



CF's writing of BOLOGNA and TAVOLINO

CW's errors on different letter types in different spelling tasks

Stimuli	Vowels	Consonants
Written spelling	42	16
Oral spelling	18	3
Delayed copying	35	7
Typing	25	15

FIGURE 5.2: Some patients produce spelling errors selectively on either consonants or vowels. This may imply separate neural resources for coding consonants and vowels.

Data from Cubelli (1991). Reproduced with permission from Springer Nature.

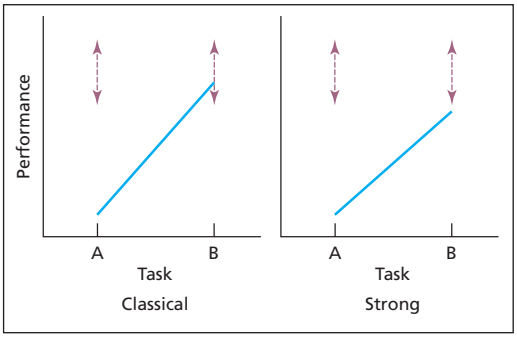


FIGURE 5.3: In a classical dissociation, performance on one task lies within the control range (shown by dotted lines). In a strong dissociation, both tasks fall outside the control range, but one task is significantly more impaired than the other.

From Shallice (1988). © Cambridge University Press. Reproduced with permission of the Licensor through PLSclear.

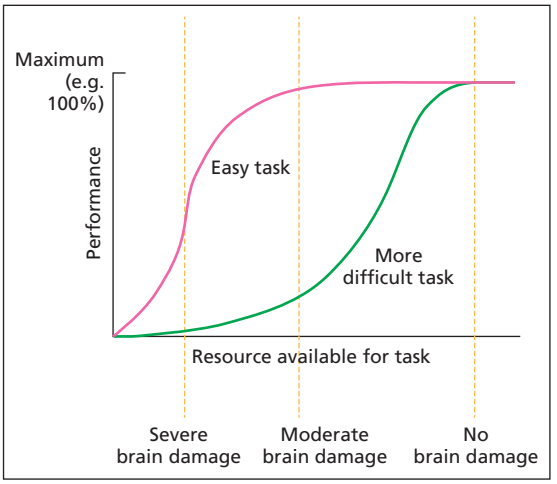


FIGURE 5.4: A task-resource artifact can arise because one task uses more of a cognitive/neural resource than the other (i.e., one task is harder). One could construe brain damage as depleting the amount of resource available. In this instance, at moderate brain damage, the patient can still perform the easy task normally. A single dissociation need not reflect different cognitive/neural substrates for the tasks.

Adapted from Shallice (1988).

In general, almost all neuropsychological studies are aimed at proving that two or more tasks have different cognitive/neural resources and disproving the task-resource and task-demand explanations even if this is not explicitly stated in these terms. In the case of Cubelli's patients, a task-demand artifact can easily be ruled out because the same task (i.e., writing) was performed in both conditions. One of the most powerful ways of discounting a task-resource artifact is to document a **double dissociation**, which merely refers to two single dissociations that have a complementary profile of abilities. To remain with the current example, Kay and Hanley's patient could write vowels better than Cubelli's patient, whereas Cubelli's patient could write consonants better than Kay and Hanley's.

So far, the discussion has emphasized the importance of dissociations between deficits, but what about *associations* of deficits? For example, if for every patient that resembled Cubelli's there were 10, 20, or 100 times as many patients who had comparable **dysgraphia** for *both* consonants and vowels, then would this diminish the findings of the dissociation? Some researchers would suggest not. There are some theoretically uninteresting reasons why two symptoms may associate together, the main reason being that they are close together in the brain and so tend to be similarly affected by brain pathology in that region. For example, patients with difficulties in recognizing faces often have difficulties in perceiving colors, but this probably reflects neuroanatomical proximity rather than suggesting a "super-module" that is specialized for both. It is the (double) dissociations between the two that count from a theoretical point of view.

Needless to say, this particular viewpoint has attracted controversy. It has been argued that it is important to know how common a particular dissociation is in order to rule out that it hasn't been observed by chance (Robertson et al., 1993). For example, if brain damage affects some written letters more than others in a random fashion, then it would still be possible to find patients who appear to have selective difficulties in writing vowels, but it would

KEY TERMS

Single dissociation
A situation in which a patient is impaired on a particular task (task A) but relatively spared on another task (task B).

Task-resource artifact
If two tasks share the same neural/cognitive resource but one task uses it more, then damage to this resource will affect one task more than the other.

Task-demand artifact
One task is performed worse than another because the task is performed suboptimally (but not because some aspect of the task is compromised).

Double dissociation
Two single dissociations that have a complementary profile of abilities.

Dysgraphia
Difficulties in spelling and writing.

be a chance occurrence rather than meaningful dissociation. Other researchers have focused more on associations between symptoms (so-called **syndromes**) rather than dissociations. The use of the double dissociation itself has been subject to criticism (see Dunn & Kirsner, 2003). Some have argued that the use of double dissociation implies an endorsement of the notion of modularity (e.g., as specified by Fodor, 1983; see Chapter 1). However, it need not. Shallice (1988) discusses why this argument is wrong by setting up the following thought trap: if modules exist, then double dissociations are a reliable way of uncovering them; double dissociations do exist, therefore modules exist. The way out of this trap, however, is to ask the question: can non-modular systems produce double dissociations? It has been demonstrated that other types of cognitive architecture, such as interactive connectionist models, can produce double dissociations (Plaut, 1995). The reason why they do so is interesting. It reflects the fact that these systems also contain units that are functionally specialized for certain types of process/information, even though the system is interactive, and even though these units may respond (to a greater or lesser degree) to a range of stimuli. Recent advances in brain imaging suggest that functional specialization is an inevitable consequence of the network architecture of the brain in which neurons processing similar kinds of information connect densely to each other (Bullmore & Sporns, 2009).

Some have argued that the reliance on double dissociations is flawed because it requires the study of "pure" cases (Dunn & Kirsner, 2003). However, it need not (Shallice, 1979). First of all, one must be careful to state what is meant by a pure case. For example, imagine that the dysgraphic patients mentioned previously also had amnesia. Would the fact that they were not "pure dysgraphic" exclude them from the study? This might depend on the theoretical stance one adopts. If one's theoretical model assumes that writing and memory are independent (as most do), then studying writing in isolation is entirely feasible.

It is worth stating that finding a double dissociation between two patients on two tasks is only part of the neuropsychologist's toolkit. To interpret their spared and impaired performance, one requires evidence from a range of other relevant tasks. For example, to fully interpret the dysgraphic patients' impairments, it would be interesting to know if they could copy vowels and consonants, or recognize them visually. The types of error that patients produce can also be an important source of information, irrespective of their performance level (i.e., how good or bad they are). For example, the independence of consonants and vowels was initially inferred from the types of errors made in dysgraphia (Caramazza & Miceli, 1990) and not from the double dissociation logic. The double dissociation is useful, but it is not a panacea.

SINGLE-CASE STUDIES IN COGNITIVE NEUROPSYCHOLOGY

Patient-based neuropsychology has tended to take two broad forms. In one tradition, which I shall call *classical neuropsychology*, attempts have been made to infer the function of a given brain region by taking

KEY TERM

Syndrome
A cluster of different symptoms that are believed to be related in some meaningful way.

ONLINE RESOURCES

Visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience) for talks by the author, Jamie Ward, including a Cognitive Neuroscience Bitesize on Non-invasive Brain Stimulation. Plus Alfonso Caramazza on "What is Cognitive Neuropsychology Good For?"

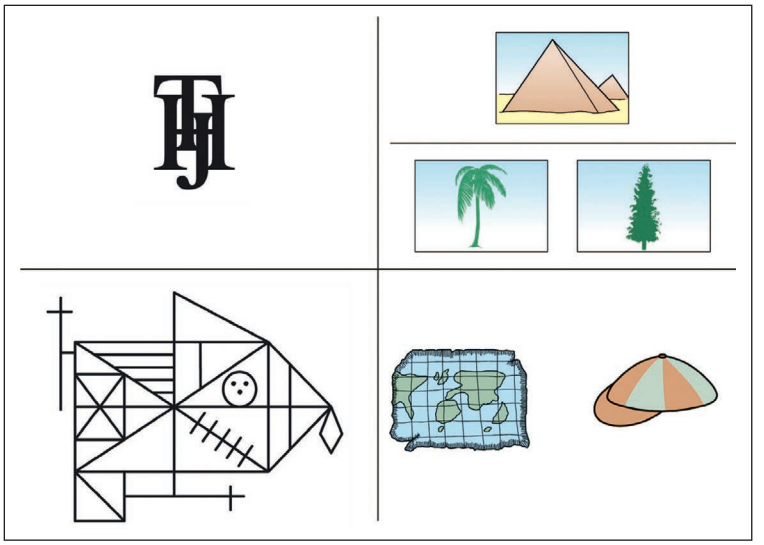


FIGURE 5.5: The purpose of a neuropsychological assessment is to ascertain a patient's level of functioning relative to that expected based on his or her premorbid functioning. Some common neuropsychological tests are shown; clockwise from top left: patients with visual recognition problems find it hard to identify overlaid letters relative to non-overlaid ones (from BORB; Riddoch & Humphreys, 1995); patients with semantic memory impairments may find it hard to match the palm tree to the pyramid (Howard & Patterson, 1992); patients with aphasia may find it hard to decide whether things rhyme (from PALPA; Kay et al., 1992); patients with memory problems may be able to copy but not remember this figure.

From Rey (1964). Reproduced by permission of Taylor & Francis Group.

KEY TERMS

Group studies
In neuropsychology, the performance of different patients is combined to yield a group average.

Single-case studies
In cognitive neuropsychology, the data from different patients are not combined.

patients with lesions to that region and examining their pattern of impaired and spared abilities. This type of research has benefited greatly from the development of imaging methods that enable more accurate lesion localization and quantification. It also provides an important source of constraint on functional imaging data. In the second tradition, which I shall call *cognitive neuropsychology*, the pattern of spared and impaired abilities in and of themselves has been used to infer the building blocks of cognition – irrespective of where they are located in the brain. Each tradition has tended to rely on its own methodology, with classical neuropsychology favoring **group studies** and cognitive neuropsychology favoring **single-case studies**. It will be argued in this chapter that group studies are more appropriate for establishing lesion-deficit associations, whereas single-case studies are particularly helpful for establishing how cognitive processes might be subdivided. Both approaches rely on detailed assessments of many kinds of cognitive function (see Figure 5.5) in order to infer the specificity of any deficit.

Caramazza's assumptions for theorizing in cognitive neuropsychology

Although the use of single cases of brain-damaged individuals to study normal cognitive/brain function began in the mid-nineteenth century, attempts to formalize the logic of this approach were lacking for many years. Caramazza (1986, 1992) provided one of the first serious attempts to do so. He suggested that three underlying, and unstated, assumptions underpinned almost all neuropsychological studies to date:

1. *The fractionation assumption*. The first assumption is that damage to the brain can produce selective cognitive lesions. Note that the assumption is stated with reference to a lesion

within a particular cognitive model and not to a lesion to a particular region of the brain (although the two may, of course, be correlated). Caramazza's arguments were concerned with using observations of brain-damaged individuals to inform theories of cognition (cognitive neuropsychology), not to localize cognitive processes in the brain (classical neuropsychology).

2. *The transparency assumption*. The **transparency assumption** states that lesions affect one or more components within the preexisting cognitive system, but they do not result in a completely new cognitive system being created. This assumption is needed because one wishes to study the abnormal in order to understand the normal, and not just to study the abnormal as an end in itself.
3. *The universality assumption*. The universality assumption is that all cognitive systems are basically identical.

KEY TERM

Transparency assumption
Lesions affect one or more components within the preexisting cognitive system but do not result in a completely new cognitive system being created.

Caramazza acknowledged that these assumptions may, under some situations, not hold true. It is a matter for empirical research to determine the extent to which they are true (for a discussion see Shallice, 2015).

Critics have pointed to a number of potential difficulties with the assumptions. Kosslyn and Van Kleek (1990) have suggested that whether selective cognitive impairments will be observed (the fractionation assumption) depends on the neural architecture. For example, selective deficits may be more likely if neurons performing a given operation are clustered together rather than distributed around the brain and if the neurons are dedicated to one operation rather than shared by many operations. Nevertheless, selective cognitive impairments *can* be observed, and so the fractionation assumption appears to hold true at one level, even if there are some cognitive processes that may be hard to uncover by the lesion method by virtue of an atypical neural architecture.

The transparency assumption is potentially the most problematic. Basically, one needs to assume that brain damage removes one component of cognition, but does not create, from scratch, a rearranged or different cognitive system. Examples of brain plasticity, and rehabilitation and recovery after brain damage, might at first appear to be convincing arguments against transparency. But they need not be. For example, imagine that a patient has severe problems in speaking after a stroke (i.e., aphasia) but that these problems ameliorate over time. This could be taken as *prima facie* evidence that the brain has somehow reorganized itself after the stroke. However, it could be that the preexisting cognitive model has just been reinstated rather than that a whole new way of performing the task has been created. As such, this would *not* be a violation of the transparency assumption. Plasticity at a neural level is a pervasive aspect of brain function (see also Chapter 11), but plasticity doesn't necessarily create alternative

cognitive systems. It is important to point out that the assumption is more likely to hold true for brain damage acquired during adulthood than childhood (Thomas & Karmiloff-Smith, 2002). It is also worth pointing out that the transparency assumption refers to the cognitive organization of the cognitive system and not necessarily its location. Consider the case of an epileptic child who has his left hemisphere removed and then learns to speak using the right hemisphere (Vargha-Khadem et al., 1997a). Is that a violation of the transparency assumption? It could be, but it need not be. It depends on whether the new right hemisphere system is cognitively equivalent to the one in the left. The transparency assumption refers to the comparability between premorbid and postmorbid cognitive systems, and not on *where* such systems are located. Although the debate remains open about the validity of this assumption, a good rule of thumb is that the transparency assumption is less likely to be violated in adult relative to child cases and when studied soon after injury relative to later in time (or if the cognitive profile after injury remains stable over time).

The universality assumption, that all cognitive systems are basically the same, may also be problematic to neuropsychology. But Caramazza has argued that it is equally problematic for other methods within cognitive neuroscience. Basically, one needs to assume that an individual (or individuals) are representative of the population at large in order to make generalizations to normal cognition. Individual differences, such as they are, are attributable to "noise" (e.g., variations in performance related to time) or other factors that may be related to the efficiency of the cognitive system (e.g., expertise) but need not reflect qualitative differences in the way the task is performed. Of course, if there are individual qualitative differences, then this is theoretically interesting. Finding a framework to explore and account for these differences is a challenge for cognitive neuroscience in general, rather than patient-based neuropsychology in particular. As one example, it has been suggested that there are different routes to reading a word aloud (a semantic route, and a phonetic route) and that there might be individual differences in how these routes are weighted: with some people using one route in preference to the other. Equivalent lesions to a given route would then produce rather different symptoms depending on how heavily that route was weighted prior to brain damage (Woollams et al., 2007).

The case for single-case studies

Caramazza and McCloskey (1988) have gone as far as to suggest that the single-case study is the *only* acceptable method in cognitive neuropsychology. The titles of the papers debating this position tell a story of their own. The original paper, entitled "The case for single patient studies" (Caramazza & McCloskey,

1988), was interpreted as the case against group studies. A subsequent paper, "The case against the case against group studies" (Zurif et al., 1989), defended group studies on the grounds that "syndromes [i.e., associations of symptoms] are what the world gives us." This provoked a paper with a particularly amusing title: "Clinical syndromes are not God's gift to cognitive neuropsychology: A reply to a rebuttal to an answer to a response to the case against syndrome-based research" (Caramazza & Badecker, 1991). To understand this heated debate, it is necessary to take a step back and consider the argument as initially laid out (see Figure 5.6).

In a non-brain-damaged population...

Subjects	S_1	S_2	S_3	S_4...	S_n
Cognitive system	M	M	M	M	M
Experiment	E	E	E	E	E
Observations	O_1	O_2	O_3	O_4...	O_n

In a brain-damaged population...

Subjects	P_1	P_2	P_3	P_4...	P_n
Cognitive system	M	M	M	M	M
Lesion	L_1	L_2	L_3	L_4	L_n
Experiment	E	E	E	E	E
Observations	O_1	O_2	O_3	O_4...	O_n

FIGURE 5.6: Caramazza has argued that it is possible to average observations (O1 to O*n*) across different non-brain-damaged participants (S1 to S*n*) because they are assumed to have the same cognitive system (M) that performs the experiment (E) in comparable ways. The same logic may not apply to brain-damaged patients (P1 to P*n*) because each patient will have a different cognitive lesion (L), which cannot be known *a priori*.

From Caramazza and McCloskey (1988). Copyright © Taylor & Francis Ltd, reprinted by permission of Taylor & Francis Ltd, www.tandfonline.com.

Consider first the logic of testing participants in the non-brain-damaged population. One may recruit a sample of participants (S1 to S*n*) and make the assumption, valid or not, that they have broadly equivalent cognitive systems (M). One may then conduct an experiment (E), making the further assumption that all participants carry it out in equivalent ways (i.e., no task-demand artifacts), and derive a set of observations (O1 to O*n*). In this instance, it is argued that it is quite feasible to average the observations of the group because it is assumed that the only difference between the participants is "noise" (i.e., variations in performance over time, differences in speed or ability).

Consider next the situation in which one wishes to test a group of brain-damaged patients (P1 to P*n*). As before, it is assumed that each has (before their lesion) essentially the same cognitive system (M) and that each is given the same experiment (E) and complies with the experiment in the same way. However, each patient may have a different lesion to the cognitive system (L1 to L*n*) and so the difference in observed performance may be attributable to differences in lesion rather than between-patient noise and, as such, averaging across patients is not possible. Determining where the lesion is in the cognitive system can only be done on the basis of empirical observation of each case in turn. It is crucial to bear in mind the distinction between a lesion to a cognitive component (which is relevant to the discussion here) and an anatomical lesion. At present, there is no magic way of working out what the precise cognitive profile of a given patient will be from a structural lesion (except in the most general terms). Thus, establishing the cognitive impairment requires cognitive testing of individual patients.

What if one were to establish that a group of patients had identical lesions to the same component of the cognitive system – could one then average across the patients? Caramazza has argued that, although legitimate, the study becomes a series of

FIGURE 5.7: The use of single cases is not peculiar to neuropsychology. For example, it is the mainstay of archaeology and anthropology. In 1974, Donald Johanson discovered a partial skeleton of a single primate, Lucy, from 3.18 million years ago, which had walked upright and had a small brain. Previous theories had suggested that brain enlargement preceded the ability to walk upright. This single case proved this not to be so. Note that Johanson did not have to provide a group of "Lucys" for his findings to be acceptable to the scientific community.

John Reader/Science Photo Library.

single-case studies, not a group study, and so the unit of interest is still the single case. To establish that they had the same lesion, one would have to carry out the same set of experiments on each individually. As such, one would not learn any more from averaging the set of patients than could be learned from a single case itself. The objection is not against the idea of testing more than one patient per se, but rather averaging the results of many patients assumed (but not proven) to be equivalent.

Some of the common objections against the use of the single-case study are that one cannot create a theory based on observations from only a single case, or that it is not possible to generalize from a single case. The counterarguments are that nobody is trying to construct whole new theories of cognition based on a single case. Theories, in neuropsychology and elsewhere, must account for a wide range of observations from different sources, both normal and brain-damaged. Nevertheless, the use of single-case methodology in the age of "big data" is undoubtedly on the decline. Medina and Fischer-Baum (2017) discuss various reasons for this including the popularity of neuroimaging, the logistics of performing in-depth investigations of one person over several months (or years) and wider concerns over replicability (even though replicability *within* the single case guards against the possibility that a pattern of data is simply noise).

Evaluation

The argument presented in the previous section has emphasized the point that single-case studies are a valid methodology, and they may have a particularly important role to play in determining what the components of cognitive systems are (Figure 5.7). The discussion has also argued that the term "lesion" can be construed both in terms of disruption to a component in a cognitive model and as a region of organic brain damage. Does this mean that group studies have no role to play at all? It will be argued that group studies do have an important role to play, and that they may be particularly suited to addressing different types of question from the single-case approach.

GROUP STUDIES AND LESION-DEFICIT ANALYSIS IN NEUROPSYCHOLOGY

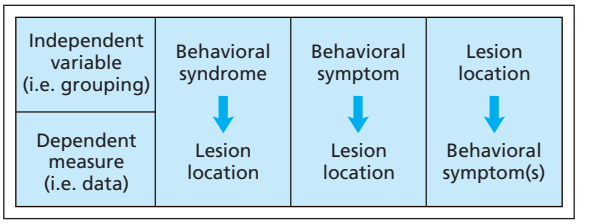


FIGURE 5.8: There are at least three different ways of grouping patients to carry out a lesion-deficit analysis.

The introduction to this chapter discussed the historical schism that exists between cognitive neuropsychology, which is aimed at developing purely cognitive accounts of cognition, and classical neuropsychology, which is aimed at developing brain-based accounts of cognition. The latter has tended to rely more on groups of patients with damage to particular brain regions in order to determine if the region is important for that task (in contrast to imaging methods which are more correlational) and to infer what precise functions that region computes. As such, this neuropsychological method has benefited greatly from the knowledge base derived from neurotypical brain imaging studies.

Ways of grouping patients

How does one decide the principle by which patients should be grouped in order to associate lesion sites with deficits? There are at least three approaches in the literature (see also Figure 5.8):

1. *Grouping by syndrome*. Patients are assigned to a particular group on the basis of possessing a cluster of different symptoms. This approach is particularly common in psychiatric studies (e.g., of schizophrenia), and there are current attempts to ensure that these diagnostic categories map effectively onto the latest findings in neurobiology and behavior (Cuthbert & Insel, 2013).
2. *Grouping by cognitive symptom*. Patients are assigned to a particular group on the basis of possessing one particular symptom (e.g., auditory hallucinations; difficulty in reading nonwords). They may also possess other symptoms, but assuming that the other symptoms differ from case to case, the method should be sensitive to the symptom under investigation.
3. *Grouping by anatomical lesion*. Patients are selected on the basis of having a lesion to a particular anatomical region. This region may have been identified as interesting by previous functional imaging studies. This method need not require that patients have damage exclusively to the region of interest. The patients may have additional damage elsewhere, but assuming that the other lesions differ from case to case, the method should be sensitive to the region in question (Damasio & Damasio, 1989).

There is no right or wrong way of deciding how to group patients, and to some extent, it will depend on the precise question

being addressed. The method of grouping cases by syndrome is likely to offer a coarser level of analysis, whereas grouping according to individual symptoms may provide a more fine-grained level of analysis. In general, the syndrome-based approach may be more appropriate for understanding the neural correlates of a given disease pathology rather than developing theories concerning the neural basis of cognition.

The method of grouping patients by symptom (2 in the previous list) and then finding out what regions of damage they have in common is made feasible by techniques that compare the location of lesions from MRI scans of different patients on a voxel-by-voxel basis, thus producing a fine-grained statistical map of the likely lesion "hot spot" (Rorden & Karnath, 2004). For example, it has been used to separate out the different contributions of frontal regions in tests of executive function (Shammi & Stuss, 1999; Stuss et al., 2002). One advantage of working forward from a symptom to a lesion location is that it could potentially reveal more than one region as being critically involved. For example, let's assume that a cognitive deficit can arise from damage to either region X or region Y. If one were to initially group patients according to whether they have damage to region X and test for a deficit (3 in the previous list), then one could falsely conclude that region X is the key region that gives rise to this deficit, and the method would not detect the importance of region Y. The main situation in which one would group patients by lesion site and then test for the presence of a particular symptom is if one has a specific testable prediction about what the region is critical for (e.g., the region has been implicated by functional imaging studies).

Caveats and complications

There are at least two caveats and complications that warrant further discussion. The first concerns the ability of current structural imaging techniques to identify lesions. The second concerns the inferences that can be drawn from lesion-deficit associations that can, if not articulated properly, lapse into neophrenology.

Damasio and Damasio (1989) discuss how certain types of neuropathology are more suited to lesion-deficit analysis than others, at least with current techniques. The most suitable lesions are those in which dead tissue is eventually replaced by cerebrospinal fluid. This is frequently the case in stroke (at least in the chronic rather than acute phase), in damage resulting from the herpes simplex encephalitis (HSE) virus and following neurosurgery. Identifying the site of a lesion caused by a tumor is particularly problematic when the tumor is *in situ* but is less problematic once it has been excised. Certain tumors (e.g., gliomas) may infiltrate surrounding tissue and so have no clear boundary, and physical strain around the tumor may cause swelling (termed **edema**). This distorts the true size and shape of the brain tissue and may render

KEY TERM

Edema
A swelling of the brain following injury.

neurons inoperative even if they are not destroyed (Figure 5.9). Similar arguments apply to the presence of leaked blood during hemorrhage and the intracranial swelling associated with closed head injury. In general, reliable lesion images are best obtained three months after onset and when the neuropsychology testing is carried out at a similar time to the structural imaging (Damasio & Damasio, 1989).

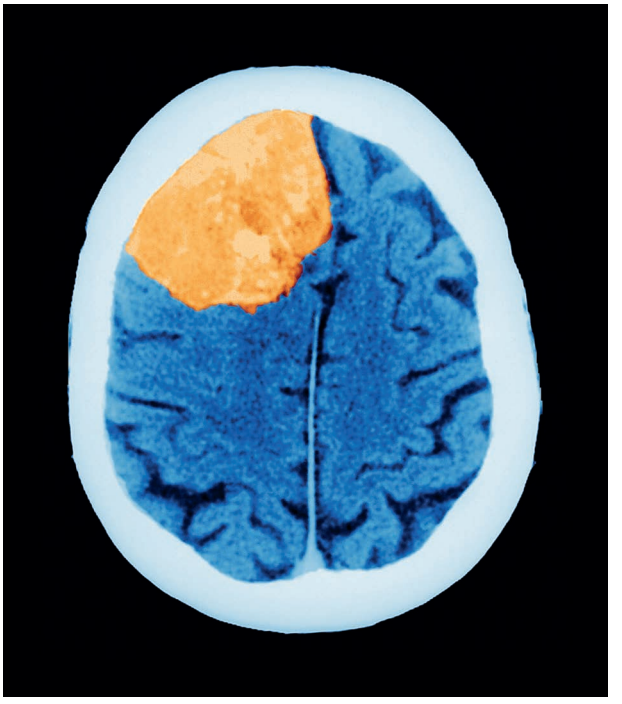


FIGURE 5.9: A tumor (here shown on a CT scan) can make it hard to estimate lesion size, and the distortion in the shape of the brain makes it hard to map onto a standard atlas.

Sovereign, ISM/Science Photo Library.

On finding that a function (F) is disrupted following a lesion to region X, it is tempting to conclude that function F is located in region X or, worse still, that the purpose of region X is to implement F. These conclusions, and the second one in particular, are tantamount to endorsing a neophrenological view of the brain structure–function relationship. Before jumping to such a conclusion, one would need to consider a number of other questions. Is this the only function of region X? Do other regions contribute to the performance of function F, or is this the only region that does so? On finding that a function (F) is disrupted following a lesion to region X, a more cautious conclusion is that region X is critical for performing some aspect of function F. This assertion does not assume that region X has a single function, or that function F has a discrete location. It is also important to note that even a very discrete brain lesion can disrupt the functioning of distant brain regions that are structurally intact; this is termed **diaschisis**. For example, structural lesions to the left frontal lobe can result in markedly reduced activity in other distant regions (e.g., left inferior posterior temporal lobe) during a letter judgment task (Price et al., 2001). This can occur even though this distant region is not lesioned and may function normally in other contexts. The implications are that damage to one region can disrupt the functioning of another, intact region when these two regions work together as a network to implement a particular cognitive function.

KEY TERM

Diaschisis
A discrete brain lesion can disrupt the functioning of distant brain regions that are structurally intact.

Evaluation

Group studies of patients can be important for establishing whether a given region is critical for performing a given task or tasks. Two broad methods are favored, depending on the hypothesis being addressed. The first method involves establishing (on a case-by-case basis) whether a patient is impaired on a given task and then

determining the lesion location(s). The second method involves selecting the group on the basis of a lesion to a predefined area and then establishing what functional deficits the group has. This second method is important for testing predictions derived from functional imaging research.

ANIMAL MODELS IN NEUROPSYCHOLOGY

The two main methods that use nonhuman animals that are considered in this textbook are single-cell recordings (discussed in Chapter 3) and lesion methods. Both of these methods have been greatly assisted by structural MRI scanning enabling individual differences in each animal's brain anatomy to be taken into consideration when placing electrodes and lesions, and also for determining the extent of lesions in vivo. When nonhuman animals are used in this way, it is typically referred to as **behavioral neuroscience** rather than cognitive neuroscience. The implication of this difference in terminology is that humans think but animals behave, or, rather, we know that humans think but we can't be so sure about other animals.

KEY TERM

Behavioral neuroscience
Cognitive neuroscience in nonhuman animals.

Although lesion methods in humans rely on naturally occurring lesions, it is possible – surgically – to carry out far more selective lesions on other animals. Unlike human lesions, each animal can serve as its own control by comparing performance before and after the lesion. It is also common to have control groups of animals that have undergone surgery but received no lesion, or a control group with a lesion in an unrelated area. There are various methods for producing experimental lesions in animals (Murray & Baxter, 2006):

1. *Aspiration*. The earliest methods of lesioning involved aspirating brain regions using a suction device and applying a strong current at the end of an electrode tip to seal the wound. These methods could potentially damage both gray matter and the underlying white matter that carries information to distant regions.
2. *Transection*. This involves cutting of discrete white matter bundles such as the corpus callosum (separating the hemispheres) or the fornix (carrying information from the hippocampus).
3. *Neurochemical lesions*. Certain toxins are taken up by selective neurotransmitter systems (e.g., for dopamine or serotonin), and once inside the cell, they create chemical reactions that kill it. A more recent approach involves toxins that bind to receptors on the surface of cells, allowing for even more specific targeting of particular neurons.
4. *Reversible "lesions."* Pharmacological manipulations can sometimes produce reversible functional lesions. For example, scopolamine produces a temporary amnesia during the time in which the drug is active. Cooling of parts of the brain also temporarily suppresses neural activity.

Studies of nonhuman animals have also enabled a more detailed anatomical understanding of the brain and, in particular, the anatomical connectivity between regions. In nonhuman animals, injecting the enzyme horseradish peroxidase into axons carries a visible tracer back to the cell bodies that send them. The tracer can be visualized at postmortem. This enables one to ascertain which regions project to a given region (Heimer & Robards, 1981). There are now a wide variety of chemically-based tract tracing methods (Lanciego & Wouterlood, 2020).

FIGURE 5.10: A family of macaque monkeys.
apple2499/iStock

While the vast majority of neuroscience research is conducted on rodents, some research is still conducted on nonhuman primates. In many countries, including in the EU, neuropsychological studies of great apes (e.g., chimpanzees) are not permitted. More distant human relatives used in research include three species of macaque monkeys (rhesus monkey, cynomolgus monkey, and Japanese macaque; Figure 5.10) and one species of New World primate, the common marmoset. There are a number of difficulties associated with the use of animal models in neuropsychology, not least the concern for the welfare of the animals. Scientists working with these species must provide a justification as to why the research requires primates rather than other animals or other methods, and they must justify the number of animals used. It is also important to have careful breeding programs to avoid having to catch animals in the wild and to protect the animals from viruses. It is important to give them adequate space and social contact. Another disadvantage of animal models is that there are some human traits that do not have obvious counterparts in other species. Language is the most obvious such trait; consciousness is a more controversial one (see Edelman & Seth, 2009).

TRANSCRANIAL MAGNETIC STIMULATION (TMS)

Attempts to stimulate the brain electrically and magnetically have a long history. Electric currents are strongly reduced by the scalp and skull and, until relatively recently, tended to be an invasive technique on people undergoing surgery. In contrast, magnetic fields do not show this attenuation by the skull. However, the limiting factor in developing this method has been the technical challenge of producing large magnetic fields, associated with rapidly changing currents, using a reasonably small stimulator (for a historical overview, see Walsh & Cowey, 1998). Early attempts at magnetic stimulation were successful at eliciting

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Legal and ethical frameworks for animal research
Search the internet or visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience) for more information on the UK's 3Rs principle (Replacement, Reduction, Refinement), the US National Institute of Health (NIH) Office of Laboratory Animal Welfare, and the European Union's Directive 2010/63/EU.

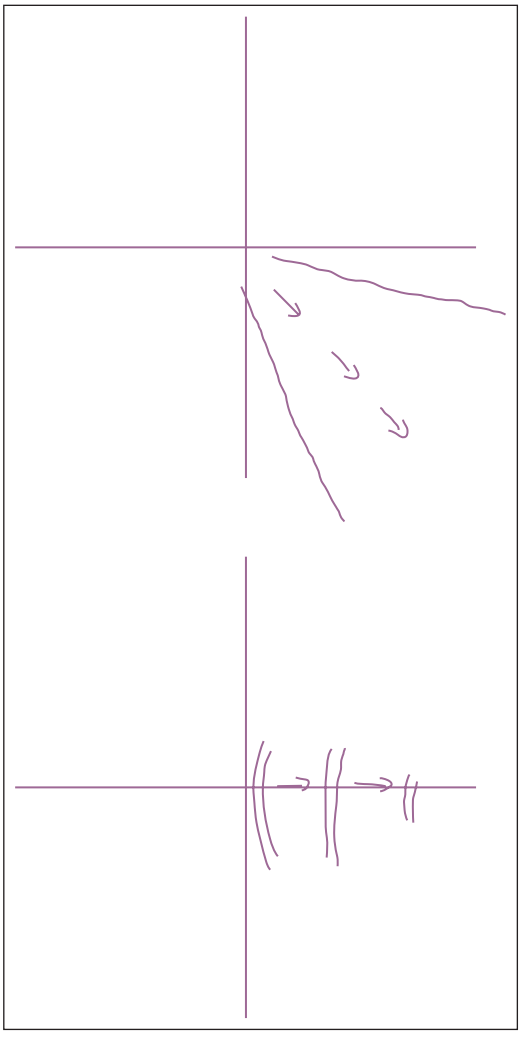

FIGURE 5.11: An example of two phosphenes produced by stimulating area V5/MT. Left hemisphere V5/MT stimulation produces right visual field phosphenes moving away from the center. The first was described as "movement of a single point in a static field" and the second as "drifting right, not continuous."

subjective flashes of light or "phosphenes" (Magnussen & Stevens, 1914), but this was probably due to stimulation of the retina rather than the brain (Barlow et al., 1947). It was not until 1985 that adequate technology was developed to magnetically stimulate focal regions of the brain (Barker et al., 1985). Since then, the number of publications using this methodology has increased rapidly. Typically, the effects of transcranial magnetic stimulation (TMS) are small, such that they alter reaction-time profiles rather than elicit an overt behavior. But there are instances of the latter. For example, if the coil is placed over the region of the right motor cortex representing the hand, then the subject may experience a sensation or involuntary movement in the left hand (given that the right motor cortex sends movement signals to the left part of the body). If the coil is placed over the right visual cortex, then the subject may report phosphenes on the left side (given that the right visual cortex represents the left side of space). Even more specific examples have been documented. Stewart et al. (1999) stimulated a part of the visual cortex dedicated to motion perception (area V5/MT) and reported that these particular phosphenes tended to move – Figure 5.11. Stimulation in other parts of the visual cortex produces static phosphenes.

How does TMS work?

TMS works by virtue of the principle of electromagnetic induction that was first discovered by Michael Faraday. A change in electric current in a wire (the stimulating coil) generates a magnetic field. The greater the *rate of change* in electric current, the greater the magnetic field. The magnetic field can then induce a secondary electric current to flow in another wire placed nearby. In the case of TMS, the secondary electric current is induced, not in a metal wire, but in the neurons below the stimulation site. The use of the term "magnetic" is something of a misnomer as the magnetic field acts as a bridge between an electric current in the stimulating coil and the current induced in the brain. Pascual-Leone et al. (1999) suggest that "electrodeless, noninvasive electric stimulation" may be more accurate, although it is a less catchy term. The induced electric current in the neurons is caused by making them fire (i.e., generate

action potentials) in the same way as they would when responding to stimuli in the environment. Although the TMS pulse itself is very brief (less than 1 millisecond), the effects on the cortex may last for several tens of milliseconds. Moreover, repeated stimulation by TMS, over several minutes, results in longer aftereffects (~20 minutes) in which synaptic transmission is temporarily affected in that region (Huang et al., 2011). As such, TMS protocols are often described as being either online (i.e., single pulse or a short train of pulses of TMS delivered around the same time as the stimulus) or offline (i.e., TMS delivered repeatedly before a task so its aftereffects influence cognition). Obviously, the former method has a better temporal resolution (refer back to Figure 5.1).

A number of different designs of stimulating coil exist (Figure 5.13), and the shape of the coil determines how focused the induced current is. One of the most common designs is the figure-of-eight coil. Although the coil itself is quite big, the focal point of stimulation lies at the intersection of the two loops and is about 1 cm^2 in area. If you have access to TMS equipment, try holding the coil a few centimeters above your arm. When the pulse is released, you should feel a slight harmless twinge on a small area of skin that is representative of the area of direct stimulation of the brain.

The "virtual lesion"

TMS causes neurons underneath the stimulation site to be activated. If these neurons are involved in performing a critical cognitive function, then stimulating them artificially will disrupt that function. Although this process is described as a "virtual lesion" or a "reversible lesion," a more accurate description would be in terms of interference. The neurons are being activated both from an internal source (the task demands themselves) and an external source (the TMS), with the latter disrupting the former. Of course, if the region is not involved in the task, then interference would not occur in this way.

WHAT IS THE "VISUAL" CORTEX OF A BLIND PERSON USED FOR?

Could whole regions of the brain normally dedicated to one type of processing (e.g., vision) take on a completely different functional characteristic (e.g., touch)? A number of studies have investigated the functioning of the visual cortex (in the occipital lobes) in people who were blind from a very early age.

Sadato et al. (1996) conducted a brain imaging study demonstrating that early blind Braille readers showed activity in their primary visual cortex (V1) during Braille reading. This was not found for late blind or sighted individuals with their eyes closed. However, functional imaging methods can reveal increases in activity that may not be functionally critical. It could be, for instance, that the blind readers are *trying* to use the visual cortex during Braille reading but that this activity is not actually contributing to task performance.

To address this, lesion methods are appropriate. Given that early blind people with late brain damage restricted to occipital regions are rare (but see Hamilton et al., 2000), TMS avails itself as the most appropriate method.

Cohen et al. (1997a) studied tactile identification of Braille letters in early blind individuals, and tactile identification of embossed letters in Roman type in both early blind and (blindfolded) sighted individuals. When they placed their finger on the letter, a train of TMS pulses was delivered. The TMS was delivered to a number of sites, including the mid-occipital ("visual" cortex), the sensorimotor (tactile/motor cortex) and "air" as the control condition. For the blind participants, TMS over midoccipital regions impaired tactile letter discrimination (Figure 5.12). This suggests that the "visual" cortex is used for touch in the early blind. Sighted people show disruption when TMS is applied over the sensorimotor cortex. It is perhaps surprising that blind people do not additionally show an effect here. It could be that, because they are more skilled, they require a higher intensity of TMS for disruption to be induced. There is evidence for plasticity in somatosensory, as well as mid-occipital, regions in the blind as the region of the brain representing their reading fingers is enlarged by as much as two or three times (Pascual-Leone & Torres, 1993). Similar TMS studies have revealed cortical enlargements are found for skilled racquet players (Pearce et al., 2000) and cortical reductions found for limb amputees (Cohen et al., 1991). These suggest that level of use is critical for plasticity.

Is it likely that any brain region can substitute for the function of another? In this instance, the function of the brain region is largely the same (i.e., it makes fine-grained spatial discriminations) even though in one instance it responds to vision and in another to touch. However, more recent research suggests that the occipital cortex in blind individuals can support tasks of a very different nature (e.g., verb generation; Amedi et al., 2004).

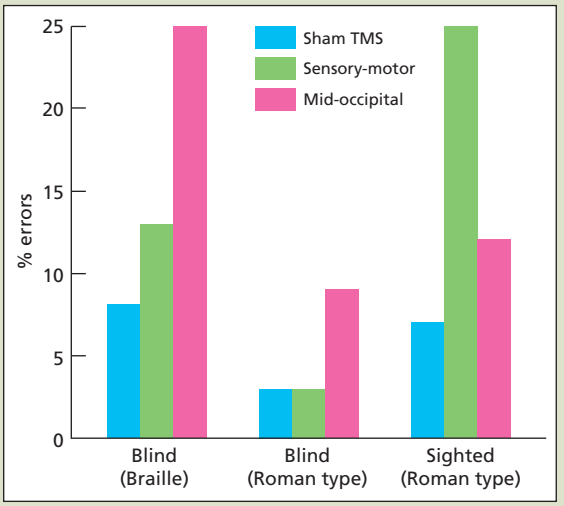

FIGURE 5.12: TMS over mid-occipital "visual" cortex impairs tactile identification in the blind, but not in blindfolded sighted people, whereas TMS over sensorimotor (tactile) cortex impairs tactile discrimination in sighted individuals.

From Cohen et al. (1997b). Reproduced with permission from Springer Nature.

TMS has a number of advantages over traditional lesion methods (Pascual-Leone et al., 1999). The first advantage is that real brain damage may result in a reorganization of the cognitive system (a violation of the transparency assumption), whereas the effects of TMS are brief and reversible. This also means that within-subject designs (i.e., with and without lesion) are possible in TMS that are very rarely found with organic lesions (neurosurgical interventions are an interesting exception, but in this instance, the brains are not strictly premorbidly "normal" given that surgery is warranted). In TMS, the location of the stimulated site can be removed or moved at will. In organic lesions, the brain injury may be larger than the area under investigation and may affect several cognitive processes.

FIGURE 5.13: The coil is held against the participant's head, and a localized magnetic field is generated during performance of the task.

University of Durham/Simon Fraser/Science Photo Library.

Will TMS completely replace traditional neuropsychological methods? Probably not. For one thing, TMS is restricted in the sites that can be stimulated, that is, those beneath the skull; stimulations elsewhere cannot be studied with TMS. Moreover, the spatial extent of the changes induced by TMS is not fully understood, and it is likely that more distant brain structures receive stimulation if they are connected to the stimulation site (Bestmann & Feredoes, 2013). In contrast, organic lesion localization using MRI is more tried and tested. Another advantage of traditional neuropsychology is that the "accidents of nature" turn up some unexpected and bizarre patterns. For example, some patients can name body parts, but not point to named parts of their body (Semenza & Goodglass, 1985); and some patients can draw a bicycle, but not recognize a drawing of a bicycle (Behrmann et al., 1994). Perhaps these sorts of pattern could also be observed with TMS, but nobody would think to look for them without the patient-based observations. Indeed, the effects of TMS "lesions" are often only observable through

Advantages of TMS over organic lesions	Advantages of organic lesions over TMS
· No reorganization/compensation	· Subcortical lesions can be studied
· Can be used to determine timing of cognition	· Lesions can be accurately localized with MRI (effects of TMS are less well understood spatially)
· Lesion is focal	
· Lesion can be moved within the same participant	· Changes in behavior/cognition are more apparent
· Can study functional integration	

slowed reaction times and not through error rates or the externally observable behavior that characterizes most neurological deficits.

Using TMS to study functional integration

The uses of TMS described so far come within the framework of functional specialization: that is, trying to understand the functional contributions of particular regions to certain aspects of cognition. A complementary approach is functional integration; that is, trying to understand how one region influences another or how one cognitive function influences another. One way in which this is achieved is by undergoing a session of focal TMS and then studying how this affects the communication between brain regions using fMRI (Bestmann & Feredoes, 2013). (Note: for safety reasons TMS cannot be done in the scanner itself without significant modification of the equipment.) Another approach is to use TMS to examine competition between brain regions. If there are different processes competing in the brain, then eliminating one process from the competition (using TMS) might have a beneficial effect on the other.

The brain divides up the visual world into different attributes such as color, shape, and motion, and these different attributes are essentially represented in different regions of the brain (see Chapter 7 for discussion). One theoretical question is: "Do these regions compete with each other, and does attending to one attribute (e.g., motion) have positive or negative consequences for irrelevant attributes (e.g., color)?" To answer this question, Walsh et al. (1998b) presented participants with arrays of different shapes made up of different colors that were either moving or static as shown in Figure 5.14. The task of the participants was to determine whether a prespecified target (e.g., a moving cross, a static cross, a green cross) was present or absent in the array as quickly as possible. TMS was delivered at area V5/MT (specialized for visual motion perception) at a number of different time intervals, but for simplicity, the overall pattern across time only will be discussed here. In the first two examples, motion is needed to discriminate between targets and distractors because relying on shape alone will not help (some Xs move and some Xs are static). Unsurprisingly, a virtual lesion to V5/MT disrupts this visual search, as has been found for organic lesions to this area (McLeod et al., 1989). The unexpected finding comes when there is no motion at all and the participants must find a target based on color and form (a green X). In this instance, a virtual lesion to V5/MT facilitates search efficiency. This suggests that different visual areas may compete with each other, and eliminating an irrelevant visual area can improve the operation of relevant ones.

Practical aspects of using TMS

When designing experiments using TMS (or when evaluating other people's choice of design), there are three main considerations:

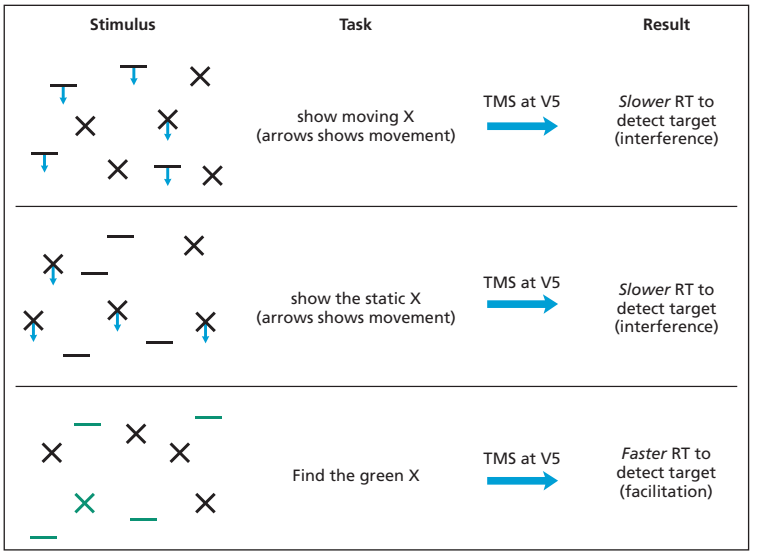

FIGURE 5.14: The participants must search for the presence or absence of a specified target (e.g., moving X) in an array of other items. TMS was applied over area V5/MT (involved in visual motion perception) at various points during search. If motion was relevant to the search task, then performance was impaired, but if motion was irrelevant to the search task, then performance was facilitated.

Adapted from Walsh et al. (1998b).

when to deliver the pulses, where to deliver the pulses, and selection of appropriate control conditions (for a good overview, see Sandrini et al., 2011). Finally, given that the brain is being stimulated, one must be fully aware of safety and ethical considerations when performing TMS experiments.

Timing issues – repetitive or single pulse?

The issue of when to deliver the pulse is crucial to the success, or otherwise, of a TMS experiment. On rare occasions, the time taken for a stimulus to be registered in a given brain region is known by previous research using other techniques. For example, single-cell recordings suggest that it takes 100 ms for a visual stimulus to be registered in the primary visual cortex (area V1), and TMS studies in which a single pulse is delivered close to this critical window can render the subject effectively "blind" to the stimulus (Corthout et al., 1999). On most occasions, timing information such as this will not be known. In this situation, there are a number of options. First, one could make the time of pulse delivery a variable in its own right. For example, if a stimulus is presented for 500 ms, the TMS pulse (or pulses) could be delivered in different time windows (0–50 ms, 50–100 ms, . . . 450–500 ms). This experimental design could thus provide important information about the timing of cognition, as well as providing information about the necessity of that region (Figure 5.15). An alternative solution is to use a train of pulses during the task (i.e., repetitive or rTMS) or to administer the task after a period of stimulation (offline TMS). In these situations, the experiment becomes potentially more powerful in its ability to detect the necessity of a region, but it would not be possible to draw conclusions about timing because it would be unclear which pulse (or pulses) was critical.

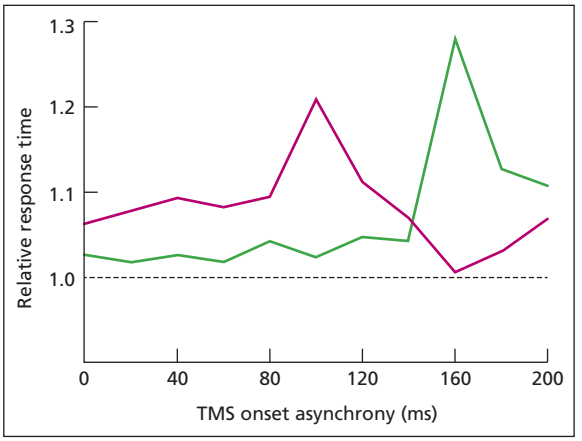

FIGURE 5.15: TMS can be used to establish *when* in a task a given region is critical. In this experiment, participants had to search for a visual target in an array that was either present or absent. TMS applied over the parietal lobes disrupted performance, but only in specific time windows, with present trials occurring earlier (100 ms; purple line) than absent trials (160 ms; green line). A temporal dissociation such as this could not be observed in patients with irreversible organic brain damage.

From Ashbridge et al. (1997). © 1997 Elsevier. Reproduced with permission.

How to hit the spot?

To conduct a TMS experiment, one needs to make some assumptions about which regions of the brain would be interesting to stimulate. In some instances, functional resolution is all that is needed. Just as with the arguments concerning classical versus cognitive neuropsychology, one may wish to establish that a given task/behavior can be selectively disrupted (in which case, the location of the stimulation site is not relevant to the type of conclusion drawn).

Positions on the head can be defined relative to landmarks, such as those used in the EEG system of electrode placement. Skull landmarks include the inion (a bony protrusion at the back of the skull), the anion (the bony ridge between the eyebrows), and the vertex (midway between the anion and inion, and midway between the ears). For example, one published way of approximately locating area V5/MT (dedicated to visual motion perception) is by marking a spot 5 cm in front of the inion and 3 cm up from it (Walsh et al., 1998a). The spot can be physically marked by placing an X on the skin, or by marking the position on a taut swimming cap.

More commonly, structural and functional MRI can also be used to locate candidate regions of stimulation taking into account individual differences in brain anatomy and skull shape (this is called *frameless stereotaxy*). A structural or functional MRI scan can be obtained prior to TMS, and then online digital registration (using specialist software) enables the position on each person's own skull to be identified. This individualized approach produces better results (i.e., larger effect sizes) than placing the TMS coil according to locations determined by skull landmarks or EEG electrode caps (Sack et al., 2009).

What is the appropriate control condition?

Two possible control conditions for TMS experiments have already been considered. First, one can compare performance when the same region is stimulated in critical and non-critical time windows. Second, one can compare stimulation in critical and non-critical regions. Some consideration needs to be given to the selection of the non-critical region. Using regions adjacent to the critical region can provide extra clues about the spatial size of the region of interest. In studies in which there is good reason to believe that the cognitive function is lateralized, one could use the same site on the opposite hemisphere as a control. A further advantage in using the control conditions mentioned previously is that peripheral effects of TMS can be minimized. These include the loud sound

of the pulse and twitches caused by inadvertent stimulation of the facial nerves and muscles. The latter can be more pronounced at some sites and so using adjacent regions or the same region on the opposite hemisphere would minimize this. Sham TMS, in which the coil is held in the air rather than against the head, is not an ideal control condition, and having no TMS at all as a control condition is also not desirable. Another control condition that can be used in TMS experiments is a task control. Thus, the same region can be stimulated at the same times, but with some aspect of the task changed (e.g., the stimuli, the instructions).

ONLINE RESOURCES

For information on jobs, news, and conferences linked to noninvasive brain stimulation, visit neuromodec.com.

Evaluation

TMS is an important addition to the cognitive neuroscientist's toolkit. It is able to ascertain the importance of a given region by stimulating that region during task performance. As such, it is related to other lesion methods that are used for establishing the importance of a given region, but it has certain advantages over the organic lesion method. The main advantage lies in the fact that the interference is short-lived and reversible. It can also be used to explore how regions interact with each other (functional connectivity) and shed light on the timing of cognitive processes.

SAFETY AND ETHICAL ISSUES IN TMS RESEARCH

Researchers need to bear in mind a number of safety issues when conducting TMS experiments. It is essential to be aware of the local regulations that apply in your own institution, but the following points are likely to be important:

- The most recent safety and ethics guidelines come from a consensus of leading researchers in the field that offers guidance on issues such as the number and intensity of pulses (Rossi et al., 2021).
- Whereas single-pulse TMS is generally considered to be safe, repetitive-pulse TMS carries a very small risk of inducing a seizure (Wassermann et al., 1996). Given this risk, participants with epilepsy or a familial history of epilepsy are normally excluded. Participants with pacemakers and medical implants should also be excluded. Credit cards, computer discs, and computers should be kept at least 1 m away from the coil.
- The intensity of the pulses that can be delivered is normally specified with respect to the "motor threshold"; that is, the intensity of the pulse, delivered over the motor cortex, that produces a just noticeable motor response.
- During the experiment, some participants might experience minor discomfort due to the sound of the pulses and facial twitches. Although each TMS pulse is loud (~100 dB), the duration of each pulse is brief (1 ms). Nonetheless, it is mandatory to protect the ears with earplugs or headphones. When the coil is in certain positions, the facial nerves (as well as the brain) may be stimulated, resulting in involuntary twitches (e.g., blinking, jaw clamping). Participants should be warned of this and

told they can exercise their right to withdraw from the study if it causes too much discomfort.

- It is generally believed that a single session of TMS has no long-term consequences. However, repeated participation in experiments could conceivably have longer-term effects – either positive or deleterious. A meta-analysis shows that TMS, relative to sham, can improve symptoms of depression in people who have previously been resistant to pharmacological treatments, although the length of the benefits was unknown (Gaynes et al., 2014). Except in cases of therapeutic intervention, it is good practice not to test the same participants many times over a short interval.

KEY TERMS

Transcranial direct current stimulation (tDCS)
Noninvasive stimulation of the brain caused by passing a weak electrical direct current through it.

Transcranial alternating current stimulation (tACS)
Noninvasive stimulation of the brain caused by passing a weak electrical alternating current through it; the frequency of the alternations can interact with the brain's own rhythmical activity.

Transcranial random noise simulation (tRNS)
Noninvasive stimulation of the brain caused by passing a weak electrical current through it, which fluctuates in direction and amplitude.

Cathodal tDCS
Decreases cortical excitability and decreases performance.

Anodal tDCS
Increases cortical excitability and increases performance.

TRANSCRANIAL ELECTRICAL STIMULATION (tES)

The use of electrical currents to stimulate the brain has a long and checkered history, with the most notorious noninvasive method being electro-convulsive therapy (ECT) which is now restricted to a small number of psychiatric patients who are unresponsive to other treatments.

Unlike ECT, the methods of transcranial electrical stimulation (tES) use a very weak electric current passed between two stimulating pads. The current can either flow in one direction **(transcranial direct current stimulation, tDCS)**, or it can rhythmically alternate in direction **(transcranial alternating current stimulation, tACS)**, or the current can randomly change direction **(transcranial random noise stimulation, tRNS)**. This is shown in Figure 5.16. tDCS is the most common of these approaches in cognitive neuroscience.

Transcranial direct current stimulation (tDCS)

Direct current involves the flow of electric charge from a positive site (an anode) to a negative site (a cathode). In tDCS, a stimulating pad (either anodal or cathodal) is placed over the region of interest, and the control pad is placed in a site of no interest (sometimes on the front of the forehead, or sometimes on a distant site such as the shoulders) – see Figure 5.17. After a period of stimulation (e.g., 10 min) a cognitive task is performed. This stimulation can be compared with sham stimulation, or anodal and cathodal stimulation can be directly contrasted. **Cathodal tDCS** stimulation tends to disrupt performance (i.e., it is conceptually equivalent to a virtual lesion approach), whereas **anodal tDCS** stimulation tends to enhance performance (Nitsche et al., 2008). For example, anodal stimulation over the visual cortex leads to an enhanced early visual ERP component (N100) and enhances the ability to detect weak visual stimuli, whereas cathodal stimulation has the opposite effects (Accornero et al., 2007; Antal et al., 2001). This is shown in Figure 5.18.

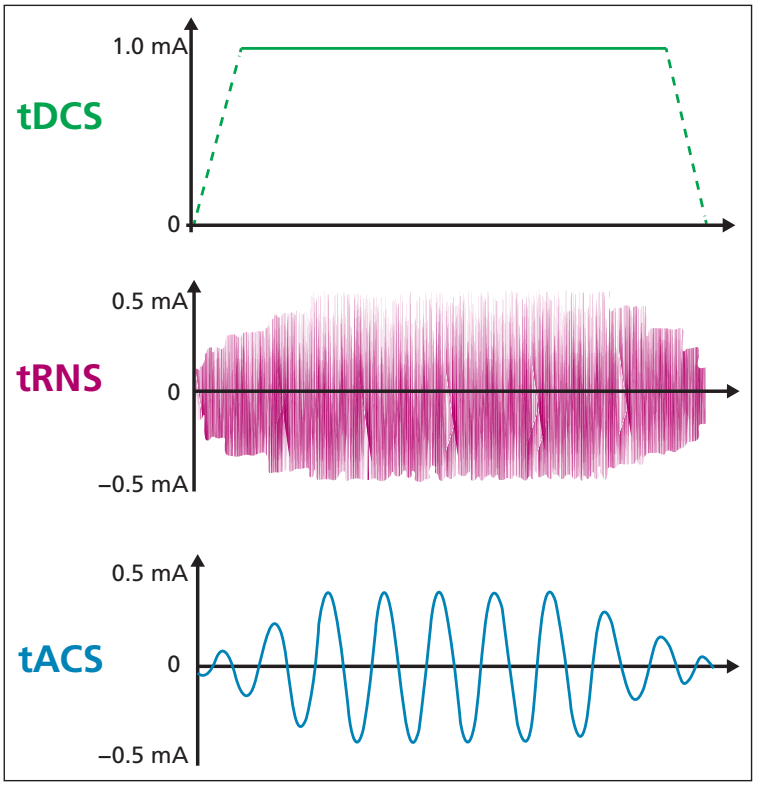

FIGURE 5.16: In transcranial electrical stimulation (tES) methods, electrical current is passed between two stimulating pads. The direction of the current can be constant (tDCS), or can vary randomly (tRNS), or can alternate rhythmically (tACS).

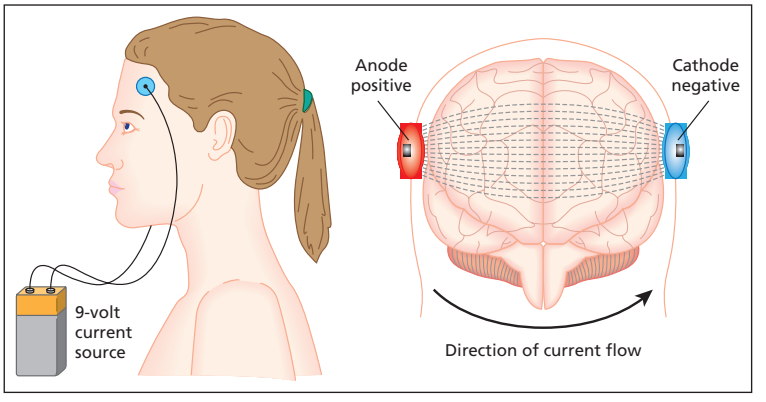

FIGURE 5.17: The method of tDCS uses a very weak electric current applied using stimulating pads attached to the scalp. Direct current involves the flow of electric charge from a positive site (an anode) to a negative site (a cathode).

Adapted from George and Aston-Jones.

ONLINE RESOURCES

Check out the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience) for videos of a series of lectures at UC Davis on brain stimulation, particularly the newer method of tDCS.

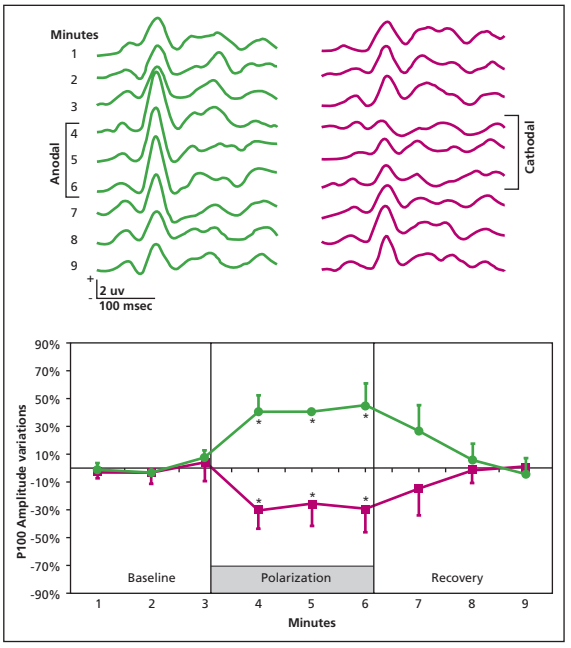

FIGURE 5.18: tDCS applied over the visual cortex (for 3 min) disrupts the amplitude of an ERP component (P100) elicited in response to viewing a black and white checkerboard. Anodal stimulation increases the amplitude, but cathodal stimulation reduces it.

From Accornero et al. (2007).

Stagg and Nitsche (2011) provide a summary of the likely neurophysiological mechanisms. It is important to consider the immediate effects of direct current stimulation and the aftereffects separately. Animal models of direct current stimulation followed by single-cell recordings have shown that anodal stimulation increases the spontaneous firing rate of neurons, whereas cathodal stimulation reduces the firing rate. The *immediate* effects of stimulation are believed to occur on the resting membrane potential rather than modulation at the synapse. However, the *aftereffects* of stimulation are likely to occur because of changes in synaptic plasticity influencing learning and perhaps affecting different neurotransmitter systems. Anodal stimulation of motor cortex affects the GABA system (this neurotransmitter has inhibitory effects), whereas cathodal stimulation affects the glutamate system (this neurotransmitter has excitatory effects). However, this may not generalize to other brain regions (Heimrath et al., 2020).

The current safety guidelines recommend upper limits on the size of the current and the surface area of the stimulating electrodes (Antal et al., 2017). If the current is concentrated on a small electrode, then it can cause skin irritation. However, unlike TMS, participants often cannot tell whether the machine is switched on or used as sham (there is no sound or twitching). As such, there is very little discomfort.

Repeated sessions of anodal tDCS are becoming increasingly used for cognitive enhancement (of normal brains) and neurorehabilitation (of damaged brains). For instance, repeated sessions of tDCS over the primary motor cortex lead to increased cortical excitability and greater hand functionality in patients with motor impairments following stroke (Hummel et al., 2005). In this study, the treatment was compared with sham and the procedure was double blind (i.e., neither participant nor experimenter knew which condition they were in). Other studies using anodal tDCS have reported improvements in language following stroke (Monti et al., 2008) and improved working memory in patients with Parkinson's disease (Boggio et al., 2006).

Transcranial alternating current and random noise stimulation (tACS, tRNS)

The same experimental setup as described for tDCS is used for tACS and tRNS, but because the direction of the current shifts back and forth, the stimulating pads continually change their status between anodal and cathodal.

Chapter 3 discussed how groups of neurons tend to fire rhythmically (at frequencies termed alpha, beta, gamma, etc.) and that this synchrony might be one way of facilitating communication between different neural populations. These naturally occurring rhythms are *measured* with EEG (or MEG). tACS would be the comparable method for *stimulating* these neural rhythms as opposed to just measuring them. By applying tACS over the visual cortex it is possible to induce phosphenes which are perceived as flickering lights (Kanai et al., 2008). Importantly, these phosphenes are only induced when tACS is applied at certain frequencies (the beta range in natural light conditions, the alpha range in dark), suggesting a causal interaction between the stimulated activity and the intrinsic rhythmic activity of the brain – see Figure 5.19.

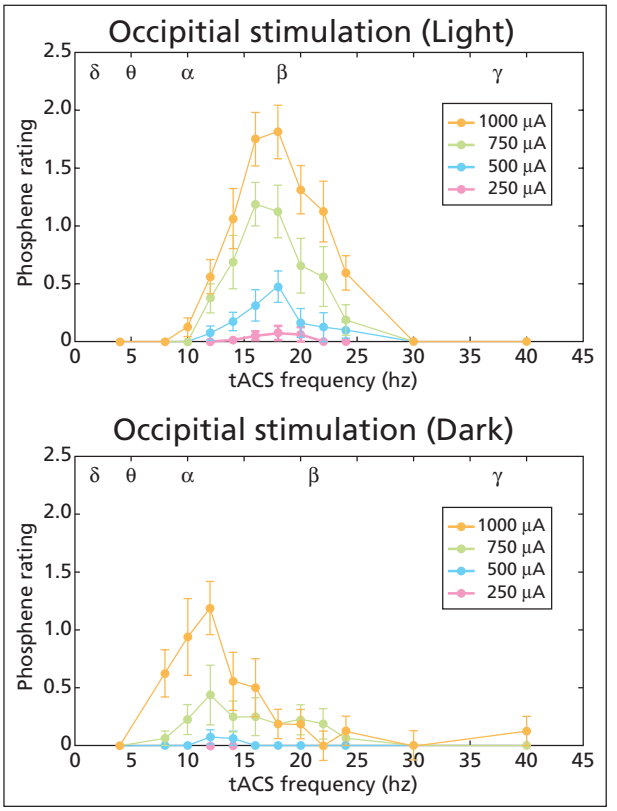

FIGURE 5.19: Transcranial alternating current stimulation (tACS) over the visual cortex can induce flickering phosphenes, but only when the current alternates at certain frequencies (the beta range during light conditions, and alpha during dark).

From Kanai et al. (2008).

tRNS is least well understood in terms of its mode of action. Intuitively, one might expect that adding electrical noise to neural activity would have a disruptive influence on cognition. However, moderate amounts of noise seem to increase cognitive performance similarly to anodal tDCS (Polania et al., 2018). For instance, moderate amounts of noise applied with tRNS to the occipital cortex enhance the ability to detect weak visual stimuli (van der Groen & Wenderoth, 2016). The explanation for this is that moderate amounts of noise can act to boost weak neural signals above a threshold for detection.

Evaluation

tES can be used to manipulate brain function in several ways in order to study the causal link between brain and cognition. It can act as a "virtual lesion" (cathodal tDCS), or it can interact with the natural rhythmic electrical activity of the brain (tACS), or it can be used to enhance cognitive function (anodal tDCS and possibly tRNS).

SUMMARY AND KEY POINTS OF THE CHAPTER

- A double dissociation between two patients occurs when patient 1 is significantly better than patient 2 on task A, and patient 2 is significantly better than patient 1 on task B. The standard interpretation of this is that task A and task B utilize some different neural resources.

- The use of single cases has led to important insights into the way in which cognitive components are organized and may be fractionated.
- Group studies of patients are important for making links between lesion location and behavioral deficits and provide an important source of converging evidence for functional imaging data.
- Transcranial magnetic stimulation (TMS) works by stimulating a region of cortex placed beneath a current-carrying coil. This stimulation temporarily interferes with ongoing cognitive activity in that region and, therefore, provides information about the necessity of that region for performing the task. This has been termed a "virtual lesion."
- Transcranial direct current stimulation (tDCS) has a poorer temporal and spatial resolution to TMS, but has the advantage of being able to facilitate cognitive function (anodal tDCS).
- Transcranial alternating current stimulation (tACS) can induce rhythmic neural activity in a brain region (e.g., to explore its effect on cognition).

EXAMPLE ESSAY QUESTIONS

- What assumptions must one accept to be able to draw inferences about normal cognition from adults with brain damage? Are these assumptions plausible?
- Critically evaluate the role of group studies in neuropsychological research.
- What are the advantages and disadvantages of using single cases to draw inferences about normal cognitive functioning?
- How have TMS and tDCS studies contributed to our knowledge of brain plasticity?
- Compare and contrast lesion methods arising from organic brain damage with TMS and tES.

ONLINE RESOURCES

Visit the Instructor & Student Resources website at routledgelearning.com/wardcognitiveneuroscience for:

- Video lectures and interviews on key topics with leading experts and author Jamie Ward, as well as demonstrations of and lectures on brain stimulation
- Multiple-choice questions and interactive flashcards to test your knowledge

CHAPTER 6

The developing brain

CONTENTS

Many people are drawn into a subject like psychology because of one nagging question: What makes us who we are? Were we predestined to become the person we are today as a result of our genetic endowment? If so, could a parent of the late twenty-first century be reading their child's genetic "blueprint" to figure out their cognitive strengths and weaknesses, their personality and temperament? Or are we shaped by our experiences and circumstances during life and during our formative years of development? These questions are central to the **nature-nurture debate**, that is, the extent to which cognition and behavior can be attributed to genes or environment. While the nature-nurture debate still has contemporary relevance and continues to excite both scientists and laypeople, this chapter will consider how many of the commonly held assumptions surrounding this debate are misguided. For example, genes do not provide a predetermined blueprint but are themselves switched on and off by the environment, and the contemporary notion of "environment" is far broader than is commonly understood. It includes biological circumstances (e.g., diet, exposure to toxins), as well as personal and social circumstances.

Historically, the pendulum has swung between opposing extremes of this debate. For example, in 1874, Francis Galton published *English Men of Science: Their Nature and Nurture*, arguing that geniuses are born and not made. As well as coining the phrase "nature or nurture," he was the first person to realize that heredity could be estimated by comparing identical and nonidentical twins.

DOI: 10.4324/9781003429975-6

KEY TERMS

Nature–nurture debate
The extent to which cognition and behavior can be attributed to genes or environment.

Neuroconstructivism
A process of interaction between environment and brain-based constraints that leads to the mature cognitive system emerging out of transformations of earlier ones (but does not assume discrete stages).

Galton's advocacy of nature over nurture would become associated with the discredited eugenics movement, which promoted selective breeding of the more cognitively able (although in practice this was often implemented by sterilization of the "feeble-minded").

In the early twentieth century, the pendulum had swung to the other extreme. Freudian theory, for example, emphasized the importance of early experiences and parenting style in development. The Russian psychologist Lev Vygotsky (1896–1934) also emphasized the role of culture and interpersonal communication in development. Behaviorist theories, such as those put forward by B. F. Skinner (1904–1990), argued that all behavior was a product of learning as a result of rewards and punishments.

Jean Piaget (1896–1980) is regarded as the founding father of modern Western developmental psychology. Piaget took a middle ground with regards to the nature-nurture debate. He regarded development as a cyclical process of interactions between the child and his or her environment (Figure 6.1). Each cycle was conceptualized as a stage in development. In his view, the genetic contribution consists of developing a brain that is readied to learn in certain ways, but progression to the next stages involves assimilating evidence from the environment and then developing new mechanisms in light of the feedback obtained. While many of Piaget's experimental studies have not stood the test of time (e.g., children show evidence of reasoning long before Piaget suggested they should), his basic approach to development has been more enduring.

FIGURE 6.1: In Piaget's sensorimotor stage (0–2 years), a child learns about the nature of objects (e.g., that they still exist when hidden) and about the nature of cause and effect (e.g., that actions have consequences on the objects around). The child then passes through other stages (preoperational, concrete, and formal operational) with greater degrees of abstraction. Although the stages can be regarded as fixed and predetermined, Piaget stressed the role of the environment to successfully develop the cognitive processes required for the next stage.

Following on from the developmental psychology tradition, developmental cognitive neuroscience has focused on brain-based explanations of developmental change (Johnson, 2005). One particular current approach is termed **neuroconstructivism** (Westermann et al., 2007). Like Piaget's approach, this assumes constant interaction between environment and genetic factors, with a mature cognitive system emerging out of transformations of earlier ones. Unlike Piaget's approach, the predetermined aspect of development is construed in terms of multiple, brain-based constraints (developmental changes in synapse formation, myelination, etc.), rather than the less well-defined notion of predetermined "stages."

This chapter will first consider the structural development of the

brain, both prenatally and postnatally. It will then go on to consider the nature of developmental change, including evidence for critical/sensitive periods and innate knowledge. An overview of the origin of genetic differences and behavioral genetics will then explore some specific examples of genetic influences in developmental cognitive neuroscience. Together with the advances made in molecular genetics, it is now becoming possible to understand how genetic influences and experience create changes in the structure and function of the brain. This is leading to an exciting rethink of the nature-nurture debate.

ADAPTING THE METHODS OF COGNITIVE NEUROSCIENCE FOR INFANTS AND CHILDREN

Methods such as fMRI and EEG are generally considered suitable for infants and children. One advantage of using these methods in younger people is that they do not necessarily require a verbal or motor response to be made.

Functional MRI

Cusack et al. (2018) provide an overview of some of the considerations needed. If one wants to compare across different ages, then the most significant problem is that the structural properties of the brain change during development. Although the volume of the brain is stable by about 5 years of age, there are differences in white and gray matter volumes until adulthood (Reiss et al., 1996). The hemodynamic response function is relatively stable after 7 years of age but differs below this age (Marcar et al., 2004). The differences in both brain structure and blood flow make it harder to compare activity in the same region across different ages. Younger children also find it harder to keep still in the scanner, and this motion can disrupt the reliability of the MR signal.

Functional near-infrared spectroscopy (fNIRS)

One relatively new method that is now being used in developmental cognitive neuroscience is functional near-infrared spectroscopy (fNIRS) (e.g., Lloyd-Fox et al., 2010). This measures the amount of oxygenated blood and is – like fMRI – a hemodynamic method. Unlike fMRI, it accommodates a good degree of movement and is more portable. The infant can sit upright on their parent's lap. However, it has poorer spatial resolution and does not normally permit whole-head coverage.

ERP/EEG

When working with young participants using ERP/EEG, a limiting factor is the child's willingness to tolerate the electrodes, the task, and the time commitment required (Thomas & Casey, 2003). Children and adults can show quite different patterns of ERP (e.g., in terms of latency, amplitude, or scalp distribution), even for tasks that both groups find easy (Thomas & Nelson, 1996), as shown in Figure 6.2. These could either reflect age-related cognitive differences (i.e., the same task can be performed in different ways at different ages) or non-cognitive differences (e.g., the effects of skull thickness, cell packing density, or myelination).

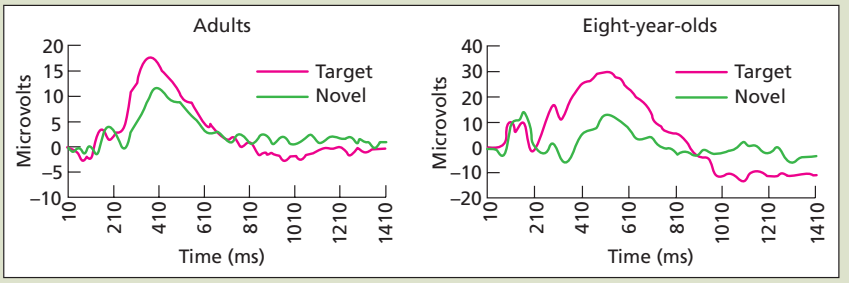

FIGURE 6.2: Adults and children show very different visual ERP waveforms, despite having equivalent behavioral performance.

Adapted from Thomas and Nelson (1996).

Brain stimulation: TMS and tES

Single and paired pulse TMS is considered to pose minimal risk in children (Gilbert et al., 2004), although *repetitive* TMS isn't recommended except for compelling therapeutic purposes (e.g., treatment of depression; Gaynes et al., 2014). Transcranial electrical stimulation (tES) is not believed to pose any greater risks or side-effects in children relative to adults (Krishnan et al., 2015) and has been used in conjunction with cognitive training to treat certain learning difficulties (Krause & Kadosh, 2013).

STRUCTURAL DEVELOPMENT OF THE BRAIN

One common idea is that the genetic code provides a blueprint for the structure of the brain. At some gross level, this must be true: all human brains are similar to each other but differ from the brains of other species. This reflects our different genetic makeup. However, the term "blueprint" is misleading as it suggests that structural details of individual brains are specified at a very fine level of detail. However, it is inconceivable that the genetic code contains a detailed wiring diagram of the brain (recall that the human brain has 86 billion neurons each with 10,000 connections, which generates a number far larger than the genome itself). Instead of the blueprint analogy, one could instead imagine the genetic code more like a recipe for making a brain. Gottlieb (1992) makes a distinction between two key ideas in development which he termed predetermined development versus probabilistic development. In *predetermined development*, genes dictate the structure of the brain, which enables the particular functions of the brain, which determines the kinds of experiences we have. This is a traditional view of how genes affect cognition. Gottlieb contrasts this with *probabilistic development* in which brain structure, and even the expression of genes, can be influenced by experience as well as vice versa. Also, the effects of genes on brain structure are themselves probabilistic (irrespective of any environmental influences) such that they specify *approximately* how many neurons to grow, and

where to grow them, but not exactly how/where neurons will grow (Hassan & Hiesinger, 2015). Thus, the same genetic program run in the same environment would not produce an exact carbon copy but, instead, some kind of variation on a theme. This is perhaps a more realistic way of understanding "identical" twins (monozygotic, MZ) who, we shall see, have very similar but not identical brains.

Probabilistic development represents the dominant view in modern developmental cognitive neuroscience, and the next sections will unpack this concept in more detail.

GOTTLIEB'S (1992) DIFFERENT VIEWS OF DEVELOPMENT

Predetermined development:

Genes → Brain structure → Brain function → Experience

Probabilistic development:

Genes ↔ Brain structure ↔ Brain function ↔ Experience

Prenatal development

The human gestation period is around 38 weeks from conception. The newly formed embryo undergoes a rapid process of cell division, followed by a process of differentiation during which the different cells become increasingly specialized (Figure 6.3). The nervous system derives from a set of cells arranged in a hollow cylinder, the **neural tube**. By around five weeks, the neural tube has organized into a set of bulges and convolutions that will go on to form various parts of the brain (e.g., the cortex, the thalamus and hypothalamus, the midbrain). Closer to the hollow of the neural tube are several proliferative zones in which neurons and glial cells are produced by division of proliferating cells (**neuroblasts** and glioblasts). Purves (1994) estimates that the fetal brain must add 250,000 neurons per minute at certain periods in early development.

The newly formed neurons must then migrate outwards toward the region where they will be employed in the mature brain. This occurs in two ways. Passively, older cells tend to be pushed to the surface of the brain. Structures such as the hippocampus are formed this way. There is also an active mechanism by which newer cells are guided to particular destinations, pushing past the older cells. Rakic (1988) identified **radial glial cells** that act like climbing ropes, ensuring that newly formed neurons are guided to their final destination. The convoluted surface of the brain, the neocortex, is formed in this way.

Regional differences in various molecular signals affect the neurons' structure, migration, and survival (see Sur & Rubenstein, 2005). Different doses of these signals determine the di-

KEY TERMS

Neural tube
The embryo's precursor to the central nervous system, consisting of a set of cells arranged in a hollow cylinder.

Neuroblasts
Stem cells for neurons.

Radial glial cells
Support cells that guide neurons from the neural tube to their final destination.

ONLINE RESOURCES

Visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience) for an animated video showing the earliest stages of the formation of neurons and the brain.

mensions of the various lobes of the brain, such that, for example, a dose above a certain threshold may instruct a new neuron to develop features characteristic of a frontal lobe neuron (e.g., in terms of its connectivity) but below that dose it may resemble a parietal neuron (Fukuchi-Shimogori & Grove, 2001). This suggests a simple mechanism for creating individual differences in brain structure and also for evolutionary development (e.g., a shifting dose could enable an evolutionary jump in frontal lobe enlargement).

The highly folded cortex is a clearly distinguishable feature of the human brain. It is visible in the last few months before birth and shows further small changes over the first two years of life (Li et al., 2014). This folding is likely to be an outcome of packing more neurons within a restricted space together with stretching the cortical surface by axonal tension (as opposed to the cortical shape being specified directly by the genome). Genetic mutations in mice that lead to overproduction of neurons also lead to the development of a more convoluted cortical surface (Haydar et al., 1999). Van Essen (1997) has proposed that the overall pattern of cortical gyri and sulci is linked to the development of axon bundles (e.g., such as those shown previously in Figure 2.4), which places the cortical surface under tension. In effect, the axons are like elastic bands that pull the cortical sheet in particular directions, giving it a characteristic shape but also allowing for variability across individuals. Axon guidance, like neural migration, is also affected by the regional concentration of different molecular signals that attract/repel different axons, ultimately biasing how/where they form (McLaughlin & O'Leary, 2005). DTI of infants born prematurely (at 30 weeks after conception, instead of 38 weeks) show that the major white matter tracts are in place at 30 weeks but continue to develop a more fine-grained pattern over the subsequent 10 weeks (Ball et al., 2014). Although the gyral pattern is broadly similar across individuals, there is variability, and twin studies suggest that gyrification is far less heritable than, for instance, brain volume (Bartley et al., 1997).

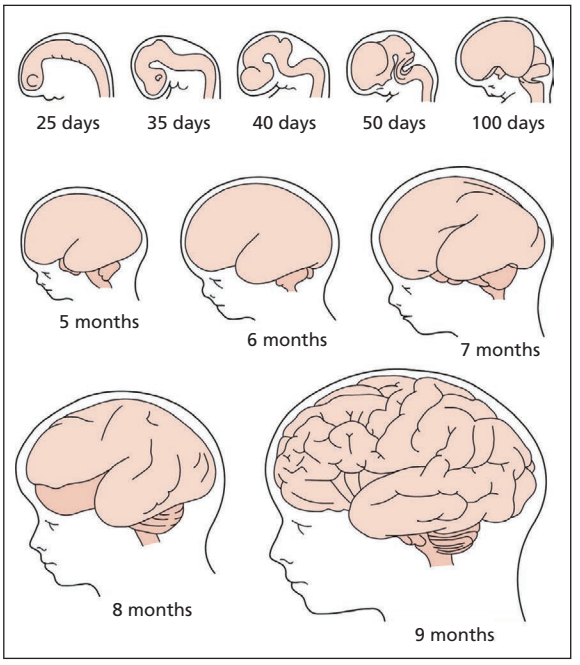

FIGURE 6.3: The embryonic and fetal development of the human brain. Cortical asymmetries between the left and right hemispheres, implicated in language acquisition, are present at 24 weeks.

From Cowan (1979). © 1979 by Scientific American, Inc. All rights reserved.

Finally, although prenatal neurons have very limited functional inputs from the environment, they can still show spontaneous electrical ac-

tivity. These enable networks to form in the brain on the basis of **Hebbian learning** ("what wires together fires together"). For instance, spontaneous waves of electrical activity emanating from the retina (but not triggered by light) are important for setting up synaptic pathways from the eyes to the lateral geniculate nucleus and the visual cortex in readiness for the processing of visual stimuli (Katz & Shatz, 1996).

KEY TERM

Hebbian learning
Strengthening of a synapse that occurs when the presynaptic and postsynaptic neurons are active at the same time ("what wires together fires together").

Postnatal development

At birth, the head makes up approximately a quarter of the length of the infant. Although the brain itself is small (450 g) relative to adult human size (1,400 g), it is large in comparison to remote human ancestors and living primates (a newborn human brain is about 75 percent of that of an adult chimpanzee). The vast majority of neurons are formed prior to birth, so the expansion in brain volume during postnatal development is due to factors such as the growth of synapses, dendrites, and axon bundles; the proliferation of glial cells; and the myelination of nerve fibers.

Huttenlocher and Dabholkar (1997) measured the synaptic density in various regions of human cortex (Figure 6.4). This is a measure of the degree to which neurons are connected to each other and is unrelated to the number of neurons per se or how active the synapses are. In all cortical areas studied to date, there is a characteristic rise and then fall in synapse formation (synaptogenesis). In primary visual and primary auditory cortex, the peak density is between 4 and 12 months, at which point it is 150 percent above adult levels, but it falls to adult levels between two and four years. In the prefrontal cortex, the peak is reached after

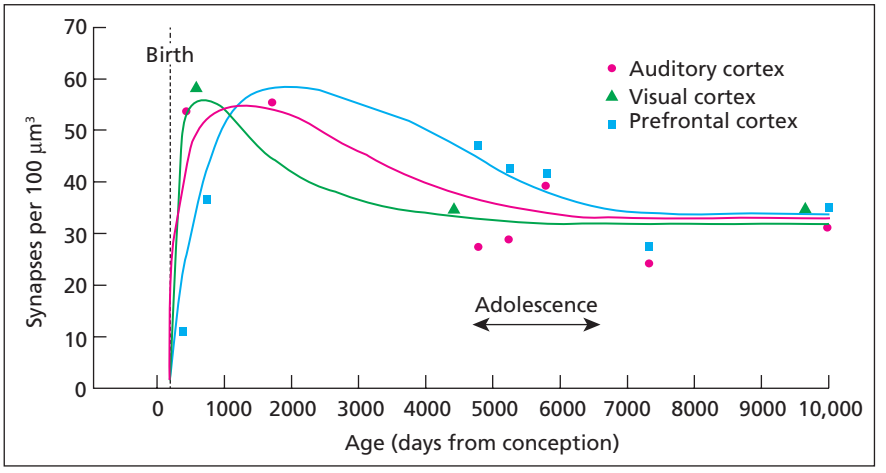

FIGURE 6.4: Synapse formation has a rise-and-fall pattern. It peaks soon after birth, although different cortical regions differ greatly in the time taken to fall again to adult synaptic levels.

From Huttenlocher and Dabholkar (1997). Reprinted with permission of John Wiley & Sons Inc.

12 months, but it does not return to adult levels until 10–20 years old. PET studies of glucose metabolism in developing brains show a similar rise and fall to studies of synaptogenesis, although the time taken to reach the peak tends to be somewhat later (Chugani et al., 1987). Glucose metabolism may be a measure of actual neural activity rather than neural structural changes. Why does the number of synapses fall during the course of development? It is not necessarily the case that more synapses reflect more efficient functioning. During development a process of fine-tuning the brain to the needs of the environment renders some connections redundant. For example, young infants can discriminate all the speech sounds (phonemes) of the world but lose this ability as they become tuned to their native language (Werker & Tees, 1984).

KEY TERMS

Myelination
An increase in the fatty sheath that surrounds axons and increases the speed of information transmission.

Plasticity
The brain's ability to change as a result of experience.

Myelination refers to the increase in the fatty sheath that surrounds axons and increases the speed of information transmission. In structural MRI, the increase in white matter volume over the first two decades of life may reflect the time course of myelination (Giedd et al., 1999). Again, the prefrontal cortex is one of the last areas to achieve adult levels of myelination, and this, together with the late fine-tuning and elimination of synapses in this region, may contribute to the development of mature social behavior during adolescence and the control of behavior in general.

Following birth, all of our everyday experiences result in tiny changes to the structure of our brain, in the form of altering the pattern of synaptic connections. Sometimes these changes are even visible at the macroscopic level. Adults who learn to juggle with three balls over a three-month period show increased gray matter density, assessed with MRI, in a region, V5/MT, specialized for detecting visual motion as well as the occipitoparietal region implicated in hand-eye coordination (Draganski et al., 2004) (Figure 6.5). This example illustrates a central concept of this chapter – namely, **plasticity**. Plasticity refers to experience-dependent changes in neural functioning. Similar findings are noted elsewhere in the book due to the spatial memory demands of driving a taxi (Maguire et al., 2000), or acquiring musical expertise (Bermudez et al., 2009). However, whilst one might intuitively expect a positive relationship between individual differences in ability and local increases in gray matter, this is not always the case. Thus, congenitally blind people have more gray matter than sighted people in their visual cortex (Jiang et al., 2009), and people with congenital amusia, linked to problems in pitch perception, have more gray matter in their auditory cortex (Hyde et al., 2007). (The term congenital means from birth onwards.) Thus, one can't take gray matter density/thickness as a simple proxy of cognitive ability as it depends on the underlying mechanisms: developmental pruning of synapses (thinner is better) or learned expertise-dependent changes (thicker is better).

Zatorre et al. (2012) discuss the potential cellular and molecular mechanisms that could underpin experience-related structural changes that are visible with MRI in humans (VBM approaches for gray matter, and DTI for white matter). First of all, they suggest that neurogenesis

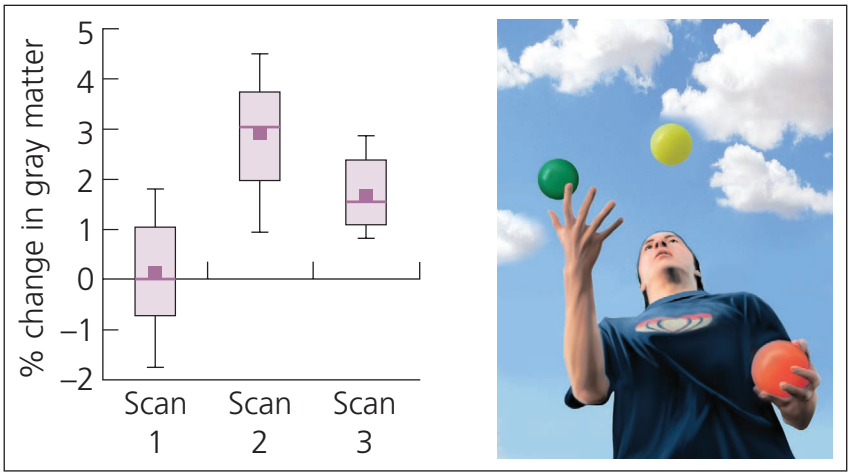

FIGURE 6.5: MRI scans were obtained at three time intervals: before learning to juggle, after three months of training, and after a further three months of no practice. The graph shows increases in gray matter density in an area associated with visual motion perception, area V5/MT.

Draganski et al. (2004). Reproduced with permission from Springer Nature

is an unlikely candidate outside of the hippocampus. However, growing more dendritic branches, synapses or axon collaterals could increase gray matter density. Glia cells can also divide or change in size or structure which could contribute to both gray matter and white matter volume, as could changes to the capillary vasculature. With regards to fractional anisotropy (in DTI), this could increase as a result of axons becoming more aligned or more myelinated.

Evaluation

Although the gross anatomical features of our brain are driven by our genes (e.g., making a human brain versus making the brain of another species), there are limits to what our genes can do. This reflects both a positive influence of the environment (including our own behaviors) but also the fact that the genetic information for constructing a brain is imprecise and, hence, variable. This is consistent with Gottlieb's (1992) idea of probabilistic development.

FUNCTIONAL DEVELOPMENT OF THE BRAIN

Having considered how brain *structure* is changed during development, the present section is primarily concerned with how brain *function* (i.e., different types of ability and knowledge) changes developmentally. In particular, several broad issues will be considered: first, the extent to which brain function is altered by major structural changes, the role of critical/sensitive periods in development, and finally, the extent to which any kind of knowledge or ability can be said to be innate.

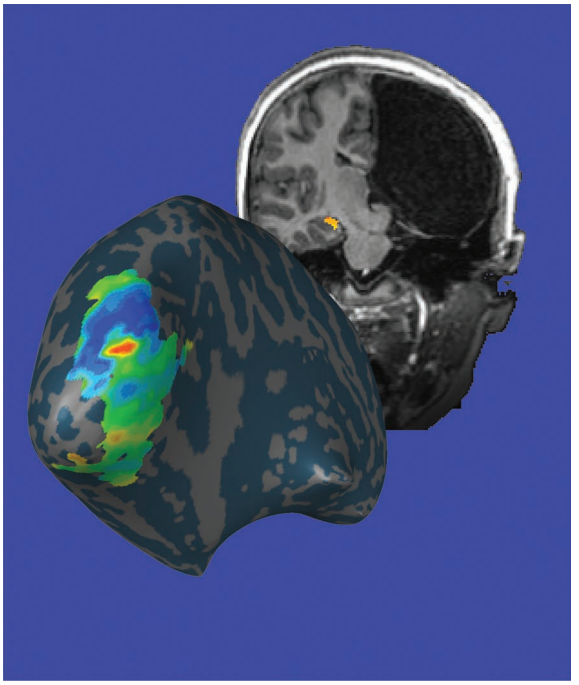

FIGURE 6.6: The structural MRI scan of a 10-year-old girl who failed to develop a right hemisphere in the womb, showing the intact LGN in the left hemisphere (yellow). Front: fMRI brain activity in her intact left visual cortex to stimuli presented in both the right visual field (green-blue) and – unusually – the left visual field (yellow-red).

From Muckli et al. (2009).

Functional brain plasticity in rewired brains

The previous section introduced the idea that whilst early development of the brain is influenced by genes, there isn't a genetic blueprint for how, exactly, each individual brain will turn out. One consequence of this is that, in the face of some major insult, the brain may be capable of reorganizing itself in some fundamentally different ways. Consider the case of AH, a 10-year-old girl, who failed to develop a right hemisphere and right eye prenatally but had only very minor visual impairments (Muckli et al., 2009). Detailed fMRI scanning revealed that visual information that would normally cross the optic chiasm into the "missing" hemisphere could be rerouted into the intact (ipsilateral) hemisphere. Neurons coding left and right sides of space were inter-mingled within the same cortical map where they are normally segregated into the different hemispheres (Figure 6.6).

In nonhuman animals, it is possible to surgically transplant a region of cortex or sever pathways such that novel ones emerge. In these extreme instances, it is possible to explore how these major structural changes impact on neural function and behavior. Prenatal visual cortex transplanted into somatosensory cortex responds to touch on a mouse's whiskers and reconnects to the somatosensory region of the thalamus (Schlagger & O'Leary, 1991). If the pathway from the cochlear to the medial geniculate nucleus (MGN) is severed in a ferret, then visual inputs (from the retina) spontaneously reroute themselves into the MGN (Sur et al., 1988). The consequence of this is that visual input into the eyes ultimately leads to activity in the auditory cortex (as well as visual cortex). Interestingly, these "auditory" neurons take on functional characteristics of visual neurons such as preferential responding to different orientations and movement directions (Sharma et al., 2000; Sur et al., 1988).

Studies such as these show that there is a high degree of structural and functional plasticity in the early brain. However, it doesn't mean that all neurons are fully interchangeable. Spontaneous patterns of activity prior to birth are already shaping neural activity and parcellating them into different networks (Katz & Shatz, 1996). In the previous example, visually rewired "auditory" cortex still retains vestiges of normal auditory cortex

connections, and the visual representations are poorer than those found in true visual cortex (Sharma et al., 2000). Moreover, these kinds of opportunities for major reorganization appear to be strictly time-limited. The next section considers in more detail the notion of critical/sensitive time periods for functional brain development.

RECOVERY OF FUNCTION AFTER EARLY BRAIN DAMAGE

Although strokes are rare in infancy and childhood, they do occur. Typically, however, the long-term effects on cognition are neither as severe nor as specific as those arising from strokes in adulthood. This is consistent with the view that plasticity and recovery is greatest earlier in life, often referred to as the **Kennard Principle** after the neurologist Margaret Kennard (Dennis, 2010). Several studies have found that children who had strokes around the time of birth go on to develop intellectual and language skills in the normal range (Aram & Ekelman, 1986; Ballantyne et al., 2008). With regards to language, it is often found that early lesions to the left hemisphere can result in later right hemisphere language as assessed using fMRI (Liegeois et al., 2004). In this study, even lesions outside of "classical" language areas (e.g., Broca's area) were just as likely to result in right hemispheric language consistent with the view that functional specialization of regions emerges gradually and in a way that is not completely predetermined. Given that the brain has very limited scope to grow new neurons, one may wonder whether accommodating language in the right hemisphere would have a detrimental outcome on traditional right hemispheric functions (e.g., visuo-spatial skills). There is some evidence for this. Lidzba et al. (2006) report that the extent of right hemispheric language (assessed by fMRI) resulting from early stroke correlated negatively with performance on visuo-spatial tasks (i.e., greater right hemisphere language is associated with poorer visuo-spatial skills). This suggests that, while early plasticity can aid recovery, this may not be completely without a cost.

Critical and sensitive periods in development

In 1909, a young Austrian boy named Konrad Lorenz and his friend (and later wife), Gretl, were given two newly hatched ducklings by a neighbor. The ducklings followed them everywhere, apparently mistaking them for their parents (see Figure 6.7). This process, now termed **filial imprinting**, was studied intensively by the adult Lorenz using goslings and earned him a Nobel Prize (see Tinbergen, 1951). Lorenz observed that there was a narrow window of opportunity, between 15 hours and 3 days, for a gosling to imprint. Once imprinted, the gosling is practically unable to learn to follow a new foster parent. The movement of a stimulus was deemed to be crucial for determining what object the gosling will imprint to. A region of the chick forebrain known as intermediate and medial of the hyperstriatum ventrale (IMHV), which may

KEY TERMS

Kennard principle
The idea that the earlier brain damage is sustained, the better the functional outcome.

Filial imprinting
The process by which a young animal comes to recognize the parent.

FIGURE 6.7: These goslings follow the Austrian professor, Konrad Lorenz, as if he is their mother! This process is called filial imprinting.

correspond to mammalian cortex, is critical for enabling imprinting (Horn & McCabe, 1984).

The studies in the previous section suggest that there is a **critical period** for imprinting. A critical period has two defining features: first, learning can only take place within a limited time window; and, second, the learning is hard to reverse in the face of later experience. Subsequent evidence suggests that the window of opportunity can be extended by lack of suitable early experience (e.g., initial absence of a moving object), and that learning can be reversed in certain circumstances. As such, many researchers prefer the more moderate terminology of a **sensitive period**. For instance, a chick imprinted to one object will often generalize to other objects of similar appearance (e.g., color and shape). By gradually changing the features of the objects to which it is exposed, the chick's final preference can be different from its initial preference, even after the end of the "critical" period (Bolhuis, 1990).

KEY TERMS

Critical period
A time window in which appropriate environmental input is essential for learning to take place.

Sensitive period
A time window in which appropriate environmental input is particularly important (but not necessarily essential) for learning to take place.

The development of visual abilities also shows evidence of a sensitive period. For example, Hubel and Wiesel (1970b) took single-cell recordings from the primary visual cortex of cats in whom one eye had been deprived of visual input in early life (by sewing it shut). They found that the cells responded to input from the sighted eye only, whereas normally reared cats possess cells that respond to inputs from both eyes. During a sensitive period between 4 and 5 weeks after birth, eye closure for 3–4 days leads to a sharp decline in the number of cells that will respond to input from both eyes.

What of "higher" cognitive abilities, such as language? Lenneberg (1967) initially argued that language acquisition has a critical period that ends abruptly at puberty. However, the ability to comprehend and produce language is likely to depend on other skills such as hearing, motor ability, working memory capacity,

and so on. Each of these basic skills may have its own sensitive period, which means that different components of language may have their own sensitive period rather than a fixed cut-off point at puberty. For example, the sensitive period for making phonemic discriminations such as the distinction between r and l occurs during infancy and is resistant to subsequent exposure (McCandliss et al., 2002). In contrast, accents are more fluid during childhood but become notoriously hard to change from the onset of adulthood.

Studies of feral children offer some support to Lenneberg's idea. Genie had been locked away by her mentally unstable family from the age of 20 months to 13 years when she was discovered in Los Angeles in 1970 (Curtiss, 1977). During this period she was severely maltreated and was not allowed to speak or be spoken to. On being rescued she was almost entirely mute, with a vocabulary of around 20 words. Within the first 18 months of being placed with a foster parent, her language was reported to have developed well on all fronts, including both vocabulary and grammar, and this was cited as evidence *against* a sensitive period (Fromkin et al., 1974). However, subsequent studies are more consistent with a sensitive period and have revealed that her language acquisition remained very poor compared with young children (Jones, 1995).

Thankfully, research in which exposure to a first language is withheld from a child is limited to a tiny number of cases. However, second language acquisition offers a richer source of evidence to test for the existence of a sensitive period. Brain imaging studies reveal that both age of acquisition and level of proficiency determine the neural substrates of second language processing in adults. One study compared syntactic and semantic language tasks in Italian-German bilinguals using fMRI (Wartenburger et al., 2003). For syntactic judgments, the age of acquisition was critical: those who learned the second language later in life showed more activity in language-related brain regions when processing syntax irrespective of their level of proficiency (Figure 6.8). This suggests a sensitive period for grammar in terms of neural efficiency (more activity is interpreted here as less efficiency). For semantic judgments, by contrast, the pattern of activity was related to proficiency level in the second language rather than age of acquisition (i.e., little influence of sensitive periods for language semantics). Hartshorne et al. (2018) examined syntactic proficiency (judging whether sentences are grammatical) in second language learners in a very large sample (two-thirds of a million) and separately modeled age of acquisition and proficiency. They estimated a sensitive period as late as 17.4 years beyond which the ability to learn syntax declines steadily.

What biological properties of the nervous system give rise to sensitive periods in development? Werker and Hensch (2015) provide an overview of three different stages.

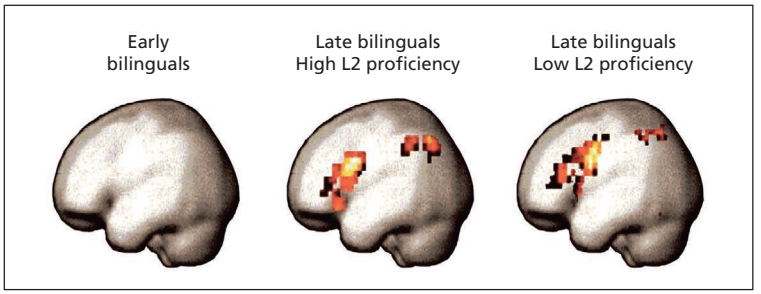

FIGURE 6.8: When brain activity linked to grammatical processing is contrasted for first (L1) and second (L2) languages, there are no differences for early bilinguals (L2 from birth). However, L2 (relative to L1) is linked to more activity in language-related regions when late bilinguals (L2 after 6 years) make grammatical judgments, irrespective of their proficiency in that language. This suggests a sensitive period for efficient grammatical acquisition.

From Perani and Abutalebi (2005).

- *Onset*. The inhibitory neurotransmitter GABA is critical for readying the cortex for learning as revealed by manipulations that increase or decrease its availability (shifting the sensitive period forwards and backwards respectively). Inhibitory interneurons are neurons that act like bridges between other neurons, and these can function as a plasticity switch that determines if/when sets of neurons cooperate. These inhibitory interneurons mature at different rates in the cortex giving rise to different sensitive periods.
- *Duration*. During the open period, synapses themselves become remodeled (protein synthesis) or removed (pruning), and this process depends on being stimulated from a suitable environment.
- *Closure*. There are various molecular brakes that reduce plasticity including myelin (which is found to some extent within the cortical sheet, and not just in tracts that connect different parts of the cortex) and epigenetic events (affecting the expression of certain genes).

That is, sensitive periods are themselves a mixture of nature and nurture where the latter refers to the availability of a suitable environment. Development will, to some extent, "wait" for an appropriate environment. Evidence for this comes from infants who are born blind or deaf and hence do not receive environmental stimulation at the normal time but undergo correction later. Human infants born with dense cataracts over both eyes show a rapid increase in visual acuity when the cataracts are surgically removed, even as late as nine months after birth (Maurer et al., 1999) although visual functioning remains weak in some domains into childhood (Le Grand et al., 2001). Attempts to correct for deafness tend to be successful up to four years (Govaerts et al., 2002), which is far beyond the normal critical period for children who were hearing at birth.

Innate knowledge?

Perhaps the most controversial topic in developmental cognitive neuroscience is the extent to which any form of knowledge or ability can be said to be innate (Karmiloff-Smith, 2006; Spelke, 1998).

This division has a long historical and philosophical tradition between so-called **empiricists** (who believed that the mind is a blank slate) and **nativists** (who believed that at least some forms of knowledge are innate).

The word *innate* itself conjures up somewhat different connotations to different researchers. For some, the word is synonymous with the idea that behavior is a product of natural selection (Ridley, 2003). The word **instinct** is often used in this context and suitable examples would be filial imprinting in birds (Tinbergen, 1951) or even language in humans (Pinker, 1994). In this usage of the word "innate," there is still a role for experience to play, perhaps within a sensitive period of development. A chick will only imprint if it is exposed to a suitable stimulus in the environment, and a child will only learn sophisticated language given suitable inputs. However, in both examples the particular content of the behavior cannot be said to be innate. The chick will as happily imprint to an Austrian professor as to its mother, and a child is capable of learning a diverse range of vocabulary and syntax, and not even the manner of production (e.g., speaking versus sign language) is strongly predetermined. In this sense of the word "innate," there is a readiness for certain knowledge to be acquired, but the knowledge itself is not strictly innate.

This leads to a consideration of the second way in which the word "innate" is applied: namely, that knowledge or behavior can be said to be innate if it comes about in the absence of appropriate experience. It is this particular usage of the term that has attracted much controversy (Spelke, 1998). The very early development of the primary visual cortex of the cat can, in this sense, be said to be innate, because it makes no difference whether the cat has visual experience or not (Blakemore & Vansluyters, 1975), as shown in Figure 6.9. Both normally developing cats and cats that have been visually deprived in *both* eyes have cells that respond to lines of particular orientations up to around three weeks after birth (Blakemore & Vansluyters, 1975). However, experience is needed for a mature system to form. In the presence of complex visual experience, these cells become even more finely tuned and resemble those of an adult by four weeks, but in the absence of appropriate visual experience, the blind cats lose this specificity.

Similar conclusions arise when one considers the development of phobias. Humans can easily learn to become fearful of certain stimuli such as snakes (e.g., by pairing with an electric shock), but it is hard to become fearful of stimuli such as flowers – a phenomenon that has been termed **prepared learning** (Seligman, 1971). In a series of studies, Mineka and colleagues studied fear conditioning in monkeys (for a review, see Ohman & Mineka, 2001). Whereas monkeys born in captivity to wild-born monkeys show fear of snakes, monkeys who were born from mothers raised in captivity do not. The fearless monkeys could acquire fear of snakes by watching videos of other monkeys reacting

ONLINE RESOURCES

Check out the Instructor & Student Resources website for an interview with Elizabeth Spelke on innateness, and a longer lecture with David Hubel on critical periods (routledgelearning.com/wardcognitiveneuroscience).

KEY TERMS

Empiricism
In philosophy, the view that the newborn mind is a blank slate.

Nativism
In philosophy, the view that at least some forms of knowledge are innate.

Instinct
A behavior that is a product of natural selection.

Prepared learning
The theory that common phobias are biologically determined from evolutionary pressures.

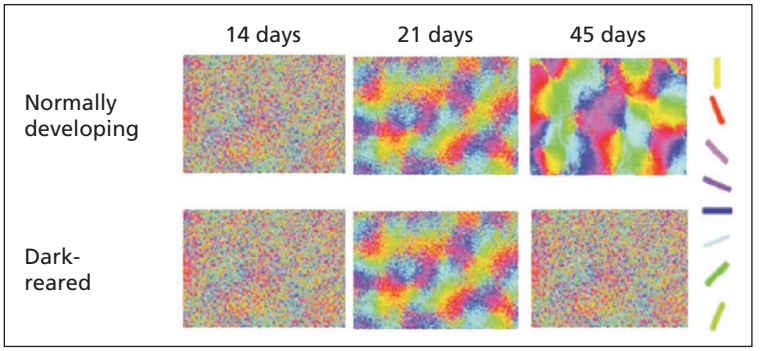

FIGURE 6.9: Orientation selectivity at 14, 21, and 45 days in the primary visual cortex of cats reared in a normal visual environment (top) and a dark-reared environment (bottom). The dark-reared cats show normal development up to 21 days but then show a decrease. The different colors represent the extent to which neurons respond to particular orientations.

Adapted from Crair et al. (1998).

with fear to snakes, but they could not acquire fear of flowers using the same method. This suggests that fear of snakes does require suitable experience, even if that fear is transmitted vicariously via other monkeys rather than through contact with snakes. That is, this behavior can be said to be innate in the sense of being a product of natural selection, but not in the sense of developing without experience.

Some preferences could, arguably, be said to be innate in the sense that they do not appear to depend on experience. Newborn infants prefer sweet tastes over neutral and sour ones (Desor et al., 1975), and they prefer some visual patterns over others (Damon et al., 2017). Harlow (1958) reported a series of ethically dubious experiments in which newborn monkeys were isolated from their natural mothers but "reared" by artificially created mothers such as a stuffed toy monkey or a metal wire monkey (Figure 6.10). The monkeys preferred to cling to the furry stuffed toy rather than the metal one, even if the metal one provided the monkey with milk. This went against the standard behaviorist doctrine at the time that maternal love was merely a learned reward for satisfying basic needs such as hunger (in which case the monkey should show affection to the wire mother).

Some abilities could also, arguably, be said to be innate in the sense that they do not appear to depend on experience. Newborn infants will imitate tongue protrusion (Meltzoff & Moore, 1977), as shown in Figure 6.11. That is, they demonstrate an understanding that a seen tongue being protruded corresponds to their own, unseen, motor ability to do the same. Meltzoff and Moore concluded that "the ability to use intermodal equivalences is an innate ability of humans" (1977, p. 78).

The studies in the previous section suggest that certain dispositions (e.g., to fear certain types of thing), preferences (e.g., sweet), and abilities (e.g., to detect edges, intermodal matching) can – in some sense of the word – be said to be innate. However, the issue of whether the specific content of knowledge (or so-called representations) is innate is much harder to substantiate. For example, newborn infants prefer to look at real faces relative to faces with the parts rearranged, but this could reflect a tendency to prefer certain symmetrical patterns (Johnson et al.,

1991). However, they will also prefer to look at a jumbled-up face provided it is top-heavy (Macchi Cassia et al., 2004). This makes it hard to argue that the specific *knowledge* of what a face looks like is innate, although one could still reasonably claim that a preference for particular kinds of pattern is an evolutionary adaptation.

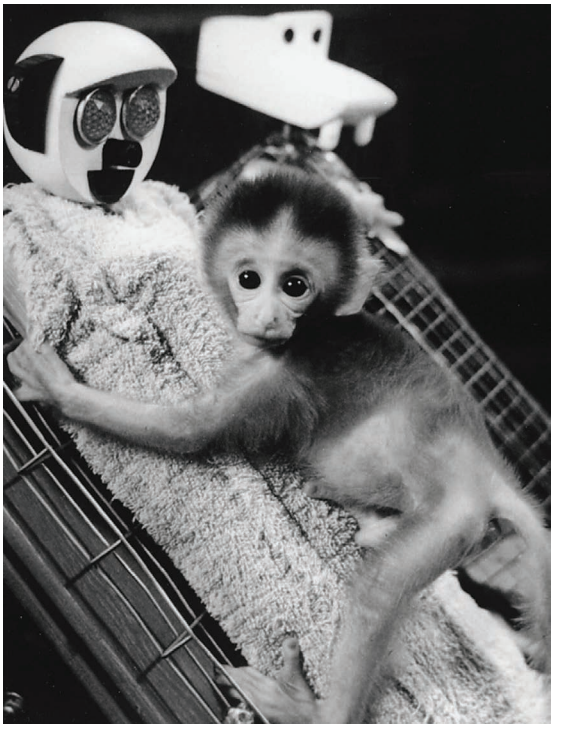

FIGURE 6.10: Harlow, in his famous article "The nature of love," argues that monkeys have an innate preference for a soft versus wire "mother" even if the wire "mother" provides the infant with milk.

From Harlow (1958). Reproduced with kind permission of Harlow Primate Laboratory, University of Wisconsin.

Evaluation

The functions of different regions of the brain depend on the underlying structure (i.e., what connects with what). Significant changes to brain structure during development can result in atypical functional specializations, although there may be a time-limited window for this to occur. Sensitive periods are important for the development of most, if not all, cognitive abilities (from vision to grammar) and reflect a mixture of innate influences and environmental exposure. Innate influences can be construed both as adaptive dispositions (i.e., instincts) or, in some cases, as a tendency for certain behaviors to develop (at least up to some point) without a suitable environment.

NATURE AND NURTURE OF INDIVIDUAL DIFFERENCES

The previous sections have focused primarily on how the brain and cognition tends to develop structurally and functionally across the population, but the remaining sections of this chapter focus on how and why there is variability from one person to another. **Behavioral genetics** is concerned with studying the inheritance of behaviors and cognitive skills. The classic methods of behavioral genetics are twin studies and adoption studies which provide ways of disentangling nature and nurture. However, genetic differences themselves (i.e., variations in the DNA sequence) can now be studied relatively easily. This holds out the promise of being able to link behavioral differences back to molecular signals involved in building the brain (e.g., axon guidance, neural migration to the cortex).

KEY TERM

Behavioral genetics
A field concerned with studying the inheritance of behavior and cognition.

Twin studies and adoption studies

Most behaviors run in families, but it is hard to know to what extent this reflects shared environment or shared genes. When

FIGURE 6.11: This 23-day-old infant imitates the tongue protrusion of the experimenter, suggesting an understanding of the link between seen actions of another and their own, unseen actions.

Photo by Andrew N. Meltzoff and E. Ferorelli, with permission from Andrew N. Meltzoff.

a child is placed into an adopted home, he or she will effectively have two sets of relatives: biological relatives with whom the child no longer shares any environment, and adopted relatives with whom the child shares an environment, but not genes. Will the child more closely resemble the biological or adoptive family, thus emphasizing a role of nature or nurture, respectively? In many cases, it is not possible to contact or test the biological relatives, but the genetic contribution can still be estimated by comparing the adopted child with non-adopted siblings in the household (i.e., both the adopted and non-adopted siblings share family environment, but not genes). Assisted fertility with donor eggs and/or sperm also represents a modern twist on the classic adoption design (Rice et al., 2009).

THE ORIGINS OF GENETIC DIFFERENCES

The human genetic code is organized onto 23 pairs of **chromosomes**, making a total of 46 chromosomes. One of the chromosomes of each pair comes from the maternal line and one from the paternal line. In each individual there are two copies of each gene normally present, one on each chromosome. However, genes may exist in different forms, termed **alleles**. The different alleles represent changes (or mutations) in the sequence of the gene that is propagated over many generations, unless natural selection intervenes. Many different allelic forms are common and benign, but they account for the individual differences that are found between humans as well as differences between species. For example, two different alleles of a single gene determine whether the earlobes will be hanging or attached. In other instances, single gene mutations are not benign, as in the case of Huntington's disease (see Chapter 10). A different allele may mean that the end-product encoded by the gene (such as enzymes) works less efficiently, more efficiently, or not at all. Alternatively, it may mean that the gene works in an entirely novel way by, for example, altering the expression of other genes. Most behavioral traits will be an outcome of the concerted action of many genes. Even though a given gene may exist in only a small number of discrete allelic types, when many such genetic variants are combined together, they may produce an outcome that is continuously distributed – such as the normal distribution found for height or IQ. Autism, dyslexia, and schizophrenia all appear to be polygenic in nature (see Tager-Flusberg, 2003).

As well as differences in alleles, individuals differ in the spacing of genes on the chromosomes (most of the genome contains non-gene segments). While it is unclear whether this contributes to observable individual differences, an analysis of the spacing of various genomic markers is central to techniques such as genetic "finger-printing" and attempts to locate candidate genes on the basis of behavioral markers (e.g., presence of schizophrenia).

During production of eggs and sperm the genes from the maternal and paternal chromosomes are "shuffled" so that a single new chromosome is created that is a combination of the original two. This mechanism prevents the number of chromosomes doubling in each generation. This provides one mechanism leading to genetic variation through producing different combinations of a finite set of alleles. This process can also go wrong if segments of DNA get deleted or duplicated. Some relatively common genetic disorders formed in this way are summarized here.

Genetic disorder	Origins	Cognitive developmental characteristics
Down's syndrome	A duplicated copy of chromosome 21	General learning difficulties (IQ < 70), poor fine motor control, delayed and impaired expressive language
Turner syndrome	A missing copy of the X-chromosome (or deletion of part of it)	Not associated with mental retardation, but verbal IQ tends to be higher than nonverbal; some difficulties in executive functions and social skills (Ross et al., 2000)
William's syndrome	A deleted segment of chromosome 7	General intellectual impairment but with some tendency for language abilities to be better than spatial abilities; high sociability, but not necessarily high social intelligence (Karmiloff-Smith, 2007)

Twin studies follow a similar logic (Figure 6.12). Twins are formed either when a single fertilized egg splits in two (monozygotic or **MZ twins**) or when two eggs are released at the same time and separately fertilized (dizygotic or **DZ twins**). MZ twins are genetically identical; they share 100 percent of their genes. DZ twins are nonidentical and share only 50 percent of their genes (i.e., the same as non-twin siblings). Given that both are assumed to share the same family environment, any difference between MZ and DZ twins is assumed to reveal genetic influences. Studies of twins reared apart combine the advantages of the standard twin study and adoption study.

There are important clarifications to the usefulness of these study designs. With regards to twin studies, it is assumed that MZ and DZ twins experience similar environments. However, MZ twins could be treated more similarly by others. Also, MZ twins often have more similar prenatal environments: many MZ twins share the same sac (called the chorion) within the placenta, but DZ twins never do. As such, MZ twins may be more likely to be exposed to the same viruses prenatally. With regards to adoption studies,

KEY TERMS

Chromosome
An organized package of DNA bound up with proteins; each chromosome contains many genes.

Allele
Different versions of the same gene.

MZ twins (monozygotic)
Genetically identical twins caused when a fertilized egg splits in two.

DZ twins (dizygotic)
Twins who share half of their genes, caused when two eggs are fertilized by two different sperm.

FIGURE 6.12: Identical twins look the same, but do they think the same?

uniball/iStock

selective placement could mean that children tend to get adopted into similar environments (e.g., with regard to race or socioeconomic status). Another issue is whether families who adopt or who give up their children for adoption are representative of the general population. Plomin et al. (2001) provide an assessment of this debate and argue that the main findings are relatively robust to these potential drawbacks.

Heritability estimates of brain and behavior

Twin studies and adoption studies are ways of establishing whether there is genetic influence. **Heritability** is an estimate of *how much* genetics contributes to a trait. In particular, heritability is the proportion of variance in a trait, in a given population, that can be accounted for by genetic differences among individuals. In twin studies, if MZ twins correlate with each other by 1.00 and if DZ twins correlate with each other by 0.50, then heritability is 100 percent. A rough estimate of heritability in a twin study can be made by doubling the difference between the MZ and DZ correlations (Plomin et al., 2001). The degree to which an MZ correlation is less than the perfect 1.0 is assumed to reflect **unshared environment** – that is, those differences that distinguish between twins (e.g., different peers, different illnesses). The remaining portion of variance is attributed to **shared environment** (e.g., family socioeconomic status, common parenting).

Figure 6.13 shows heritability estimates of various psychological abilities and conditions. It is to be noted that these are comparable to many heritability estimates from non-psychological traits and functions that we might naively expect to be "more biological." In a meta-analysis of 50 years of twin studies, Polderman et al. (2015) calculated the heritability of cognitive abilities to be .468 and for psychiatric conditions to be .463. This contrasts with .436 and .545 for cardiovascular and respiratory functioning, respectively (of course, the brain is as much a part of our biology as our heart and lungs).

The concept of heritability, although useful, is easily misunderstood. It measures how much variability is due to genetic factors within a given population, not the contribution it makes in a given individual. If the heritability of height is about 0.69 (Hemani et al., 2013), it doesn't mean that 69 percent of a person's height has come from their genes and 31 percent from their environment. It means that 69 percent of the differences in height between different people, within that population, are due to their genes. To give another example, most people have ten fingers and this is genetically specified. However, the heritability measure for number of fingers is low, because the *variability* in the number of fingers is due primarily to environmental reasons – industrial accidents and so on (Ridley, 2003).

KEY TERMS

Heritability
The proportion of variance in a trait, in a given population, that can be accounted for by genetic differences among individuals.

Unshared environment
The proportion of variance in a trait, in a given population, that can be accounted for by events that happen to one twin but not the other, or events that affect them in different ways.

Shared environment
The proportion of variance in a trait, in a given population, that can be accounted for by events that happen to both twins, affecting them in the same way.

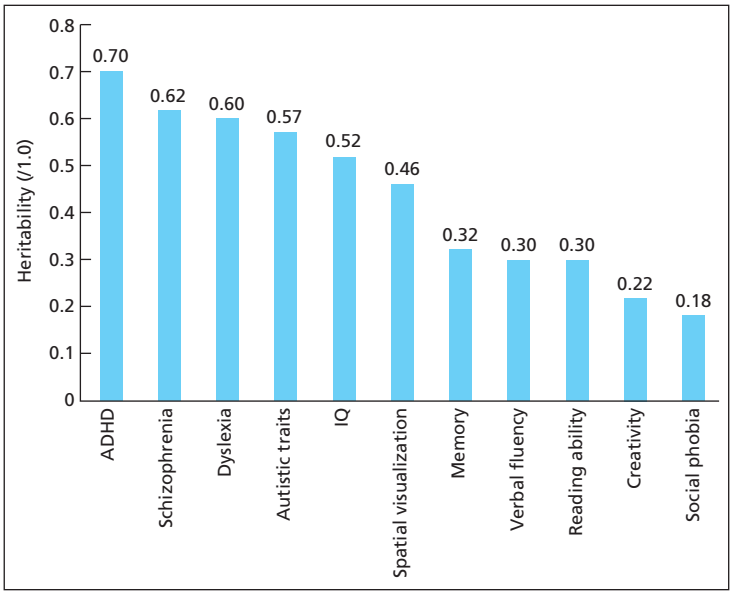

FIGURE 6.13: The approximate heritability of various psychological abilities and conditions: attention deficit and hyperactivity disorder, ADHD (Eaves et al., 1997); schizophrenia (Gottesman, 1991); dyslexia (Hawke et al., 2006); autistic traits (Hoekstra et al., 2007); IQ (Bouchard & McGue, 1981); spatial visualization, memory, verbal fluency (Nichols, 1978); reading ability in elementary school (Thompson et al., 1991); creativity (Nichols, 1978); and social phobia (Kendler et al., 1992).

To consider a cognitive example, the fact that heritability for reading ability in elementary school pupils is 0.30 (Thompson et al., 1991) does not mean that 30 percent of a child's ability is due to genes and 70 percent due to environment. Reading requires an appropriate environment (i.e., living in a literate culture), otherwise literacy will not exist at all. It also requires an appropriate brain architecture that will support reading. Both are equally essential. The measure of heritability may also vary according to the population studied. If one were to measure reading ability in a country in which education was not universal, then heritability would almost certainly be lower because reading ability would be an outcome of opportunity, that is, an environmental factor. It is curious, but true, that the more that our societies are based upon equal opportunities, the more that genetic differences will matter (proportionally speaking). To give one final example, the heritability for reading disability, or dyslexia, in Western societies is higher, at 0.60 (Hawke et al., 2006), than for reading ability per se, because the diagnostic criteria for dyslexia typically assume adequate opportunity and intellect; that is, variability in environmental factors is minimized by the selection criteria.

Heritability estimates can also be applied to structural and functional brain differences as well as to cognitive and behavioral traits (Jansen et al., 2015). For instance, Figure 6.14 shows the

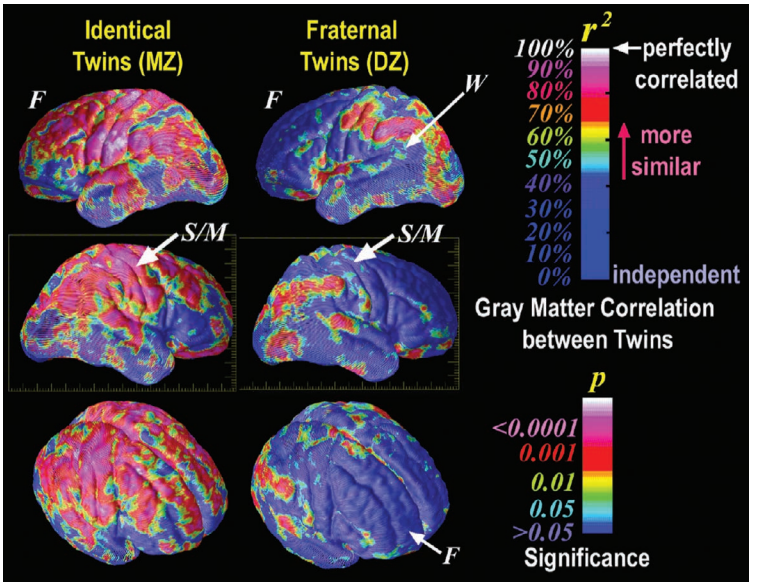

FIGURE 6.14: Correlations in gray matter density between pairs of MZ twins (left column) and DZ twins (right column) for three different views of the brain (F = frontal pole, W = Wernicke's area, S/M = somatosensory/motor cortex).

Thompson et al. (2001). Reproduced with permission from Springer Nature.

correlation in localized gray matter volumes between MZ and DZ twins (heritability is, of course, related to the difference of the two sets of correlations). The correlations tend to be far greater in MZ twins. Heritability estimates for total brain volume are 0.94 (Bartley et al., 1997). For cortical surface area they range from .30 to .43 depending on the region (Chen et al., 2012), and for gray matter and white matter density using VBM they range from .69 to .85 (Hulshoff Pol et al., 2006). The Human Connectome Project aims to have detailed MRI and MEG scans from 1,200 people comprising sets of twins (Van Essen et al., 2013), and initial research has shown that whole brain measures of functional connectivity have a far stronger heritable (genetic) component than do effects of shared environment (Colclough et al., 2017). There was still a sizeable influence of non-shared environment, which could include things such as measurement error and variability in implementing the genetic program, which, as noted before, does not specify a precise connectome but provides guiding constraints for its construction.

ONLINE RESOURCES

Check out the Instructor & Student Resources website for TED talks on the fascinating topic of epigenetics (routledgelearning.com/wardcognitiveneuroscience).

Linking genetic differences to brain and behavior

Heritability is a statistical measure that doesn't say anything directly about particular genes or their function. In order to do that, one needs to link relevant data from cognitive neuroscience with individual differences in the genetic code itself (i.e., variations in the DNA sequence). Taking cheek swabs remains the most common and most simple way of extracting cells for human genetic analysis (Figure 6.15). Cells on the inside of the cheek are loose and can be removed by light abrasion with a swab. Recall that the genetic code is the same across all the cells in the body,

so it makes no difference whether it is extracted from a cheek cell or a neuron itself. Sterile kits are cheaply available, and swabs can be obtained remotely with participants returning their DNA sample via post. The two approaches that one could adopt for analysis of genetic differences are called **genotype-first** and **phenotype-first**. In conducting this kind of research it is important to obtain accurate information about the ethnicity of your genetic sample (or have a homogeneous sample) as the prevalence of many polymorphisms can vary considerably depending on race.

FIGURE 6.15: DNA can be obtained from cheek cells using commercially available swab kits. The sequence of DNA in an individual is the same in all the cells of their body – so cheek cells are as useful as neurons for this purpose.

Science History Images/Alamy Stock Photo

An example of a genotype-first approach would be to take a single gene that is known to exist in multiple variants (polymorphisms) and that may be relevant to a given research question (i.e., based on previous research). As an example from the literature, oxytocin is a hormone involved in prosocial interactions (including falling in love). Oxytocin binds to receptors in the brain which are coded by a gene with a relatively common mutation (termed "A" and "G" variants that reflect a single difference in the DNA sequence). It is possible to group participants according to their genotype (AA, GG, AG) and then show that they differ on behavioral measures such as parenting style (Bakermans-Kranenburg & van Ijzendoorn, 2008) or neural responses, in fMRI, to rewards (Damiano et al., 2014). The advantage of this genotype-first approach is that the genetic analysis is limited to one specific gene and so is relatively straightforward to conduct (commercial companies can provide this service to the neuroscience community). It also avoids the problem of multiple comparisons when testing multiple genes (the problem of Type I errors).

An example of a phenotype-first approach would be to take a given trait that is known to vary in the population (e.g., empathy) or to take a clinically defined condition (e.g., autism) and to determine which portions of the genome contribute most to variations in that trait (as a continuous measure) or the presence/absence of a condition (as a binary measure). One method that uses this approach is termed a **genome-wide association study (GWAS)** and tends to involve many thousands of participants. This method is based on the fact that there are many small variations in the genome across individuals termed single nucleotide polymorphisms (SNPs, pronounced "snips"). These SNPs are not of interest in their own right but provide useful

KEY TERMS

Genotype-first
An analysis approach in which different genotypes (e.g., different alleles) are used to explore for phenotypic variation.

Phenotype-first
An analysis approach in which different phenotypes are used to explore genetic differences.

Genome-wide association study (GWAS)
A phenotype-first approach in which the presence/absence, or continuous variation, in a trait is linked to variations at many different sites in the genetic code.

clues as to which parts of the genome contain a "hot spot" (i.e., regions where individuals with the same phenotype have genetic similarities that deviate from chance). To give an example of this approach, Ma et al. (2009) studied 487 Caucasian families (1,537 individuals) with autism and examined their genomes using over one million SNPs. Figure 6.16 shows the way that these data can be visualized: the genome is plotted on the x-axis and (log) probability values on the y-axis (it is also called a Manhattan Plot). They found 96 genetic locations (SNPs) that have $P < 10^{-4}$ (.0001) and 6 that have $P < 10^{-5}$ (.00001). This suggests that genes close to these locations are commonly implicated in the development of autism. The same approach can be applied to brain-based data itself, although this approach is still in its infancy because sufficiently large samples (thousands) of scanned people have not been readily available. To give one example, the UK Biobank has health, behavioral, and genetic data on half a million participants and is collecting brain scans (MRI) on up to 100,000 of them. A preliminary GWAS (albeit with N = 8,428) revealed 148 areas of the human genome that were linked to brain structure and function, including those involved in axon guidance (e.g., the ROBO3 gene affects development of midbrain tracts), white matter repair (e.g., relevant to disorders such as multiple sclerosis), and iron transport relevant to neuro-vascular coupling (Elliott et al., 2018). However, identifying these genes is only the starting point. The ultimate aim is to be able to link different levels of explanation together coherently, along the lines of Gottlieb's (1992) simple framework described earlier: Genes ↔ Brain structure ↔ Brain function ↔ Experience.

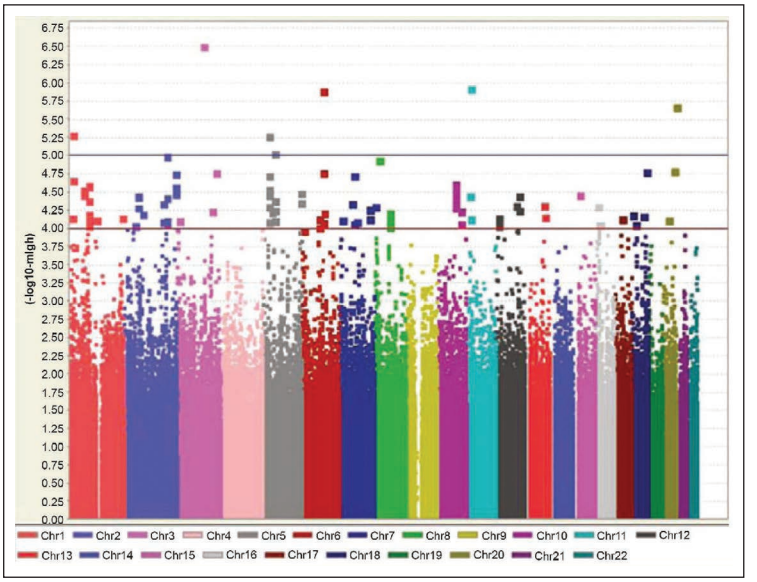

FIGURE 6.16: This genome-wide association study (GWAS) of autism divides the genome into different regions (Chr 1 to 22 refer to the different chromosomes) and measures the statistical probability (plotted on the y-axis) that variability in the presence of the trait is linked to variability in that region of the genome. The values of 4.00 and 5.00 refer to $P < 10^{-4}$ (.0001) and $P < 10^{-5}$ (.00001), respectively.

LINKING GENES TO COGNITION: THE CASE OF FOXP2, SPEECH, AND GRAMMAR

In 1990, a remarkable family came to the attention of the scientific community. Around half of the members of the so-called KE family had problems in producing speech and language, and moreover, the pattern of inheritance was consistent with a single gene mutation (Figure 6.17). Affected family members would come out with sentences like "The boys eat four cookie" and "Carol is cry in the church." Indeed, early reports of the family suggested that they may have problems in specific aspects of grammar (Gopnik, 1990; Gopnik & Crago, 1991), that is, a potential "gene for grammar." Since then, the affected mutation in the FOXP2 gene has been identified, the nature of the speech problems have been described in more detail, and the neural substrates have been explored in both humans and other species (for a review, see Fisher, 2017).

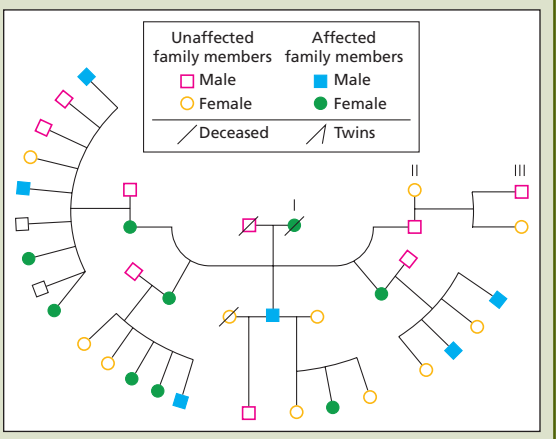

FIGURE 6.17: The family tree of three generations of the KE family shows that around half of the members have significant problems in speech and language. This problem has now been linked to a mutation in a single gene called FOXP2. Does this gene have a role to play in the evolution of human language?

Watkins et al. (2002). By permission of Oxford University Press.

While the core deficit in the family remains debated, the deficits are certainly not limited to grammar. Affected KE family members, relative to unaffected ones, score poorly on tests of pronunciation, grammar, semantics, verbal IQ, and even nonverbal IQ, although the scores from the two groups overlap (Vargha-Khadem et al., 1995). Tests of oral praxis and orofacial praxis (e.g., copying tongue protrusions or lip pouting) do produce nonoverlapping test scores, suggesting that **orofacial dyspraxia** is a core deficit. There is reduced volume in the basal ganglia (caudate nucleus) that correlates with their level of orofacial dyspraxia (Watkins et al., 2002). The basal ganglia have a key role in the control of voluntary movement. The basal ganglia, and the caudate in particular, have also been linked to implicit rule learning in artificial grammars (Lieberman et al., 2004), suggesting a possible link to the grammatical deficits. Inserting different versions of the FOXP2 gene into the mouse affects the plasticity of basal ganglia circuits, with human versions increasing plasticity (see Fisher, 2017). Other families with specific language impairment (SLI) of developmental origin do not appear to have the FOXP2 gene affected (Newbury et al., 2002), although some of them do perform poorly on grammar in the absence of orofacial dyspraxia (Falcaro et al., 2008). As such, there are likely to be multiple genes that affect grammar, and at present, there are no known genes that specifically affect only grammar.

What do studies of the *normal* version of the FOXP2 gene reveal about its possible function? The product of the FOXP2 gene is what is called a transcription factor, that is, its molecular function is to affect the expression of other genes. As such, its effects may be wide-ranging, and it is expressed in various tissues in the body, not just the brain. Haesler et al. (2004) found that FOXP2 expression in birds who need to learn their vocalization (e.g., canaries) had greater expression in the avian equivalent of the basal ganglia during song learning than song production. Intriguingly, the FOXP2 proteins of chimpanzees, gorillas, and rhesus macaques are identical to each other but differ from humans in terms of two small sequence changes, one of which is likely to be functional and has been dated to 200,000 years ago, about the time that anatomically modern humans emerged (Enard et al., 2002). The final word concerning the function of this gene has yet to be written.

KEY TERMS

Orofacial dyspraxia
An impaired ability to perform the coordinated movements that are required for speech.

Epigenetics
Changes (e.g. in behavior) that occur as a result of changes in gene expression.

Mechanisms for gene–environment interplay

The new frontier of the nature-nurture debate is concerned with how genes and environments influence each other mechanistically. In their book *Rethinking Innateness*, Elman and colleagues (1996) put it this way: "The answer is not Nature *or* Nurture; it's Nature *and* Nurture. But to say that is to trade one platitude for another; what is necessary is to understand the nature of the interaction" (p. 357). At least three broad scenarios have been identified (Rutter et al., 2006), namely: epigenetics, gene–environment correlations, and gene–environment interactions.

Epigenetics

Although the structure of the genetic code for each person is fixed at conception, the functioning (or "expression") of the genetic code is highly dynamic. Different genes become active or inactive at different times of life (e.g., causing us to go through puberty, or our hair to turn gray). The expression of the genetic code is also influenced by the environment – a phenomenon termed **epigenetics**. In epigenetic marking the genes are not changed but get tagged with a chemical marker that dampens (e.g., a methyl group) or accentuates (e.g., an acetyl group) their expression. At present, epigenetic markers have to be explored in vitro. A lack of availability of human brain tissue, and the difficulty in linking it to cognitive or behavioral measures, has resulted in limited progress in humans (Miller, 2010). It is also unclear how epigenetic differences that can be more easily measured in the DNA of other tissues (e.g., blood cells) would relate to those of neurons. Thus, epigenetic differences tend to be studied in animal models (e.g., Meaney, 2001).

One well-known example of epigenetic effects concerns the influence of abuse or poor caregiving (neglect) in early development. In rats, mothers vary in the amount of care (licking and grooming) given to their pups. Low care is linked to an increased, and lasting, stress

response in the pups to both neutral and stressful events (e.g., Meaney, 2001). The effect has been related to an epigenetic reduced expression of a gene coding for a glucocorticoid receptor, leading to an increased stress response (Weaver et al., 2004). In humans, McGowan et al. (2009) examined the postmortem brains of people who had committed suicide versus control brains. They found epigenetic influences on the gene coding for the glucocorticoid receptor in suicide victims who had experienced early neglect/abuse, but this was not found on the other suicide victims or the controls – see Figure 6.18. This confirms that the epigenetic effects were linked to early abuse/neglect rather than other factors contributing to suicide (e.g., adult mental health).

Gene–environment correlations (rGE)

Gene–environment correlations (rGE) are genetic influences on people's exposure to different environments (Plomin et al., 1977). For example, people will seek out different environments (e.g., drug taking and novelty seeking) depending on their genotype (Benjamin et al., 1996; Kotler et al., 1997). Benjamin et al. (1996) reported a link between long versions of the D4 dopamine receptor gene and personality questionnaires that measure novelty seeking (Figure 6.19) and extraversion (but linked negatively to conscientiousness). However, in order to properly understand these results that link genes and behavior, it will be important to situate them within models of brain function which, perhaps surprisingly, remains to be done (Robbins, 2018). There is unlikely to be a simple mapping between neurotransmitter function and behavior.

Gene–environment correlations have often been studied in the context of parenting styles, and this has led to the notions of evocative and passive processes (see Figure 6.20). An evocative process, in this context, is one in which a child's negative behavior leads to a harsher parenting style. A passive correlation is that both a risk for negative child behaviors and negative parenting behaviors are transmitted genetically. Although these differences are hard to pull apart in most families, there are some "natural experiments" that lend themselves to this approach. For instance, adopting a child or assisted fertility with donor embryos eliminates the possibility of passive correlations but provides positive evidence of evocative rGE effects where the child's behavior influences parenting style (Harold et al., 2013).

Gene–environment interactions (G X E)

Gene X environment interactions (G X E) occur when susceptibility to a trait depends

KEY TERMS

Gene–environment correlations
Genetic influences in people's exposure to different environments.

Gene X environment interactions
Susceptibility to a trait depends on a particular combination of a gene and environment.

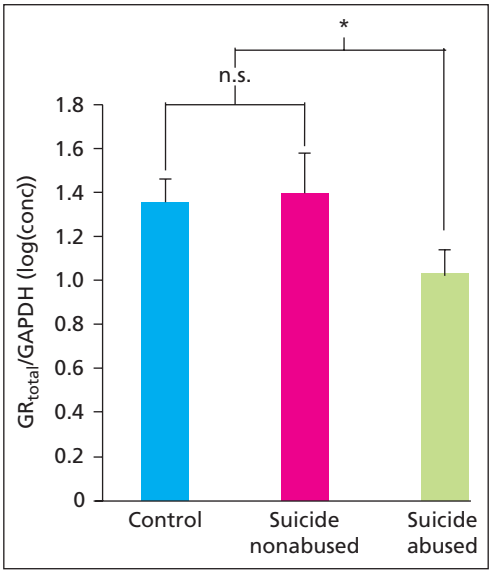

FIGURE 6.18: Abuse in early childhood, rather than suicide-related mental illness, is linked to lower expression of the stress-related glucocorticoid receptor gene in the human hippocampus. This is evidence of an influence of the social environment on the functioning of the genome, that is, epigenetics.

From McGowan et al. (2009). Reproduced with permission from Springer Nature.

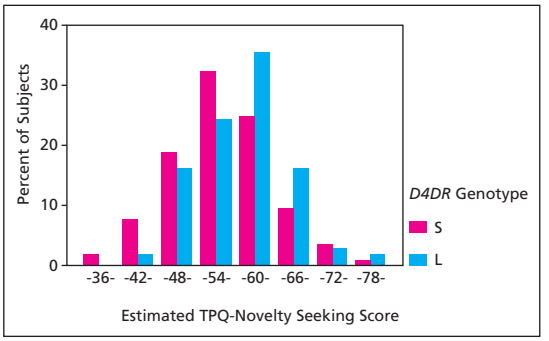

FIGURE 6.19: The D4 dopamine receptor gene (D4DR) exists in short and long (S, L) polymorphisms, and the long variant is linked to higher questionnaire scores of novelty seeking (TPQ = tridimensional personality questionnaire).

From Benjamin et al. (1996). Reproduced with permission from Springer Nature.

on a particular combination of a gene and environment. The effects of the gene and environment together exceed what would be expected from the sum of the parts. Three classic demonstrations of G X E were reported in the early 2000s that attracted much attention at the time but have subsequently led to controversy. These included interactions between childhood abuse and variants of monoamine oxidase A gene in eliciting antisocial behavior (Caspi et al., 2002); interactions between short and long versions of a serotonin transporter gene and adverse life events in eliciting depression (Caspi et al., 2003); and interactions between the COMT gene and cannabis use in eliciting symptoms of schizophrenia (Caspi et al., 2005). All studies involved a sample of over 1,000 consecutive births from Dunedin, New Zealand, that have been systematically studied at subsequent time points (between 3 and 50 years, so far). Hence, this sample has had a detailed assessment of their health and environment throughout life (Poulton et al., 2015). These studies are described briefly next and then reevaluated in terms of subsequent evidence and debates.

Caspi et al. (2002) reported that children with the low-activity (L) variant of the monoamine oxidase A (MAOA) gene who were maltreated are more likely to show antisocial behavior as an adult. That is, the effect of having this combination of gene and environment exceeds what one would expect from the simple sum of the effect of the gene alone and the effect of the environment alone. The gene codes for an enzyme involved in the metabolism of dopamine, norepinephrine, and serotonin. A different mutation in this gene had previously been found in a large Dutch family with a strong history of violence in its male members (Brunner et al., 1993). The effect is more pronounced in men because the gene is coded on the X-chromosome. Men (XY) have only a single copy of the gene, whereas women (XX) have two copies, one of which can compensate for the other.

Caspi et al. (2003) examined the serotonin transporter gene (5-HTT) that occurs in two variants termed short and long. Carriers of the short allele show a higher prevalence of depression and suicidal thoughts following a negative life event (such as divorce).

In their third study, Caspi et al. (2005) reported a gene X environment interaction between variants of the COMT gene and cannabis smoking in triggering symptoms linked to schizophrenia (e.g., hearing voices that others couldn't hear). A common mutation at one place in the COMT gene leads to the substitution of an amino acid (from valine, Val, to methionine, Met), such that the presence of a Val allele is linked to more efficient dopamine

breakdown. The presence of the Val/Val genotype together with the smoking of cannabis during adolescence was linked to greater report of symptoms at age 26 (see Figure 6.21). The effect was not found for cannabis smoking at a later age, suggesting a sensitive period.

It is not hard to see why these studies attracted so much attention. In all three examples these were essentially "normal" genes (i.e., present in a large proportion of the population) that, given a particular environment, leads to an increased vulnerability of a psychiatric problem but without a need for simple reductionism (e.g., a "gene for depression") or determinism (i.e., that an outcome is guaranteed). So why the subsequent controversy? The original studies relied on the identification of candidate genes (a genotype-first approach) but this approach has largely been overtaken by GWAS (a phenotype-first approach). Ideally the two approaches should converge to give the same answers but the results of GWAS have tended not to confirm the involvement of the genes that were expected from this earlier research, despite having far larger sample sizes (for a discussion see Dick et al., 2015). Others have taken a similar phenotype-first approach as the original authors (e.g., regarding schizophrenia and COMT) and whereas some groups replicate the original findings (Nieman et al., 2016), others do not (Zammit et al., 2007). However, in support of the original claims, there has also been converging evidence from experimental paradigms exploring the effects of these genetic differences. For instance, carriers of the different versions of the MAOA gene (high or low activity) brought up in typical environments, i.e., without a history of maltreatment, show structural differences in regions such as orbitofrontal cortex as well as functional differences when processing fear and anger (Meyer-Lindenberg et al., 2006).

Although the status of these particular findings remains for future research to corroborate (or definitively discard), there is a general consensus in the literature that gene X environment interactions do

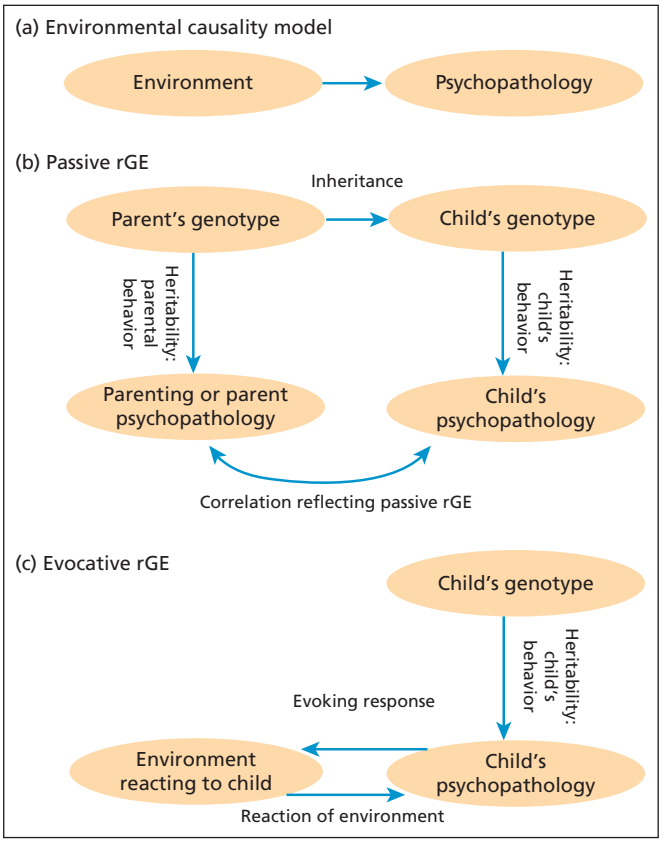

FIGURE 6.20: Different ways in which child psychopathology and environment might be related. (a) The environment directly causes psychopathology (irrespective of genetics); (b) both the parent and child have similar genotypes that predispose toward certain behaviors; (c) the child's genotype predisposes toward both psychopathology and predisposes toward particular parenting responses.

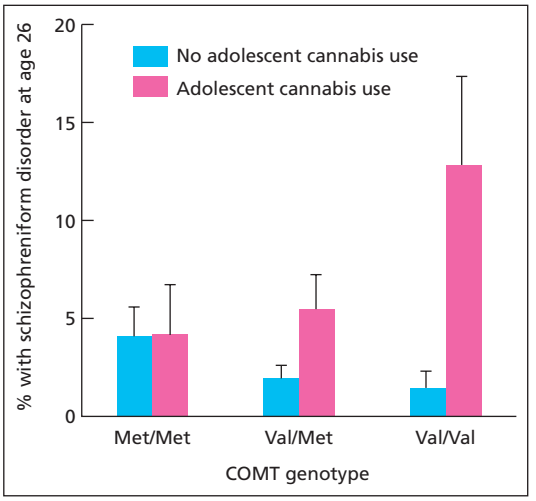

FIGURE 6.21: The COMT gene is involved in the metabolism of the neurotransmitter dopamine, and the gene exists in two main forms (termed Val and Met). Each person has two copies of the gene. If you have a Val copy of the gene *and* you smoke cannabis during adolescence, then there is an increased risk of displaying symptoms of schizophrenia at age 26 – a gene X environment interaction.

Reprinted from Caspi et al. (2005). © 2005, with permission from Elsevier.

exist. For instance, Dick et al. (2015) argue that G X E for single genes are likely to be linked to small effect sizes (because the genetic influences from GWAS are of this order of magnitude), but that the overall effects of multiple genes could be large. This is effectively what the earlier research on heritability estimates showed (i.e., the degree of heritability can vary according to environment) but where heritability was a summed estimate of all genetic effects. Others have argued that inconsistency in the G X E results reflects inconsistencies and uncertainties in how to measure relevant environmental influences (Rutter, 2012). It may depend on the severity of the environmental trigger or the timing of it (e.g., during a sensitive period) in ways that are not fully understood or that were not always taken into account by subsequent replication attempts. Belsky and Beaver (2011) have argued that previous research has incorrectly over-emphasized the importance of *adverse* environments but that, instead, some genetic influences may make people more susceptible to environmental influences per se (both good and bad ones). They conceptualize this in terms of genetic differences in environmental plasticity (how this concept relates to neural plasticity is unknown). For example, Figure 6.22 shows the relationship between self-regulation in adolescents and quality of parenting as a function of how many "plastic" genes are present (including the 5-HTT and MAOA polymorphisms discussed already). Note that the G X E interaction extends to both sides of the graph, that is, people with more of these genes are more sensitive to parenting style per se, whether the parenting style is unusually good or unusually bad.

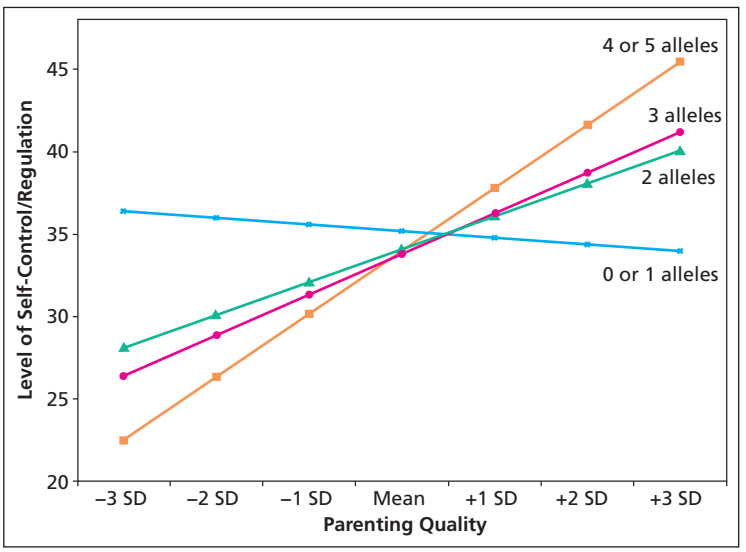

FIGURE 6.22: There is a relationship between parenting quality and level of self-control/emotion regulation in adolescents, but the strength of that relationship depends on the child's genetic predisposition (number of genes that are found to have a more "plastic" allele: 0/1, 2, 3, or 4/5).

From Belsky and Beaver (2011).

Evaluation

Twin and adoption studies have provided an important means for estimating how much variability in a trait is due to genetic influences (heritability) or environmental influences. These approaches can be applied to data from cognitive neuroscience (e.g., inter-individual variability in structural and functional MRI scans) as well as traditional behavioral genetic approaches. Heritability estimates, however, can't be used to infer causal mechanisms (i.e., to determine whether a trait is caused by genes or environment). There are several mechanisms by which genes and environments interact, including epigenetics (changes in gene expression), gene–environment correlations (genetic influences on people's exposure to different environments), and gene–environment interaction (in which a combination of a gene and environment together are crucial). These can now be studied at the whole genome level using large participant databases shared amongst the research community.

SUMMARY AND KEY POINTS OF THE CHAPTER

- Structural changes in the brain occur throughout life. Genes not only influence prenatal development (e.g., the formation of large numbers of synapses around birth) but have a lifelong influence. Genes act as a guiding influence for the development of the brain but do not provide a detailed "blueprint."
- There is good evidence from both animal studies and human research for sensitive periods in development in which the brain is optimally readied to acquire certain skills or knowledge. However, these periods may be more flexible than were first thought.
- The word "innate" can mean at least two different things: either referring to instincts that have been shaped by natural selection (language being one candidate) or referring to knowledge/skills/resources acquired in the absence of experience (candidates include certain preferences and dislikes, and the existence of orientation-selective cells in the visual cortex).
- Twin and adoption studies provide one way of showing that there is a genetic contribution for a given trait. However, the concept of "heritability" is not a pure measure of genetics because the amount of variance in a trait that is due to genetic factors will also depend on the amount of variance that is due to non-genetic factors.

- Genetic disorders can often affect some cognitive abilities more than others. However, genes are rarely highly specific for psychological/cognitive traits. This is because genes interact with other genes, and there is a complex interplay between genes and environment. Sometimes a gene makes certain environments more likely to be sought out (a gene–environment correlation), and sometimes a gene leads to a susceptibility that also depends crucially on environmental circumstance (a gene–environment interaction).

EXAMPLE ESSAY QUESTIONS

- What is the evidence for sensitive periods in development and what kinds of neural mechanism could give rise to them?
- To what extent can any kind of behavior be said to be innate?
- What is meant by the term "heritability" and how can it be measured?
- How might gene–environment interplay contribute to developmental conditions and psychiatric disorders?

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CHAPTER 7

The seeing brain

CONTENTS

Students who are new to cognitive neuroscience might believe that the eyes do the seeing and the brain merely interprets the image on the retina. This is far from the truth. Although the eyes play an undeniably crucial role in vision, the brain is involved in actively constructing a visual representation of the world that is not a literal reproduction of the pattern of light falling on the eyes. For example, the brain divides a continuous pattern of light into discrete objects and surfaces, and translates the two-dimensional retinal image into a three-dimensional interactive model of the environment. In fact, the brain is biased to perceive objects when there is not necessarily an object there. Consider the Kanizsa illusion (Figure 7.1) – it is quite hard to perceive the stimulus as three corners as opposed to one triangle. The brain makes inferences during visual perception that go beyond the raw information given.

Psychologists make a distinction between **sensation** and **perception**. Sensation refers to the effects of a stimulus on the sensory organs, whereas perception involves the elaboration and interpretation of that sensory stimulus based on, for example,

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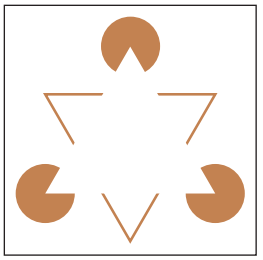

FIGURE 7.1: Do you automatically perceive a white triangle that isn't really there? This is called the Kanizsa illusion.

knowledge of how objects are structured. This chapter will consider many examples of the constructive nature of the seeing brain, from the perception of visual attributes, such as color and motion, up to the recognition of objects and faces.

FROM EYE TO BRAIN

Light is converted into neural signals by the retina, and there are several routes by which this information is carried to the brain. Different routes serve different functions. The dominant route for detailed, conscious visual perception in humans is the geniculostriate route.

EYE–BRAIN MYTH 1

Do not make the mistake of believing that the retina of the left eye represents just the left side of space, and the retina of the right eye represents just the right side of space. (If you are still confused, close one eye and keep it fixed – you should be able to see both sides of space with a minor occlusion due to the nose.) Rather, the left side of the left eye and the left side of the right eye both contain an image of objects on the right side of space. The right side of the left eye and the right side of the right eye both contain an image of objects on the left side of space.

KEY TERMS

Sensation
The effects of a stimulus on the sensory organs.

Perception
The elaboration and interpretation of a sensory stimulus based on, for example, knowledge of how objects are structured.

Retina
The internal surface of the eyes that consists of multiple layers. Some layers contain photoreceptors that convert light to neural signals, and others consist of neurons themselves.

Rod cells
A type of photoreceptor specialized for low levels of light intensity, such as those found at night.

Cone cells
A type of photoreceptor specialized for high levels of light intensity, such as those found during the day, and specialized for the detection of different wavelengths.

Receptive field
The region of space that elicits a response from a given neuron.

The retina

The **retina** is the internal surface of the eyes that contains specialized photoreceptors that convert (or *transduce*) light into neural signals. The photoreceptors are made up of **rod cells**, which are specialized for low levels of light intensity, such as those found at night, and **cone cells**, which are more active during daytime and are specialized for detecting different wavelengths of light (from which the brain can compute color). The highest concentration of cones is at a point called the *fovea*, and the level of detail that can be perceived (or visual acuity) is greatest at this point. Rods are more evenly distributed across the retina (but are not present at the fovea).

There is already a stage of neural computation that takes place at the retina itself. Bipolar cells in the retina are a type of neuron that behave in one of two ways: detecting light areas on dark backgrounds (ON) or detecting dark areas on light backgrounds (OFF). A higher level of processing, by retinal ganglion cells, has a more complex set of on and off properties. Most retinal ganglion neurons have a particular characteristic response to light that is termed a *center-surround* receptive field. The term **receptive field** denotes the region of space that elicits a response from a given neuron. One intriguing

feature of the receptive fields of these cells, and many others in the visual system, is that they do not respond to light as such (Barlow, 1953; Kuffler & Barlow, 1953). Rather, they respond to *differences* in light across the center and surround of their receptive field, as shown in Figure 7.2. Light falling in the center of the receptive field may excite the neuron, whereas light in the surrounding area may switch it off, but when the light is removed from this region, the cell is excited again (on-center off-surround cells). Other retinal ganglion cells have the opposite profile (off-center on-surround cells). Light over the entire receptive field may elicit no net effect because the center and surround inhibit each other. These center-surround cells form the building blocks for more advanced processing by the brain, enabling detection of, among other things, edges and orientations.

The output of the retinal ganglion cells is relayed to the brain via the *optic nerves.* The point at which the optic nerve leaves the eye is called the **blind spot**, because there are no rods and cones present

KEY TERM

Blind spot
The point at which the optic nerve leaves the eye. There are no rods and cones present there.

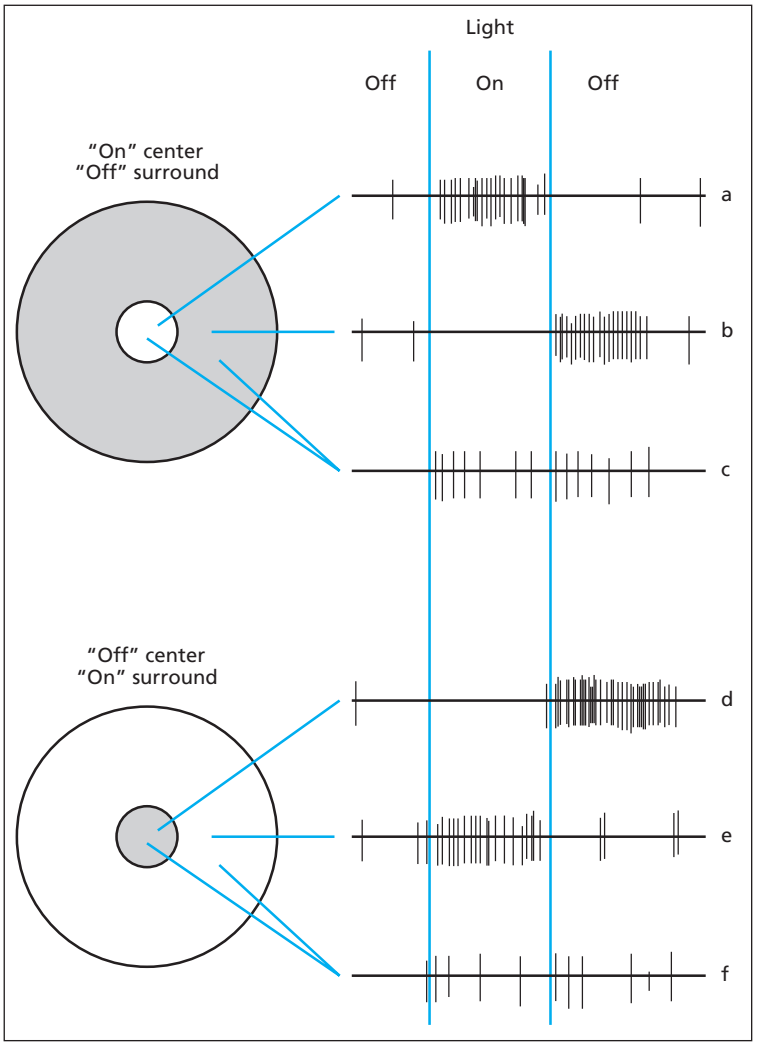

FIGURE 7.2: Receptive fields of two retinal ganglion cells. The cell in the upper part of the figure responds when the center is illuminated (on-center, a) and when the surround is darkened (off-surround, b). The cell in the lower part of the figure responds when the center is darkened (off-center, d) and when the surround is illuminated (on-surround, e). Both cells give on- and off-responses when both center and surround are illuminated (c and f), but neither response is as strong as when only center or surround is illuminated.
From Hubel (1963)

FIGURE 7.3: To find your blind spots, hold the book about 50–70 cm away. With your left eye open (right closed), look at the +. Adjust the distance of the book (or move your head) while looking at the + (do not move your eyes). At a certain distance, the dot will disappear from sight . . . this is when the dot falls on the blind spot of your retina. Reverse the process: Close your left eye and look at the dot with your right eye. Move the image slowly closer to you, and the + should disappear.

there. If you open only one of your eyes (and keep it stationary), there is a spot in which there is no visual information. Yet one does not perceive a black hole in one's vision (try the experiment in Figure 7.3). This is another example of the brain filling in missing information.

The primary visual cortex and geniculostriate pathway

Although there is a single channel of neural output from each eye, via the optic nerve, this subsequently splits into multiple branches (in the optic tract and beyond) with the net result being that there are a number of different pathways from the retina to the brain (Stoerig & Cowey, 1997). The dominant visual pathway in the human brain travels to the **primary visual cortex** at the back, or posterior, of the brain, via a processing station called the lateral geniculate nucleus (LGN), as shown in Figure 7.4. The LGN is part of the thalamus, which has a more general role in processing sensory information; there is one LGN in each hemisphere. The primary visual cortex is also referred to as V1, or as the striate cortex because it has a larger than usual stripe running through one layer that can be seen when stained and viewed under a microscope. This particular route is called the geniculo-striate pathway.

KEY TERM

Primary visual cortex (or V1)
The first stage of visual processing in the cortex; the region retains the spatial relationships found on the retina and combines simple visual features into more complex ones.

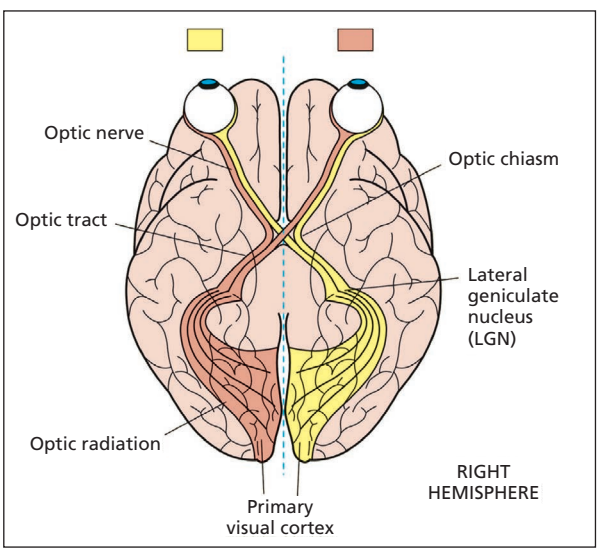

FIGURE 7.4: Connections from the retina to the primary visual cortex – the geniculostriate pathway.

From Zeki (1993). © Blackwell Publishing. Reproduced with permission.

The neural representation in the lateral geniculate nucleus divides up information on the retinal surface in a number of interesting ways. Objects in the right side of space (termed the right visual field) fall on the left side of the retina of *both* eyes and project to the left lateral geniculate nucleus. The representation in the lateral geniculate nucleus thus contains information from both the left and right eyes. This information is segregated into the six different neuronal layers of this structure, three for each eye. The layers of the lateral geniculate nucleus are not only divided according to the eye (left or right) but also contain a further subdivision. The upper four

layers have small cell bodies and have been termed *parvocellular*, or P layers, whereas the lower two layers contain larger cell bodies and have been termed *magnocellular*, or M layers. Parvocellular cells respond to detail and are concerned with color vision. Magnocellular cells are more sensitive to movement than color and respond to larger areas of visual field (Maunsell, 1987). A third type of cell (K or konio) has been documented in the LGN that lies between the magnocellular (magno) and parvocellular (parvo) layers (Hendry & Reid, 2000). These cells show much less functional specificity than magno and parvo cells and have a different pattern of connectivity.

EYE–BRAIN MYTH 2

If you think that the response of neurons on the retina or in the brain is like the response of pixels in a television screen, then think again. Some visual neurons respond when light is taken away, or when there is a *change* in light intensity across the region that they respond to. Other neurons in extrastriate areas respond only to certain colors, or movement in certain directions. These neurons often have very large receptive fields that do not represent a very precise pixel-like location at all.

ONLINE RESOURCES

Check out Jamie Ward's Cognitive Neuroscience Bitesize on Early Visual Processes in the Brain by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

The neurons in V1 transform the information in the lateral geniculate nucleus into a basic code that enables different kinds of visual information to be extracted by later stages of processing. First of all, neurons need to be able to represent how light or dark something is. In addition, neurons need to represent the color of an object to distinguish, say, between fruit and foliage of comparable lightness/darkness but complementary in color. Edges also need to be detected, and these might be defined as abrupt changes in brightness or color. These edges might be useful for perceiving the shape of objects. Changes in brightness or color could also reflect movement of an object, and it is conceivable that some neurons may be specialized for extracting this type of visual information. Depth may also be perceived by comparing the two different retinal images.

The properties of neurons in the primary visual cortex were elucidated by pioneering work by David Hubel and Torsten Wiesel (1959, 1962, 1965, 1968, 1970a), for which they were awarded the Nobel Prize in Medicine in 1981. The method they used was to record the response of single neurons in the visual cortex of cats and monkeys. As with many great discoveries, there was an element of chance. Hubel and Wiesel noted that an oriented crack in a projector slide drove a single cell in V1 wild, that is, it produced lots of action potentials (cited in Zeki, 1993). They then

KEY TERMS

Simple cells
In vision, cells that respond to light in a particular orientation (or points of light along that line).

Complex cells
In vision, cells that respond to light in a particular orientation but do not respond to single points of light.

Hypercomplex cells
In vision, cells that respond to particular orientations and particular lengths.

systematically went on to show that many of these cells responded only to particular orientations. These were termed **simple cells**. The responses of these simple cells could be construed as a combination of the responses of center-surround cells in the lateral geniculate nucleus (Hubel & Wiesel, 1962), as shown in Figure 7.5. The cells also integrate information across both eyes and respond to similar input to either the left or right eye. Many orientation-selective cells were found to be wavelength-sensitive too (Hubel & Wiesel, 1968), thus providing a primitive code from which to derive color.

Just as center-surround cells might be the building blocks of simple cells, Hubel and Wiesel (1962) speculated that simple cells themselves might be combined into what they termed **complex cells**. These are orientation-selective too but can be distinguished from simple cells by their larger receptive fields and the fact that complex cells require stimulation across their entire length, whereas simple cells will respond to single points of light within the excitatory region. Outside of V1, another type of cell, termed **hypercomplex cells**, which can be built from the responses of several complex cells, was observed (Hubel & Wiesel, 1965). These cells were also orientation-sensitive, but the length was also critical. The receptive fields of hypercomplex cells may consist of adding excitatory complex cells, but with inhibitory complex cells located at either end to act as "stoppers." In sum, the response properties of cells in V1 enable more complex visual information (e.g., edges) to be constructed out of more simple information.

The take-home message of the work of Hubel and Wiesel is of a hierarchically organized visual system in which more complex visual features are built (bottom-up) from more simple ones. However, this is only half of the story. Information from more complex representations also propagates *down* the hierarchy. For instance, in the Kanizsa illusion, there are cells in V2 (but not V1) that respond to the illusory "white edges" of the triangle (Von der Heydt et al., 1984). This is assumed to reflect feedback information to V2 from regions in the brain that represent shapes and surfaces (Kogo & Wagemans, 2013).

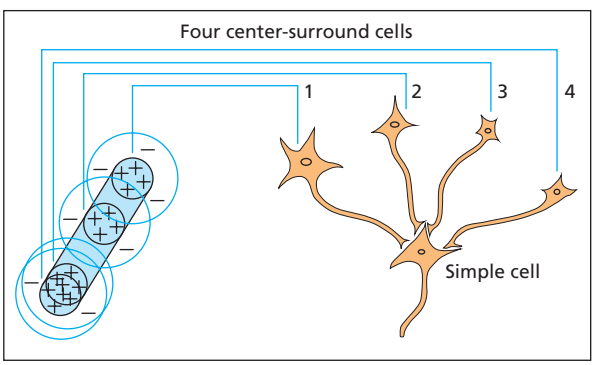

FIGURE 7.5: A simple cell in V1 responds to lines of particular length and orientation. Its response may be derived from a combination of responses from different cells with center-surround properties such as those located in the lateral geniculate nucleus.

From Zeki (1993). © Blackwell Publishing. Reproduced with permission.

Cortical and non-cortical routes to seeing

To date, around ten different pathways from the eye to the brain have been discovered (Figure 7.6), of which the pathway via the lateral geniculate nucleus to V1 is the most well understood and appears to make the

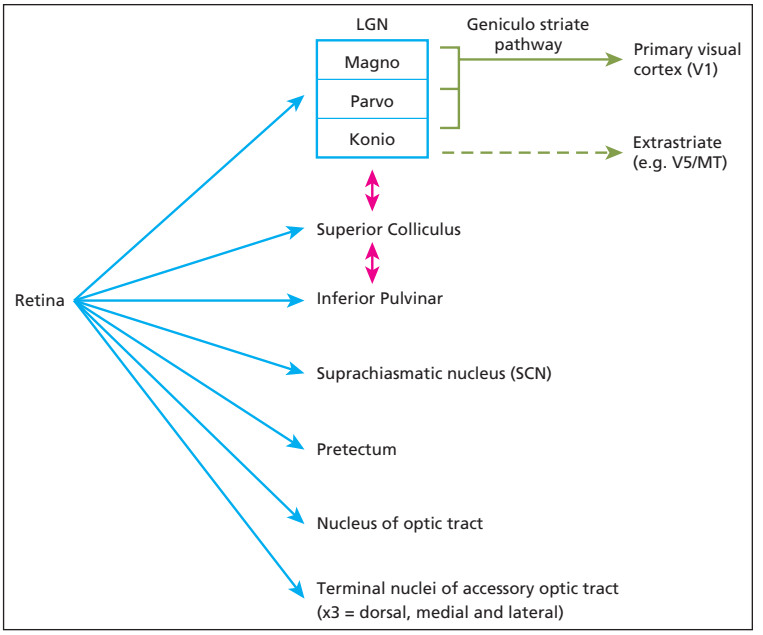

FIGURE 7.6: There are believed to be ten different routes from the retina to different regions of the brain.

largest contribution to human visual perception (Stoerig & Cowey, 1997). The other routes are evolutionarily more ancient. Evolution appears not to have replaced these routes with "better" ones but has retained them and added new routes that enable finer levels of processing or that serve somewhat different functions. For example, a visual route from retinal ganglion cells to the suprachiasmatic nucleus (SCN) in the hypothalamus provides information about night and day that is used to configure a biological clock (Klein et al., 1991). Other routes, such as via the superior colliculus and inferior pulvinar, are important for orienting to stimuli (e.g., a sudden flash of light) by initiating automatic body and eye movements (Wurtz et al., 1982). These latter routes are faster than the route via V1 and can thus provide an early warning signal; for instance, to threatening or unexpected stimuli. This can explain how it is possible to unconsciously turn to look at something without realizing its importance until after orienting. More recently, an alternative pathway from the LGN (via the K-cells) to the cortex has been documented that projects to a part of the brain that is specialized for process of visual motion (area V5/MT) without first projecting to V1 (Sincich et al., 2004). This may account for the fact that some patients with cortical blindness can still discriminate motion.

Evaluation

V1 contains cells that enable a basic detection of visual features, such as edges, that are likely to be important for segregating

the scene into different objects. There is some evidence for a hierarchical processing of visual features such that responses of earlier neurons in the hierarchy form the building blocks for more advanced responses of neurons higher up in the hierarchy. A number of other routes operate in parallel to the geniculostriate route to V1. These may be important for early detection of visual stimuli, among other things.

CORTICAL BLINDNESS AND "BLINDSIGHT"

KEY TERMS

Hemianopia
Cortical blindness restricted to one half of the visual field (associated with damage to the primary visual cortex in one hemisphere).

Quadrantanopia
Cortical blindness restricted to a quarter of the visual field.

Scotoma
A small region of cortical blindness.

Retinotopic organization
The receptive fields of a set of neurons are organized in such a way as to reflect the spatial organization present in the retina.

Loss of one eye, or the optic nerve of that eye, results in complete blindness in that eye. The spared eye would still be able to perceive the left and right sides of space and transmit information to the left and right primary visual cortex. But what would be the consequences of *complete* damage to one side of the primary visual cortex itself? In this instance, there would be cortical blindness for one side of space (if the left cortex is damaged, then the right visual field would be blind, and vice versa). The deficit would be present when using either the left or right eye alone, or both eyes together. This deficit is termed **hemianopia** (or homonymous hemianopia). *Partial* damage to the primary visual cortex might affect one subregion of space. As the upper part of V1 (above a line called the calcarine fissure) represents the bottom side of space, and the lower part of V1 represents the top part of space, damage here can give rise to cortical blindness in a quarter of the visual field (so-called **quadrantanopia**). Blindness in a smaller region of space is referred to as a cortical **scotoma**. These are illustrated in Figure 7.7. Note that the layout of visual information in V1 parallels that found on the retina. That is, points that are close in space on the retina are also close in space in V1. Areas such as V1 are said to be **retinotopically organized**.

EYE–BRAIN MYTH 3

The image on the retina and the representation of it in V1 are "upside down" with respect to the outside world. As such, one might wonder how the brain turns it the right way up. This question is meaningless because it presupposes that the orientation of things in the outside world is in some way "correct" and the brain's representation of it is in some way "incorrect." There is no "correct" orientation (all orientation is relative), and the brain does not need to turn things around to perceive them appropriately. What does need to happen is that neurons coding the position of space in the visual field need to interface appropriately with, for instance, neurons that guide reaching movements of the hand upwards or downwards such that visual spatial information is appropriately calibrated with other kinds of non-visual spatial information.

The previous section described how there are several visual routes from the eye to the brain. Each of these routes makes a different contribution to visual perception. Taking this on board, one might question whether damage to the brain (as opposed to the eyes) could really lead to total blindness unless each and every one of these visual pathways coincidentally happened to be damaged. In fact, this is indeed the case. Damage to the primary visual cortex does lead to an inability to report visual stimuli presented in the corresponding affected region of space and can be disabling for such a person. Nevertheless, the other remaining visual routes might permit some aspects of visual perception to be performed satisfactorily in exactly the same regions of space that are reported to be blind. This paradoxical situation has been referred to as **blindsight** (Weiskrantz et al., 1974).

Patients exhibiting blindsight deny having seen a visual stimulus even though their behavior implies that the stimulus was in fact seen (for a review, see Cowey, 2010). For example, patient DB had part of his V1 removed to cure a chronic and severe migraine (this was reported in detail by Weiskrantz, 1986). When stimuli were presented in DB's blind field, he reported seeing nothing. However, if asked to point or move his eyes to the stimulus, then he could do so with accuracy, while still maintaining that he saw nothing. DB could perform a number of other discriminations well above chance, such as orientation discrimination (horizontal, vertical, or diagonal), motion detection (static or moving), and contrast discrimination (gray on black versus gray on white). In all these tasks DB felt as if he was guessing even though he clearly was not. Some form/shape discrimination was possible but appeared to be due to detection of edges and orientations rather than shape itself. For example, DB could discriminate between X and O, but not between X and A, and not between squares and rectangles that contain lines of similar orientation (but see Marcel, 1998).

How can the performance of patients such as DB be explained? First of all, one needs to eliminate the possibility that the task is being performed by remnants of the primary visual cortex. For example,

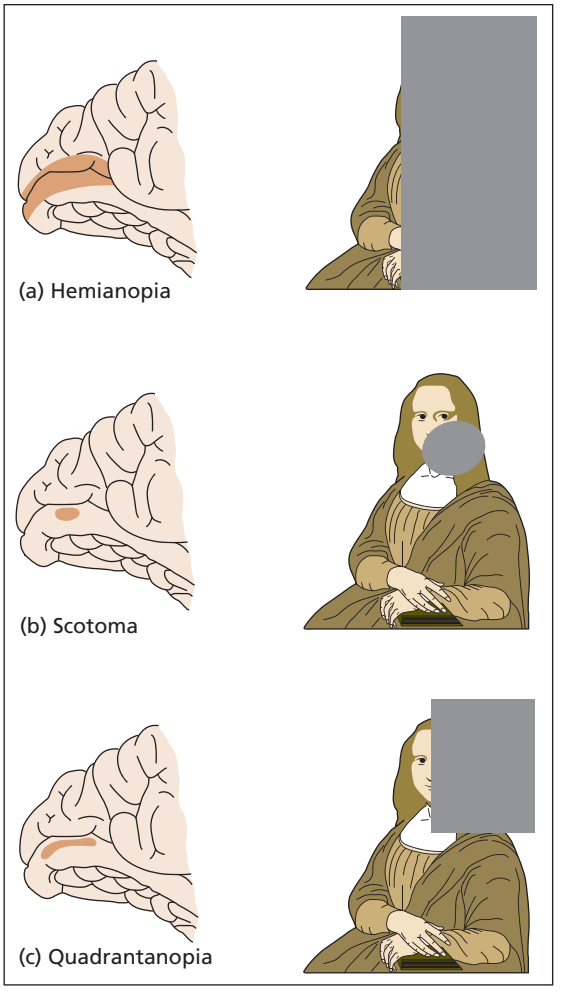

FIGURE 7.7: Partial damage to the primary visual cortex (V1) can result in blindness in specific regions (shown here in gray). This is because this region of the brain is retinotopically organized. Area V1 is at the back of the brain and on the middle surface between the two hemispheres.

Adapted from Zeki (1993).

KEY TERM

Blindsight
A symptom in which the patient reports not being able to consciously see stimuli in a particular region but can nevertheless perform visual discriminations (e.g., long, short) accurately.

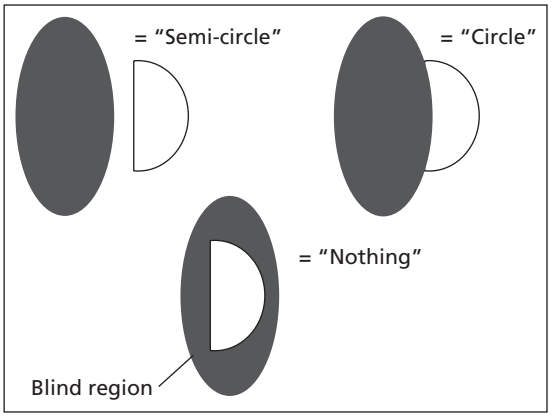

FIGURE 7.8: If a visually presented semicircle abuts a cortical scotoma (the shaded area), then the patient might report a complete circle. Thus, rather than seeing a gap in their vision, patients with blindsight might fill in the gap using visual information in the spared field. If the semicircle is presented inside the scotoma, it isn't seen at all, whereas if it is away from the scotoma, it is perceived normally.

Adapted from Torjussen (1976).

there could be islands of spared cortex within the supposedly damaged region (Campion et al., 1983). However, many patients have undergone structural MRI, and it has been established that no cortex remains in the region corresponding to the "blind" field (Cowey, 2010). Another explanation is that light from the stimulus is scattered into other intact parts of the visual field and is detected by intact parts of the primary visual cortex. For example, some patients may be able to detect stimuli supposedly in their blind field because of light reflected on their nose or other surfaces in the laboratory (Campion et al., 1983). Evidence against this comes from the fact that performance is superior in the "blindsight" region to the natural blind spot (found in us all). This cannot be accounted for by scattered light (see Cowey, 2010). Thus, the most satisfactory explanation of blindsight is that it reflects the operation of other visual routes from the eye to the brain rather than the residual ability of V1. For instance, the ability to detect visual motion in blindsight might be due to direct projections from the LGN to area V5/MT that bypasses V1 (Hesselmann et al., 2010).

This account raises important questions about the functional importance of conscious versus unconscious visual processes. If unconscious visual processes can discriminate well, then why is the conscious route needed at all? As it turns out, such questions are misguided because the unconscious routes (used in blindsight) are not as efficient and are only capable of coarse discriminations in comparison to the finely tuned discriminations achieved by V1 (see Cowey, 2010). At present, we do not have a full understanding of why some neural processes but not others are associated with conscious visual experiences (e.g., Leopold, 2012). Nevertheless, studies of patients with blindsight provide important clues about the relative contribution and functions of the different visual pathways in the brain (Figure 7.8).

Blindsight ≠ normal vision – awareness of vision
Blindsight = impaired vision + no awareness of vision

FUNCTIONAL SPECIALIZATION OF THE VISUAL CORTEX BEYOND V1

The neurons in V1 are specialized for detecting edges and orientations, wavelengths, and light intensity. These form the building blocks for constructing more complex visual representations based on form (i.e., shape), color, and movement. Some of the principal anatomical connections between these regions are shown

in Figure 7.9. One important division, discussed in more detail in later chapters, is between the **ventral stream** (involved in object recognition and memory) and the **dorsal stream** (involved in action and attention). The ventral stream runs along the temporal lobes, whereas the dorsal stream terminates in the parietal lobes.

The occipital cortex outside V1 is known as the *extrastriate cortex* (or prestriate cortex). The receptive fields in these extrastriate visual areas become increasingly broader and less coherently organized in space, with areas V4 and V5/MT having very broad receptive fields (Zeki, 1969). The extrastriate cortex also contains a number of areas that are specialized for processing specific visual attributes such as color (area **V4**) and movement (area **V5 or MT**, standing for medial temporal). To some extent, the brain's strategy for processing information outside of V1 is to "divide and conquer." For example, it is possible to have brain damage that impairs color perception (cerebral **achromatopsia**) or movement perception (cerebral **akinetopsia**) that preserves other visual functions. These regions are shown in Figure 7.10.

V4: the main color center of the brain

Area V4 is believed to be the main color center in the human brain because lesions to it result in a lack of color vision, so that the world is perceived in shades of gray (Heywood et al., 1998; Zeki, 1990). This is termed cerebral achromatopsia. It is not to be confused with color blindness in which people (normally men) have difficulty discriminating colors such as reds and greens because of a deficiency in certain types of retinal cells. Achromatopsia is rare because there are two V4 areas in the brain, and it is unlikely that brain damage would symmetrically affect both hemispheres. Damage to one of the V4s would result in one side of space being seen as colorless (left V4 represents color for the right hemifield and vice versa). Partial damage to V4 can result in colors that appear

KEY TERMS

Ventral stream
In vision, a pathway extending from the occipital lobes to the temporal lobes involved in object recognition, memory, and semantics.

Dorsal stream
In vision, a pathway extending from the occipital lobes to the parietal lobes involved in visually guided action and attention.

V4
A region of the extrastriate cortex associated with color perception.

V5 (or MT)
A region of the extrastriate cortex associated with motion perception.

Achromatopsia
A failure to perceive color (the world appears in grayscale), not to be confused with color blindness (deficient or absent types of cone cell).

Akinetopsia
A failure to perceive visual motion.

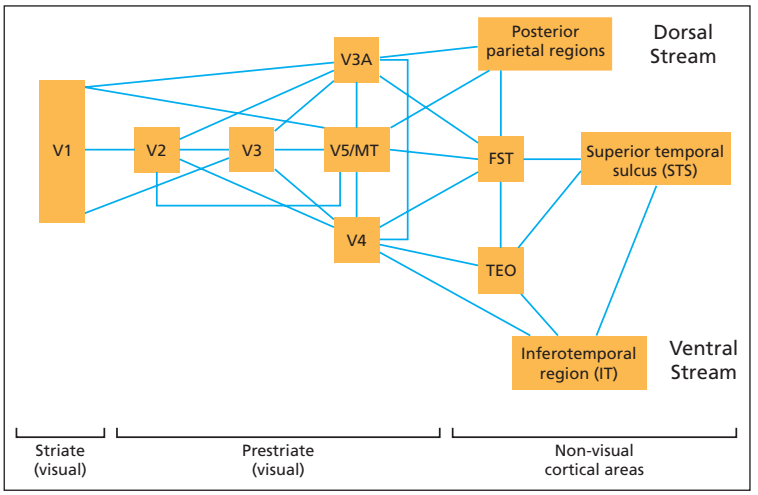

FIGURE 7.9: Information from V1 is sent in parallel to a number of other regions in the extrastriate cortex, some of which are specialized for processing particular visual attributes (e.g., V5/MT for movement). These extrastriate regions interface with the temporal cortex (involved in object recognition) and the parietal cortex (involved in space and attention).

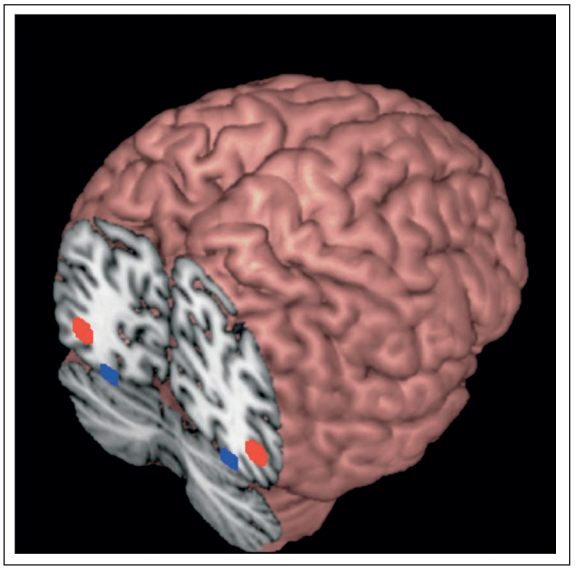

FIGURE 7.10: Area V5/MT (in red) lies near the outer surface of both hemispheres and is responsible for perception of visual motion. Area V4 (in blue) lies on the under surface of the brain, in each hemisphere, and is responsible for the perception of color. This brain is viewed from the back.

"dirty" or "washed out" (Meadows, 1974). In people who have not sustained brain injury, area V4 can be identified by functional imaging by comparing viewing patterns of colored squares (so-called Mondrians, because of a similarity to the work of that artist) with their equivalent grayscale picture (Zeki et al., 1991). The grayscale pictures are matched for luminance such that if either image were viewed through a black-and-white camera, they would appear identical to each other.

Why is color so important that the brain would set aside an entire region dedicated to it? Moreover, given that the retina contains cells that detect different wavelengths of visible light, why does the brain need a dedicated color processor at all? To answer both of these questions, it is important to understand the concept of **color constancy**. Color constancy refers to the fact that the color of a surface is perceived as constant even when illuminated in different lighting conditions and even though the physical wavelength composition of light reflected from a surface can be shown (with recording devices) to differ under different conditions. For example, a surface that reflects a high proportion of long-wave "red" light will appear red when illuminated with white, red, green, or any other type of light. Color constancy is needed to facilitate recognition of, say, red tomatoes across a wide variety of viewing conditions. The online viral phenomenon known as "The Dress" is also an example of color constancy (see Figure 7.10). If the viewer interprets the dress as being illuminated by yellowish light, then the fabric color is perceived as black and blue, but if it is interpreted as being illuminated by blue light, then the color is perceived as white and gold (Lafer-Sousa et al., 2015). The close cropping of the image helps to create the initial ambiguity in the background lighting condition.

KEY TERM

Color constancy
The color of a surface is perceived as constant even when illuminated in different lighting conditions.

The derivation of color constancy appears to be the function of V4 (Zeki, 1983). Neurons in V4 may achieve this by comparing the wavelength in their receptive fields with the wavelength in other fields. In this way, it is possible to compute the color of a surface while taking into account the illuminating conditions of the whole scene (Land, 1964, 1983). Cells in earlier visual regions (e.g., V1) respond only to the local wavelength in their receptive field, and their response would change if the light source were changed even if the color of the stimulus was not (Zeki, 1983), a finding that has been replicated in humans using fMRI (Brouwer & Heeger, 2009). Achromatopsic

patients with damage to V4 are able to use earlier visual processes that are based on wavelength discrimination in the absence of color experience. For example, patient MS could tell if two equiluminant colored patches were the same or different if they abutted to form a common edge, but not if they were separated (Heywood et al., 1991). This occurs because wavelength comparisons outside of V4 are made at a local level. Although earlier visual regions respond to wavelength, V4 has some special characteristics. The neurons in V4 tend to have larger receptive fields than earlier regions. Moreover, evidence from fMRI shows that voxels that are sensitive to one color (e.g., red) tend to have graded selectivity to perceptually neighboring colors (e.g., violets, yellows), but this is not found in earlier visual regions (Brouwer & Heeger, 2009). It suggests that V4 implements a relational coding between colors (analogous to a color wheel) that may also be helpful for color constancy.

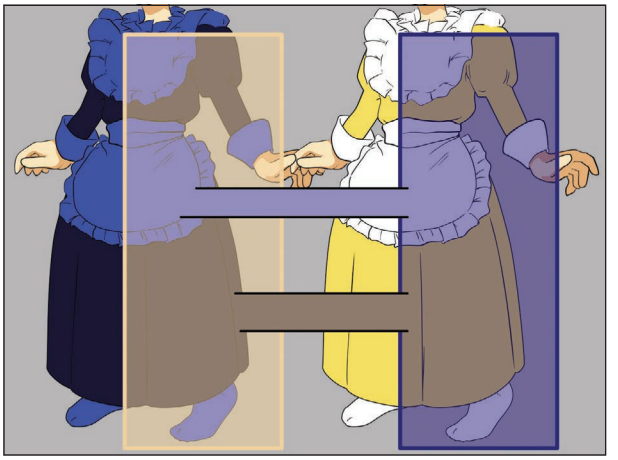

FIGURE 7.11: What color is "The Dress"? The original image went viral on social media because some people perceive it as black and blue, and others as white-gold. This image shows how the same dress can be perceived differently depending on whether the ambient lighting is assumed to be bright or dark.
Natallia Krechka/Alamy Stock Vector

Although V4 has been described as "the main color center in the human brain," it does not follow that it only processes color information. Evidence from macaque single-cell recordings suggests neurons in V4 also respond to visual features such as shape and texture (Roe et al., 2012). Moreover, it should be pointed out that V4 is not the only color-responsive region of the brain. For example, Zeki and Marini (1998) compared viewing of appropriately colored objects (e.g., a red tomato) with inappropriate ones (e.g., a blue tomato) in humans and found activation in, among other regions, the hippocampus, which may code long-term memory representations. Memory representations of color can also activate the visual cortex: viewing a grayscale banana can induce a pattern of activity consistent with yellow in regions such as V1 and V4 (Bannert & Bartels, 2013).

V5/MT: the main movement center of the brain

If participants in a PET scanner view images of moving dots relative to static dots, a region of the extrastriate cortex called V5 (or MT) becomes particularly active (Zeki et al., 1991). Earlier electrophysiological research on the monkey had found that all cells in this area are sensitive to motion, and that 90 percent of them respond preferentially to a particular direction of motion and will not respond at all to the opposite direction of motion (Zeki, 1974). None were color-sensitive.

Patient LM lost the ability to perceive visual movement after bilateral damage to area V5/MT (Zihl et al., 1983). This

condition is termed akinetopsia (for a review, see Zeki, 1991). Her visual world consists of a series of still frames: objects may suddenly appear or disappear, a car that is distant may suddenly be seen to be near, and pouring tea into a cup would invariably end in spillage as the level of liquid appears to rise in jumps rather than smoothly.

Other studies have suggested that other types of movement perception do not rely on V5/MT. For example, LM is able to discriminate biological from non-biological motion (McLeod et al., 1996). The perception of **biological motion** was traditionally assessed by attaching light points to the joints and then recording someone walking/running in the dark (Figure 7.12). When only the light points are viewed, most people are still able to detect bodily movement (relative to a condition in which these moving lights are presented jumbled up). LM could discriminate biological from non-biological motion, but could not perceive the overall direction of movement. Separate pathways for this type of motion have been implied by functional imaging (Vaina et al., 2001).

KEY TERM

Biological motion
The ability to detect whether a stimulus is animate or not from movement cues alone.

LM was able to detect movement in other sensory modalities (e.g., touch, audition), suggesting that her difficulties were restricted to certain types of visual movement (Zihl et al., 1983). However, functional imaging studies have identified supramodal regions of the brain (in the parietal cortex) that appear to respond to movement in three different senses – vision, touch, and hearing (Bremmer et al., 2001).

Evaluation

One emerging view of visual processing in the brain beyond V1 is that different types of visual information get parsed into more specialized brain regions. Thus, when one looks at a dog running across the garden, information about its color resides in one region, information about its movement resides in another, and information about its identity (this is my dog rather than any dog) resides in yet another, to name but a few. The question of how these different streams of information come back together (if at all) is not well understood but may require the involvement of non-visual processes related to attention (see Chapter 9).

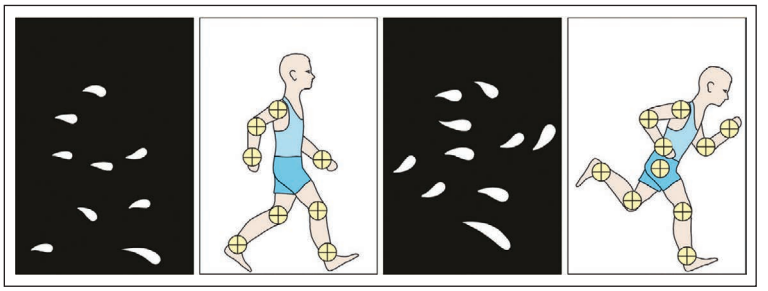

FIGURE 7.12: When this array of dots is set in motion, most people can distinguish between biological and non-biological motion.

HOW DOES THE BRAIN RESPOND TO VISUAL ILLUSIONS?

When you look at the top part of Figure 7.13 do you have a sense of motion in the circles even though the image is static? This image is called the Enigma illusion. When you look at the bottom image, do you see one vase or two faces? Does this image appear to spontaneously flip between one interpretation and the other, even though the image remains constant? Examples such as these reveal how the brain's perception of the world can differ from the external physical reality. This is, in fact, a normal part of seeing. Visual illusions are in many respects the norm rather than the exception, even though we are not always aware of them as such.

A functional imaging study has shown that parts of the brain specialized for detecting real movement (area V5/MT) also respond to the Enigma illusion (Zeki et al., 1993). It has been suggested that the illusion of movement is driven by tiny adjustments in eye fixation (Troncoso et al., 2008). An fMRI study using bi-stable stimuli such as the face–vase has shown how different visual and non-visual brain structures cooperate to maintain perceptual stability. The momentary breakdown of activity in these regions is associated with the timing of the subjective perceptual flip (Kleinschmidt et al., 1998). TMS over the right parietal lobes affects the rate of switch between bi-stable images with adjacent regions either promoting stability or generating instability (Kanai et al., 2011). This suggests different top-down biasing influences on perception.

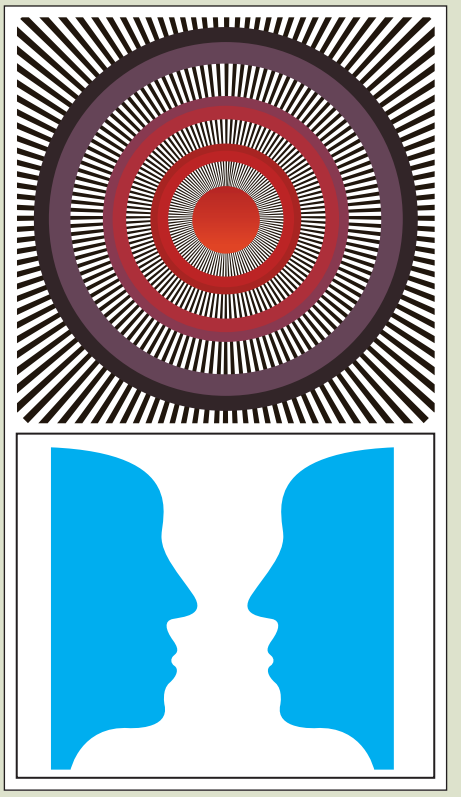

FIGURE 7.13: Do you see movement in the image on the top when you stare at the center? Do you see a vase or faces on the bottom? How does the brain interpret such ambiguities?
Godong/Alamy Stock Photo

RECOGNIZING OBJECTS

For visual information to be useful, it must make contact with knowledge that has been accumulated about the world. There is a need to recognize places that have been visited and people who have been seen and to recognize other stimuli in the environment in order to, say, distinguish between edible and non-edible substances. All of these examples can be subsumed under the process of "object recognition." Although different types of object (e.g., faces) may

ONLINE RESOURCES

To learn more about visual illusions and how they are created by the brain, check out illusionoftheyear.com and visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience).

recruit some different mechanisms, there will nevertheless be some common mechanisms shared by all objects, given that they are extracted from the same raw visual information.

Figure 7.14 outlines several basic stages in object recognition that, terminology aside, bear a close resemblance to Marr's (1976) theory of vision:

1. The earliest stage in visual processing involves basic elements such as edges and bars of various lengths, contrasts, and orientations. This stage has already been considered previously.
2. Later stages involve grouping these elements into higher-order units that code depth cues and segregate surfaces into figure and ground. Some of these mechanisms were first described by the Gestalt psychologists and are considered in the next section. It is possible that this stage is also influenced by top-down information based on stored knowledge. These visual representations, however, represent objects according to the observer's viewpoint and object constancy is not present.
3. The viewer-centered description is then matched onto stored three-dimensional descriptions of the structure of objects (**structural descriptions**). This store is often assumed to represent only certain viewpoints and thus the matching process entails the computation of object constancy (i.e., an understanding that objects remain the same irrespective of differences in viewing condition). There may be two different routes to achieving object constancy, depending on whether the view is "normalized" by rotating the object to a standard orientation.
4. Finally, meaning is attributed to the stimulus, and other information (e.g., the name) becomes available. This will be considered primarily in Chapter 12.

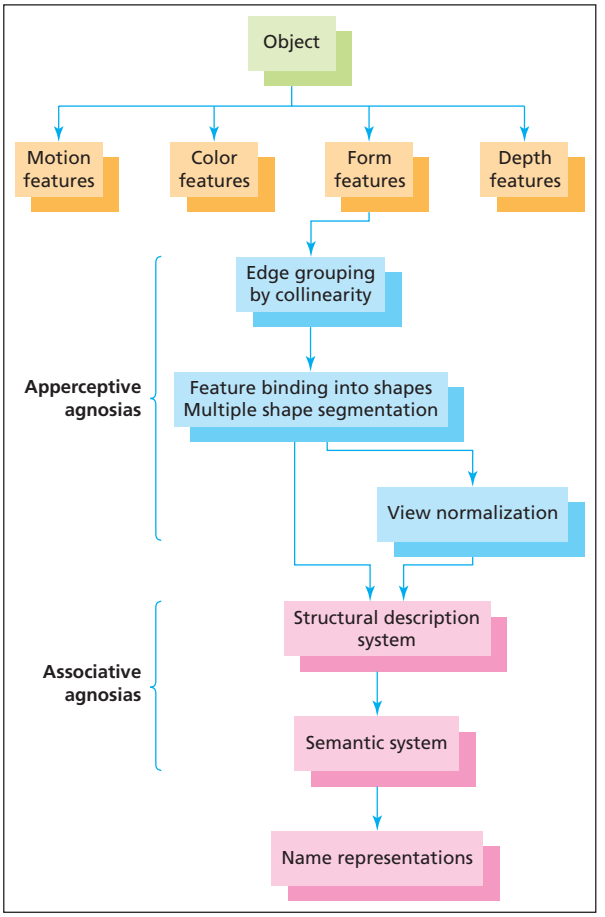

FIGURE 7.14: A simple model of visual object recognition.

From Riddoch and Humphreys (2001). Reproduced by permission of Taylor & Francis Group.

Disorders of object recognition are referred to as visual agnosia, and these have been traditionally subdivided into **apperceptive agnosia** and **associative agnosia**, depending

on whether the deficit occurs at stages involved in perceptual processing or stages involving stored visual memory representations (Lissauer, 1890). This classification is perhaps too simple to be of much use in modern cognitive neuroscience. Models such as the one of Riddoch and Humphreys (2001) acknowledge that both perception and the stored properties of objects can be broken down into even finer processes. It is also the case that most contemporary models of object recognition allow for interactivity between different processes rather than discrete processing stages. This is broadly consistent with the neuroanatomical data (see earlier) of connections between early and late visual regions and vice versa.

Parts and wholes: Gestalt grouping principles

In the 1930s, Gestalt psychologists identified a number of principles that explain why certain visual features become grouped together to form perceptual wholes (Figure 7.15). These operations form a key stage in translating simple features into three-dimensional descriptions of the world, essential for object recognition. The process of segmenting a visual display into objects versus background surfaces is also known as **figure-ground segregation**. The Gestalt approach identified five basic principles to account for how basic visual features are combined:

1. *The law of proximity* states that visual elements are more likely to be grouped if they are closer together. For example, the dots in (a) in the figure tend to be perceived as three horizontal lines because they are closer together horizontally than vertically.
2. *The law of similarity* states that elements will be grouped together if they share visual attributes (e.g., color, shape). For example, (b) tends to be perceived as vertical columns rather than rows, because elements in columns share both shape and color.

KEY TERMS

Structural descriptions
A memory representation of the three-dimensional structure of objects.

Apperceptive agnosia
A failure to understand the meaning of objects due to a deficit at the level of object perception.

Associative agnosia
A failure to understand the meaning of objects due to a deficit at the level of semantic memory.

Figure-ground segregation
The process of segmenting a visual display into objects versus background surfaces.

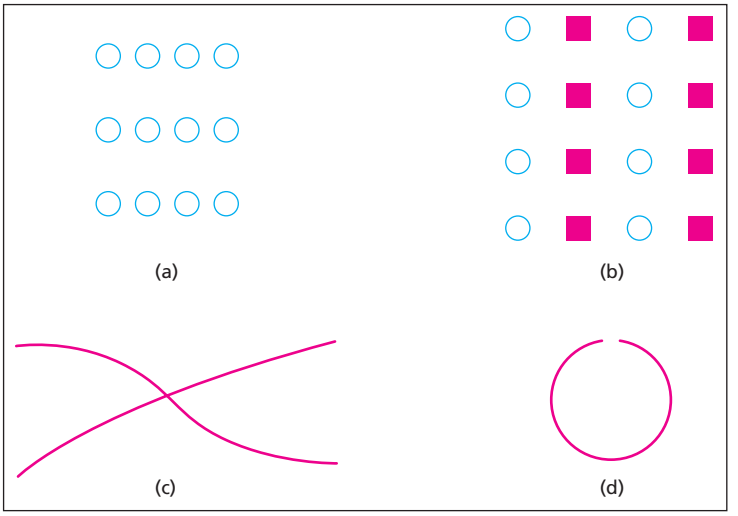

FIGURE 7.15: The Gestalt principles of (a) law of proximity, (b) law of similarity, (c) law of good continuation, and (d) law of closure.

3. *The law of good continuation* states that edges are grouped together to avoid changes or interruptions; thus, (c) is two crossing lines rather than > and <.
4. *The law of closure* states that missing parts are "filled in"; thus (d) has circular properties in spite of the gap. This law, and the previous one, is important for recognizing objects that are partly occluded.
5. *The law of common fate* states that elements that move together tend to be grouped together. A good example of this comes from studies of biological motion perception (e.g., Johansson, 1973). Light points attached to bodily joints are perceived as movement of a single human figure when viewed in the dark.

Perceptual grouping occurs at multiple levels within the visual hierarchy (and via interactions between those levels). For instance, grouping of light points based on the known structure and dynamics of the human body occurs only at later stages of visual processing, in this case in the superior temporal sulcus (Grossman et al., 2000). In other instances, there is evidence of grouping effects at the earliest stages of visual processing. Cells in V1 tuned to particular orientations fire more when these orientations are part of the figure rather than the ground as shown by animal single-cell electrophysiology (Lamme, 1995). Human fMRI shows that V1, as well as higher visual regions, are sensitive to the law of good continuation (Altmann et al., 2003). In general, whether grouping occurs early or late will depend on the nature of the stimulus and the extent to which it depends on stored knowledge of objects (e.g., shape of the human body) or less specific knowledge (e.g., the general properties of surfaces, such as occlusion).

KEY TERM

Lateral occipital complex (LOC)
A region of the brain that is specialized for processing object shapes.

One region that is involved in computing the shape of objects is termed the **lateral occipital complex (LOC)**, which lies next to the motion-sensitive area V5/MT. This region responds in fMRI studies to objects more than textures, but it doesn't distinguish between real objects and made-up ones (Malach et al., 1995). This suggests that it is involved in computing shape but does not act as a memory store of structural descriptions. fMRI activity shows adaptation between occluded and non-occluded images of an object suggesting that they are treated as the same, that is, the missing parts are filled in (Kourtzi & Kanwisher, 2001). Disruption of this region with TMS affects the ability to match objects by shape but not by orientation (Chouinard et al., 2017), and it impairs the ability to categorize objects whilst enhancing the ability to categorize scenes (Mullin & Steeves, 2011). The latter suggests competition between different regions specialized for different aspects of vision.

Case HJA: seeing the parts but not the whole

Perhaps the most detailed study of visual agnosia in the literature is case HJA, which was reported in a number of studies by Humphreys, Riddoch, and colleagues (Humphreys & Riddoch, 1987; Riddoch et al., 1999). HJA was a businessman who suffered a bilateral stroke that left him with severe difficulties in recognizing

objects, but with preserved sensory discriminations of length, orientation, and position. A number of tests conducted on HJA support the conclusion that he has difficulty in integrating parts into wholes – a type of apperceptive agnosia on the simple model in Figure 7.14. The evidence in support of this interpretation is summarized in the next table (and see Figure 7.16). These results support the conclusion that HJA has difficulties in using perceptual grouping mechanisms to translate his intact perception of lines into more complex visual descriptions required to access stored knowledge. His visual system does not permit him to take advantage of Gestalt-based grouping mechanisms that support normal object recognition. Humphreys and Riddoch have termed this **integrative agnosia**. It isn't the case that no grouping at all occurs. There is evidence that local contours may be grouped together, for instance, based on the Gestalt principle of continuation (Giersch et al., 2000). This is consistent with the claim that some forms of grouping, and figure-ground segmentation, occur at earlier stages in the visual stream (with these stages largely spared in HJA).

HJA's spared abilities	HJA's impaired abilities
• He is able to copy drawings of objects that he cannot recognize, suggesting that he can "see" them at some level.	• He is unable to recognize pictures, but gives a reasonable description of their parts. For example, when shown a carrot: "The bottom point seems solid and the other bits are feathery. It does not seem logical unless it is some sort of brush."
• He is able to draw objects from memory, suggesting that he can access structural descriptions from memory, but not vision.	• When shown degraded pictures, he does not benefit from Gestalt principles in the same way as other people do (Boucart & Humphreys, 1992).
• He is able to recognize objects from modalities other than vision and has good verbal knowledge about them.	• He is unable to perform an object decision task in which "novel" objects are created by recombining the parts of real objects.

Accessing structural descriptions: object constancy

One of the most important aspects of object recognition is to be able to recognize an object across different viewpoints and different lighting conditions – this is termed **object constancy**. It is generally agreed that object constancy is brought about by matching the constructed visual representation with a store of object descriptions in memory that carry information about the invariant properties of objects. The mechanism by which this

KEY TERMS

Integrative agnosia
A failure to integrate parts into wholes in visual perception.

Object constancy
An understanding that objects remain the same, irrespective of differences in viewing condition.

ONLINE RESOURCES

Check out Jamie Ward's Cognitive Neuroscience Bitesize on Object Recognition – The Ventral Stream by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

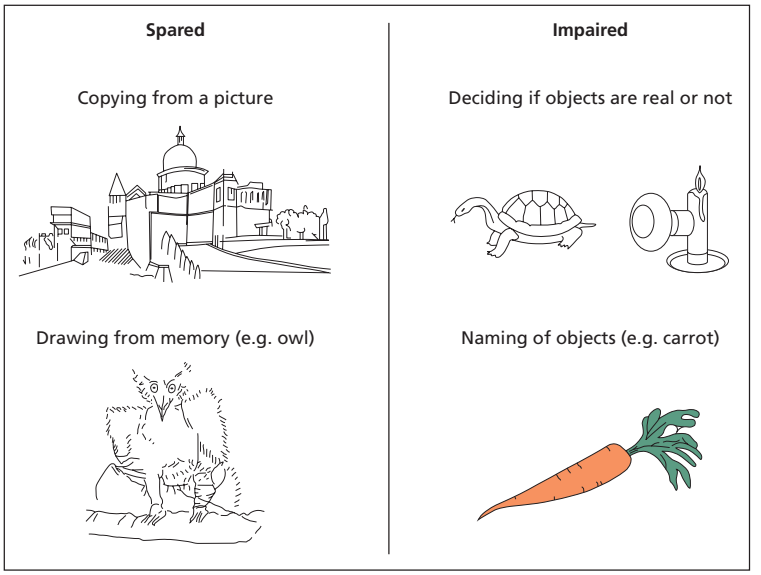

FIGURE 7.16: HJA is impaired at deciding if objects are real or made up and naming objects. However, he can copy drawings and draw objects from memory.

Adapted from Humphreys and Riddoch (1987) and Riddoch and Humphreys (1995).

matching process occurs has traditionally been divided into viewpoint-invariant and viewpoint-dependent mechanisms. Viewpoint-invariant theories, such as that of Biederman (1987), argue that particular object parts or features (e.g., the tines of a fork) are mapped directly to structural descriptions. Regions sensitive to shape, such as LOC, may be important for this (Hayworth & Biederman, 2006). Others have argued that the most important mechanism is more holistic and involves extracting the principal axis of an object (Marr & Nishihara, 1978). Thus, seeing an object from an unusual view (e.g., a foreshortened fork) would first require a "mental rotation" into a normal viewpoint. Naming times for objects presented in unusual views are slower (Palmer et al., 1981), but this could potentially reflect less familiarity with these viewpoints rather than a view normalization procedure (Karnath et al., 2000). Evidence from cognitive neuroscience points to the existence of both viewpoint-invariant and viewpoint-dependent mechanisms.

The inferotemporal cortex (IT) takes its input from the geniculostriate pathway and appears to code the type of information important for object constancy. For example, single-cell recordings from macaques show that these cells respond to specific object attributes (e.g., junctions) and have large receptive fields that almost always cover the fovea and typically extend to both hemifields (Gross, 1992; Gross et al., 1972). Thus, the neurons tend to code for specific visual information but are less concerned with the location of the object – an ideal condition for computing object constancy. In humans, the fMRI-based technique of multi-voxel pattern analysis (MVPA, see Chapter 4) has been applied to activity in this region in order to discriminate different classes of visually presented objects (e.g., chairs, cats, bottles; Haxby et al., 2001).

Object constancy can be assessed more directly using fMRI by presenting pairs of stimuli of the same object that differ in size (e.g., big v. small), viewpoint (e.g., top view v. side view), or exemplar (e.g., mug v. cup). The logic behind this approach is that the response of neurons tends to decrease over time if the same stimulus is repeated. This is termed **adaptation** and is related to the behavioral phenomenon of priming (faster responses for repeated items). Thus, one can correlate reductions in fMRI signal with repetition of particular object attributes but in which sameness refers to the same viewpoint, the same size or the same type of object (see Figure 7.17). Vuilleumier et al. (2002a) found that the left inferotemporal (or fusiform) region responds irrespective of viewpoint or size, whereas viewpoint (but not size) was important for the comparable region in the right hemisphere. This is evidence that there are at least two routes to object constancy – one that is sensitive to viewpoint and one that is not. Vuilleumier et al. (2002a) found that adaptation to visual objects with the same name (e.g., two kinds of telephone) is not found within the visual system but in language-related regions (Broca's region). Other studies, using the same object in different configurations such as a perched bird versus the same bird in flight, also fail to adapt in these inferotemporal regions or LOC, suggesting that these regions code superficial visual information (Kim et al., 2009).

KEY TERM

Adaptation (or repetition suppression)
A reduced neural response to a stimulus, or stimulus feature, that is repeated.

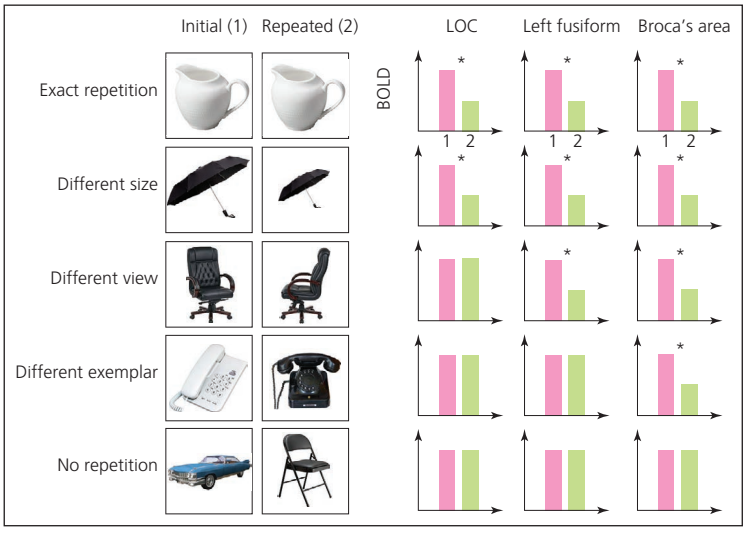

FIGURE 7.17: The response of neurons (e.g., BOLD response in fMRI) tends to be lower for repeated stimuli (time 1 and time 2): this is termed adaptation or repetition suppression. By varying which aspect of a stimuli is repeated (size, viewpoint, exemplar), it is possible to identify different brain regions that are tuned to different features. Regions that respond to the same object, irrespective of size, illumination, and viewpoint, are implicated in object constancy. LOC (lateral occipital complex) shows adaptation for the same shape, whereas the left fusiform area also shows evidence of adaptation across viewpoints, and Broca's area shows adaptation for the same exemplar/name. * = significant adaptation.

Adapted from Vuilleumier et al. (2002a) and Vuilleumier, P., Henson, R. N., Driver, J., & Dolan, R. J. (2002). With permission from Springer Nature.

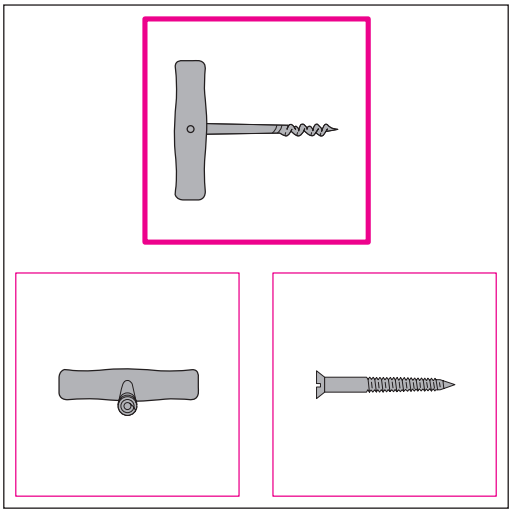

FIGURE 7.18: A test of object recognition that requires matching to an unusual view.

From Riddoch and Humphreys (1995). Reproduced by permission of Taylor & Francis Group.

Further research using fMRI repetition priming confirms viewpoint-insensitive regions within the inferotemporal cortex but also finds regions within the parietal lobes that are sensitive to object viewpoint but not to object identity (Valyear et al., 2006). The latter enables acting upon objects, but may also be involved in mentally rotating objects onto their principal axis to aid recognition. In support of this, some brain-damaged patients with right parietal lobe lesions are able to recognize and name objects from the usual view but are impaired at recognizing objects presented in unusual views, as shown in the example in Figure 7.18 (Humphreys & Riddoch, 1984; Warrington & Taylor, 1973). They may also have problems in determining whether an object is the same following a rotation or reflection (Martinaud et al., 2016).

Category specificity in visual object recognition?

It has already been suggested that higher visual areas of the brain may be specialized for processing particular visual attributes such as color and motion. But are there higher visual areas of the brain that are specialized for recognizing different categories of object such as animals, faces, places, words, and bodies? Chapter 1 outlined Fodor's (1983) theory that many cognitive functions are carried out by domain-specific modules. The term "domain specific" refers to the fact that the module is hypothesized to process one, and only one, type of information (e.g., there may be a module that processes faces but not other types of stimuli). Evidence in favor of this strong position has been mustered from dissociations of spared and impaired performance in the recognition of different classes of object, and from the observation that different regions of the brain are optimized for responding to certain classes of stimuli. The notion that the brain represents different categories in different ways is termed **category specificity**. A parallel debate exists in the literature concerning whether the semantic representation of objects is represented categorically (see Chapter 12), as well as for the structural descriptions of objects. The alternative to the domain-specific hypothesis is that different categories of stimuli require somewhat different kinds of processing (e.g., words are recognized by parts, and faces recognized holistically), and that such differences may be relative rather than absolute.

KEY TERM

Category specificity
The notion that the brain represents different categories in different ways (and/or different regions).

This chapter discusses the domain-specific hypothesis with regards to faces. Chapter 13 discusses a similar proposal with regards to recognizing visual words (Dehaene et al., 2002; Petersen et al., 1990). In addition to faces and text, functional imaging studies have

identified other regions that appear to be relatively specialized for the visual recognition of particular categories, as shown in Figure 7.19. These include the **parahippocampal place area (PPA)**, which responds to scenes more than objects (Epstein & Kanwisher, 1998), and the *extrastriate body area* (EBA), which responds to the human body more than to faces, scenes, or objects (Downing et al., 2001). Although these studies argue in favor of some degree of category specificity, it is unclear whether they support domain specificity in the strong form (i.e., that the regions are only involved in recognizing stimuli from one category). The strongest evidence for domain-specificity in object recognition so far has come from face processing, and this is considered next.

KEY TERM

Parahippocampal place area (PPA)
A region of the visual ventral stream that responds to scenes more than objects.

RECOGNIZING FACES

Although faces are a type of visual object like any other, there is some reason to believe that the process of face recognition may be

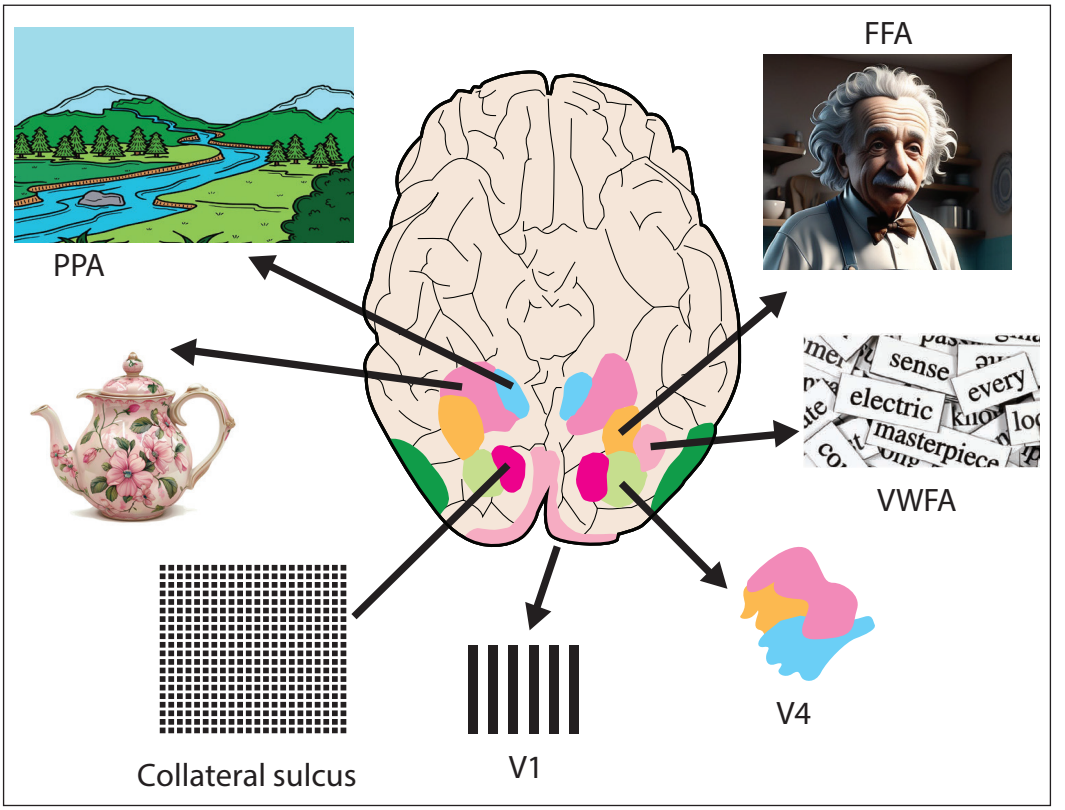

FIGURE 7.19: The human visual ventral stream (here showing the underside of the brain) contains regions that are relatively specialized for processing different kinds of visual object. Where does this specialization come from? Here we focus on faces and the FFA (fusiform face area). Note also: VWFA = visual word form area (specialized for text), PPA = parahippocampal place area (specialized for scenes).

KEY TERMS

Face recognition units (FRUs)
Stored knowledge of the three-dimensional structure of familiar faces.

Person identity nodes (PINs)
An abstract description of people that links together perceptual knowledge (e.g., faces) with semantic knowledge.

different from other aspects of object recognition. First of all, the goal in face recognition is normally to identify one particular face (e.g., "that is Donald Trump!") rather than categorizing a face as such (e.g., "that visual object is a face!"). Second, researchers have suggested that faces might be special either because of the type of processing they require or because they are a distinct category. Although there is good evidence to suggest that faces do have a different neural substrate from most other objects and can be disproportionately spared or impaired, the reasons why this is so remain a matter of controversy.

Models of face processing

Bruce and Young (1986) proposed a cognitive model of face recognition that has largely stood the test of time (Figure 7.20). They assume that the earliest level of processing involves computation of a view-dependent structural description, as postulated for object recognition more generally. Following this, a distinction is made between the processing of familiar and unfamiliar faces. Familiar faces are recognized by matching to a store of face-based structural descriptions (which they term **face recognition units**). Following this, a more abstract level of representation, termed **person identity nodes**, accesses semantic (e.g., their occupation) and name information about that individual. A separate route (termed directed visual processing) was postulated to deal with unfamiliar faces. A number of other face-processing routes are postulated to occur in parallel to the route involved in recognizing familiar people. Evidence from neurological patients suggests that recognition of emotional expression, age, and gender is independent of familiar face recognition (Tranel et al., 1988; for electrophysiological data, see Hasselmo et al., 1989), as is the ability to use lip-reading cues (Campbell et al., 1986).

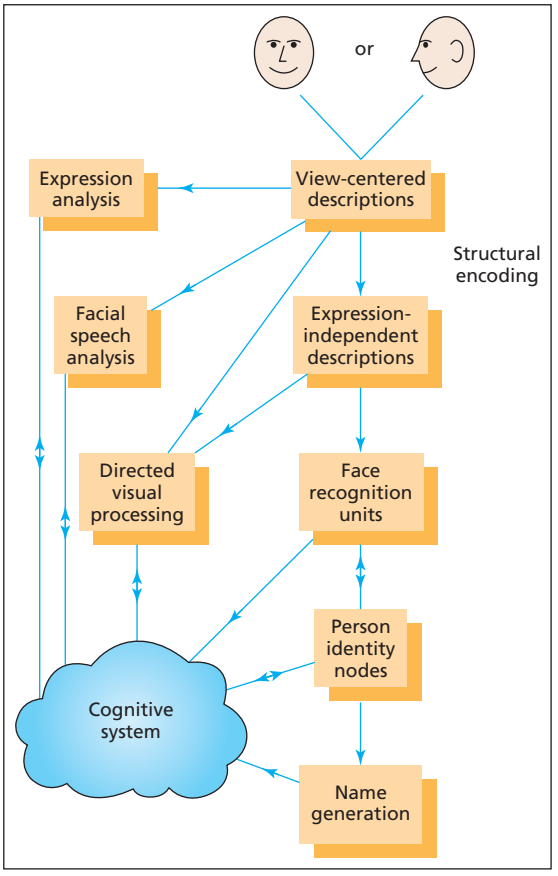

FIGURE 7.20: The Bruce and Young (1986) model of face recognition. Structural encoding is common to all faces. But there is then a distinction between processing familiar faces (right-sided route) versus generic properties of faces such as expressions.

From Parkin (1996).

The model of Haxby et al. (2000) – shown in Figure 7.21 – presents a neuroanatomically inspired model of face perception that contrasts with the purely cognitive account offered by Bruce and Young (1986). In their model, Haxby et al. (2000) consider the core regions involved in face perception to lie in the fusiform gyrus in humans (corresponding to the in-

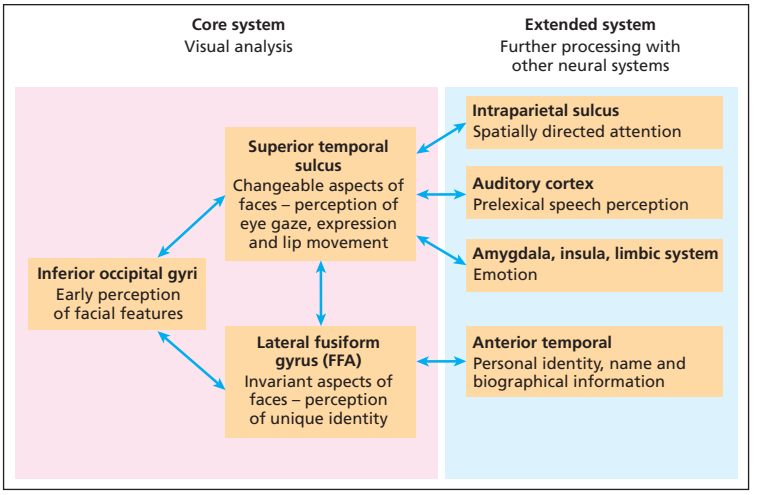

FIGURE 7.21: The model of Haxby et al. (2000) divides the neural substrates of face processing into a number of core mechanisms (relatively specialized for faces) and an extended system in which face processing makes contact with more general cognitive mechanisms (e.g., concerning emotion, language, action).

ferotemporal cortex identified in primates) and the superior temporal sulcus. The **fusiform face area (FFA)** is assumed to be involved in recognizing familiar faces. The superior temporal sulcus (STS) is assumed to process dynamic aspects of faces (such as expression, and lip and gaze movements) that are common to familiar and unfamiliar faces alike. They also identify an "extended system" to denote other areas of the brain that receive inputs from the core face perception system but are not essential for face perception (e.g., regions supporting semantic knowledge of people).

Evidence that faces are special

The Bruce and Young (1986) model has a number of similarities with models of object recognition, including distinctions between apperceptive and associative stages, and distinctions between view-independent and view-dependent codes. However, in other respects, faces may differ from other objects. Broadly speaking, two lines of evidence have been presented to back up the claim. First, that faces have a distinct neural substrate; second (and related to the first), that faces can thus be selectively impaired.

Impairments of face processing that do not reflect difficulties in early visual analysis are termed **prosopagnosia** (Bodamer, 1947). The term prosopagnosia is also sometimes used specifically to refer to an inability to recognize familiar faces. As such, care must be taken to describe the putative cognitive mechanism that is impaired rather than relying on simple labeling. The case study reported by De Renzi (1986) had profound difficulties in recognizing the faces of people close to him, including his family, but could recognize them by their voices or other non-facial information. He once

KEY TERMS

Fusiform face area (FFA)
An area in the inferior temporal lobes that responds more to faces than other visual objects and is implicated in processing facial identity.

Prosopagnosia
Impairments of face processing that do not reflect difficulties in early visual analysis (also used to refer to an inability to recognize previously familiar faces).

remarked to his wife: "Are you [wife's name]? I guess you are my wife because there are no other women at home, but I want to be reassured." In contrast, the patient could perform perceptual matching tests involving faces normally. Within the Bruce and Young (1986) model, his deficit would be located at the face recognition unit stage. The patient's ability to recognize and name other objects was spared.

The FFA responds to faces more than other stimuli, including bodies, and may be particularly important for recognizing known faces (Kanwisher et al., 1997; Kanwisher & Yovel, 2006). It is for this reason that Kanwisher and colleagues have suggested that this is a strong candidate for domain specificity (i.e., contains neurons that process only one particular kind of information). The FFA is found bilaterally, with a generally more robust response on the right. Unlike earlier regions in the occipital gyrus that also demonstrate some face specificity, the FFA demonstrates categorical perception. **Categorical perception** refers to the tendency to perceive ambiguous or hybrid stimuli as either one thing or the other (rather than as both simultaneously or as a blend). Rotshtein et al. (2005) studied this using morphed images of Margaret Thatcher and Marilyn Monroe in an fMRI adaptation study. Consider the pair of images on the left of Figure 7.22. Both images are physically different from each other by 30 percent but both tend to be perceived as "Maggie." Now consider the pair of images on the right of Figure 7.22. Both of these images are also physically different from each other by 30 percent, but whereas the upper face tends to be categorized as "Maggie," the lower face tends to be categorized as "Marilyn." The FFA showed adaptation only when the identity was perceived to change (i.e., the second pair – categorical perception), but earlier occipital regions showed adaptation to any physical change (i.e.,

KEY TERM

Categorical perception
The tendency to perceive ambiguous or hybrid stimuli as either one thing or the other (rather than as both simultaneously or as a blend).

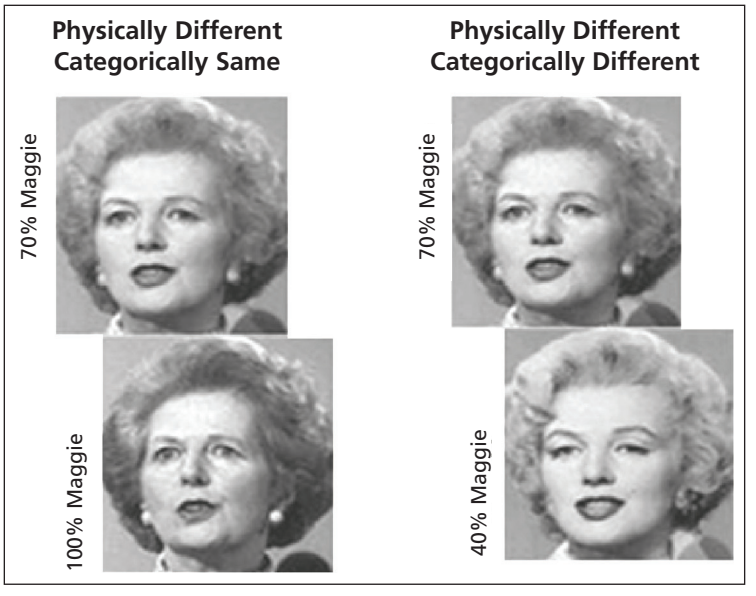

FIGURE 7.22: Morphing from Maggie to Marilyn! Both the left and the right pair of images differ from each other by 30 percent, but a change in identity is perceived to occur in the right pair only. The FFA is sensitive to changes in identity whereas occipital regions are sensitive to the degree of physical change.

From Rotshtein et al. (2005). Reproduced with permission from Springer Nature.

both the first and second pair – continuous perception). That is, the FFA appears to process the constancy of faces across different images and viewing conditions.

Why are faces special?

This section considers four accounts of why faces might be special. These accounts are not necessarily mutually exclusive, and there might be several factors that contribute.

Task difficulty

Faces are complex visual stimuli that are very similar to each other (e.g., they all consist of mouth, nose, eyes, etc.), so are faces special simply by virtue of added task difficulty relative to other kinds of objects? A number of reports of patients with visual agnosia without prosopagnosia would appear to speak against this view (Rumiati et al., 1994). Farah et al. (1995a) attempted to address the issue of task difficulty directly by creating an object recognition task (using spectacle frames) of comparable difficulty to a face recognition task in controls (both tasks performed at 85 percent correct). They found that their prosopagnosic participant, LH, was impaired on the face task (62 percent), but not the frames task (92 percent), ruling out a task-difficulty explanation.

Holistic versus part-based perceptual processing

Perhaps faces are treated differently from other types of objects because they require a special type of processing, rather than being special because they are faces as such. The most influential theory along these lines has been proposed by Farah (1990; Farah et al., 1998). Her thesis is that *all* object recognition lies on a continuum between recognition by parts and recognition by wholes (Figure 7.23, left). Recognition of faces may depend more on holistic processing, whereas recognition of written words may depend on more part-based processing (e.g., identifying the sequence of letters in the word); recognition of most other objects lies somewhere in between. Farah's initial source of evidence came from a meta-analysis of cases with visual agnosia, prosopagnosia, and difficulties in visual word recognition (pure alexia; see Chapter 13). She found no convincing cases of isolated object agnosia (without prosopagnosia or alexia) or prosopagnosia with alexia (without object agnosia), supporting the claim that these lie on a continuum (Farah, 1990). Subsequent research has reported these dissociations (De Renzi & di Pellegrino, 1998; Humphreys & Rumiati, 1998). These cases support an alternative view in which there are separate stores of structural descriptions for objects, faces, and words (right of Figure 7.23) rather than a continuum between two types of underlying perceptual processes. Face-selective regions of the cortex respond to both whole faces and face

ONLINE RESOURCES

Do you think you have developmental (or congenital) prosopagnosia? Or perhaps you never forget a face and could be a super-recognizer? Visit the Instructor & Student Resources website to find out (routledgelearning.com/wardcognitiveneuroscience) and explore our test library (testable.org/ward).

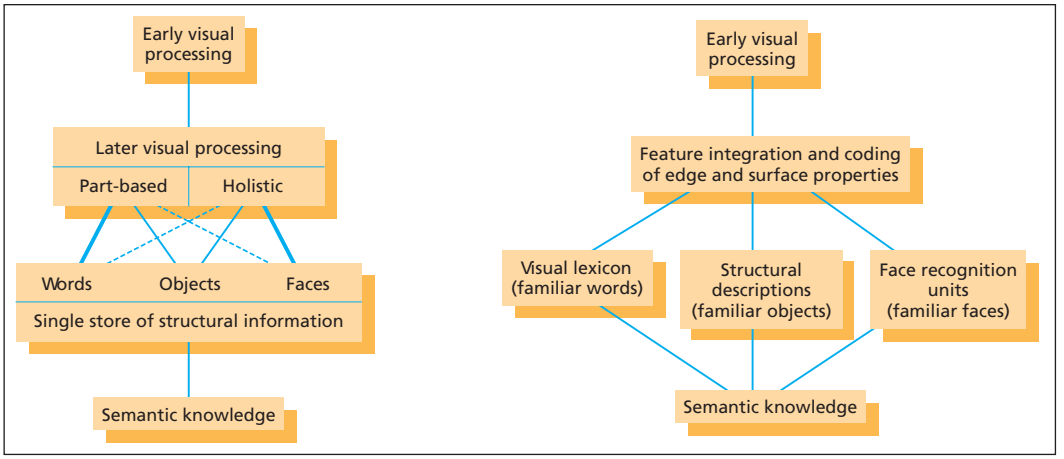

FIGURE 7.23: In Farah's model, differences between recognition of words, objects, and faces reflect different weightings of part-based versus holistic perception (left). Other models have suggested, on the basis of dissociations between object agnosia, prosopagnosia, and alexia, that there may be separate stores of structural knowledge for these categories (right).

parts in both human fMRI (Harris & Aguirre, 2008) and monkey electrophysiology (Freiwald et al., 2009), which is also challenging for the claim that faces rely more on holistic processing.

Others have defended the importance of holistic processing of faces, noting that, whilst faces can be processed by both parts and wholes, individuals who employ a holistic strategy have better face recognition (Richler et al., 2011). It has also been pointed out that apparent dissociations between objects and faces don't always use comparable tasks, as discussed further in the next section.

Visual expertise at within-category discrimination

A somewhat different account from that of Farah has been put forward principally by Gauthier and colleagues (Gauthier & Logothetis, 2000; Gauthier & Tarr, 1997; Gauthier et al., 1999). Their account has two key elements: (1) that faces require discrimination within a category (between one face and another), whereas most other object recognition requires a superordinate level of discrimination (e.g., between a cup and comb); and, consequently, that (2) we become "visual experts" at making these fine within-category distinctions through prolonged experience with thousands of exemplars. Like Farah's explanation, this account assumes that faces are special because of processing demands rather than because faces are a domain-specific category.

The evidence for this theory comes from training participants to become visual experts at making within-category discriminations of non-face objects, called "Greebles" (see Figure 7.24). As participants become experts, they move from part-based to holistic processing, as has often been proposed for faces (Gauthier &

Tarr, 1997). In addition, they have shown that Greeble experts activate the FFA (Gauthier et al., 1999), and similar findings have been reported for experts on natural categories such as cars (McGugin et al., 2012). In addition, Greeble recognition has a characteristic N170 ERP signal normally only found for faces (Rossion et al., 2002). Gauthier and Logothetis (2000) reported similar training studies in monkeys and found that certain cells (claimed to be analogous to face cells) became sensitive to the whole configuration after training even though non-facial stimuli were used.

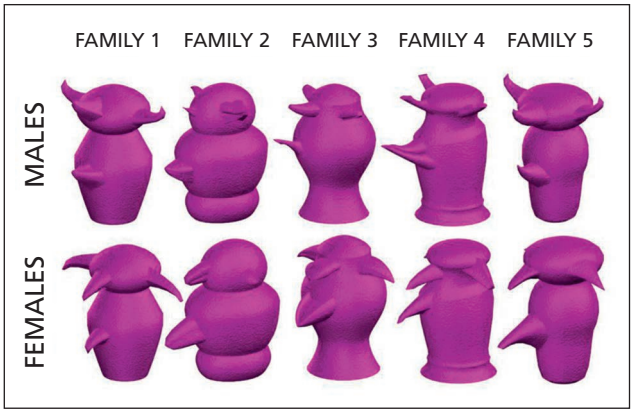

FIGURE 7.24: Examples of "Greebles." Greebles can be grouped into two genders and come from various families. To what extent does discriminating against Greebles resemble discriminating against faces?

Images provided courtesy of Michael J. Tarr (Carnegie Mellon University, Pittsburgh), see www.tarrlab.org.

Faces are a distinct category

Although it might indeed be the case that faces make different processing demands on certain perceptual mechanisms relative to other classes of stimuli, there is some evidence to suggest that these accounts are not sufficient to explain the whole picture. Some have argued that what is additionally required is the assumption that faces really are a distinct category and are represented as such in the adult brain. For example, there is evidence of dissociations between faces and other expert categories from ERP studies (Carmel & Bentin, 2002) and human neuropsychology (McNeil & Warrington, 1993; Sergent & Signoret, 1992). Sergent and Signoret (1992) reported a prosopagnosic patient, RM, who had a collection of over 5,000 miniature cars. He was unable to identify any of 300 famous faces, or the face of himself or his wife, or match unfamiliar faces across viewpoints. Nevertheless, when shown 210 pictures of miniature cars he was able to give the company name, and for 172 he could give the model and approximate year of manufacture. Thus, although the FFA may tend to represent within-category exemplars (Gauthier et al., 2000), there could still be scope for finer-grained categorical dissociations. McNeil and Warrington (1993) reported patient WJ, who was unable to distinguish previously familiar faces from unfamiliar ones. Following his stroke, he acquired a flock of 36 sheep, which testing revealed that he could distinguish from unfamiliar sheep. This case was taken to support the view that faces are a special category independent of the type of perceptual processing, but skeptics may argue that the sheep recognition task could be performed in different ways (e.g., recognizing markings rather than holistic configuration) or that the level of expertise is not

matched (e.g., 36 sheep versus many thousands of faces). In addition to prosopagnosia acquired from brain injury, there are some people for whom face recognition ability doesn't develop (congenital prosopagnosia). Many of these cases appear to have some difficulties in object recognition when tested on comparably demanding tests (Geskin & Behrmann, 2017).

Evaluation

There is good evidence to suggest that face recognition can be spared or impaired relative to the recognition of other objects. To account for this, it might be necessary to assume that faces engage different types of perceptual mechanism related to holistic versus part-based processing and might require expert within-category discriminations. Whereas these accounts might be necessary to explain the data, they might not be sufficient. There remains some evidence to suggest that there is indeed a separate store of structural descriptions for familiar faces.

THE MARGARET THATCHER ILLUSION

What is wrong with this face (Figure 7.25)? Turn it upside down and have a look. In the so-called Thatcher illusion, the holistic configuration of the face, in its inverted orientation, disrupts the ability to detect local anomalies in the stimulus such as an inversion of the eyes and mouth (Thompson, 1980). The success of the illusion is based on two properties of the face recognition system. First, that faces usually have an upright orientation and may be stored in the brain as such. This explains why the anomaly is detected upon inversion. Second, that faces are processed holistically rather than piecemeal from parts.

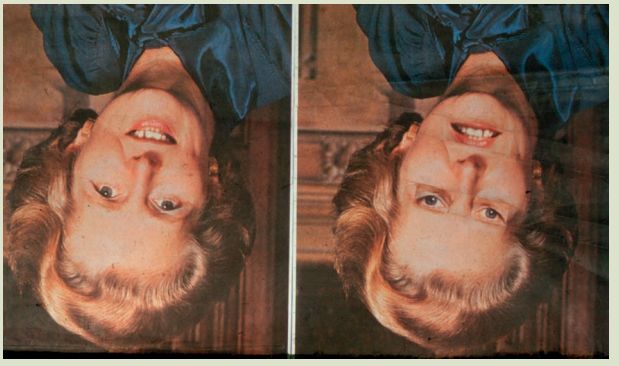

FIGURE 7.25: These are two images of the former British Prime Minister, Margaret Thatcher (but the illusion works with any face). What is wrong with one of them? Turn it the right way up to find out.

From Thompson (1980). © Pion Limited, London. Reproduced with permission.

For most adults, inverted faces are much harder to identify (Yin, 1969). But prosopagnosic patients such as LH may show no advantage of upright over inverted faces, suggesting this information is lost (Farah et al., 1995b). Greeble experts tend to show an advantage for processing upright Greebles (Gauthier & Tarr, 1997). Infants show a preference for a "top-heavy" configuration of facial features from birth but, beyond that, they do not have a strong preference for the correct configuration (Macchi Cassia et al., 2004).

VISION IMAGINED

Close your eyes and imagine a horse galloping left to right through a green field and jumping over a fence. To what extent is this "visual imagery" task achieved by using the same mechanisms used to visually perceive horses, color, movement, and so on? Historically, this debate was framed in terms of whether visual imagery is more like perception or more like language. In the latter case, imagery would be more like semantic memory, which would store information *about* vision, but not necessarily using a visual code. Pearson and Kosslyn (2015) argue that this debate is very much ended, with the evidence coming down in favor of visual imagery utilizing visual representations. But what kinds of visual representations? Object-level (visual ventral stream) or simpler features (V1) or both? And by what mechanism? Is there simply a reversal of the normal flow of visual information, as shown in Figure 7.26?

One claim that has been made about mental imagery is that V1 is necessary for it (Kosslyn et al., 1995, 1999). Kosslyn et al. (1995) compared an imagery condition of visualizing objects of different sizes relative to a non-imagery baseline. They found that there was activity in V1 and, moreover, that the locus of activity was related to the size of the imagined stimulus. (Recall that V1 is retinotopically organized so that images that cover a large area on the retina will cover a large area on V1 although the central portion of space is also disproportionately magnified.) Imagery of learned artworks can be decoded, using multi-voxel pattern analysis, from fMRI activity in this region (Naselaris et al., 2015). To establish the functional necessity of V1 for imagery, Kosslyn et al. (1999) conducted a TMS study on participants who were making imagery judgments about a previously learned array

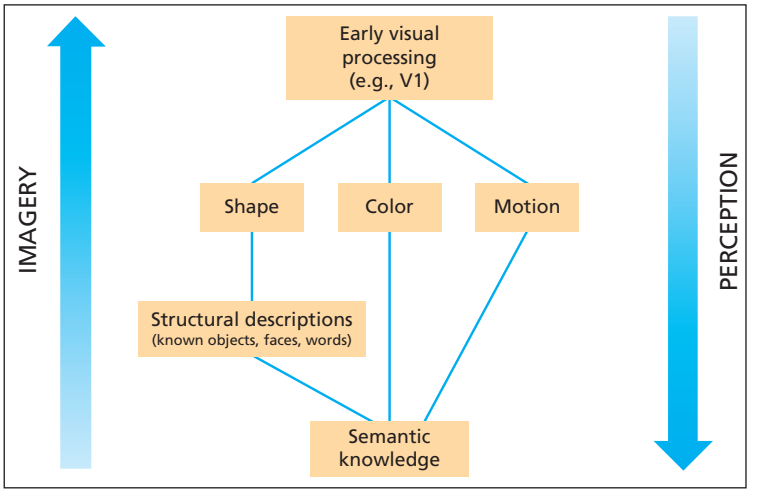

FIGURE 7.26: Imagery may involve some of the same structures as perception, but activated in the reverse ("top-down") direction.

of line gratings (e.g., parallel lines of different width, length, and orientation). They found that TMS over V1 did indeed disrupt mental imagery.

Although V1 may be important for certain aspects of visual imagery (e.g., retinotopic), other regions of visual cortex are important too, depending on the content of the visual image. For instance, imagining a shape (e.g., X v. O) activates regions such as lateral occipital complex (LOC; Stokes et al., 2011), whereas imagery of moving objects activates V5/MT and can even deactivate V1 (Kaas et al., 2010). A patient with cortical blindness due to V1 damage was still able to imagine faces and places (Stokes et al., 2011), whereas a patient with achromatopsia and prosopagnosia may have problems imagining colors and faces (Levine et al., 1985). As such, visual imagery can be fractionated along similar lines as visual perception.

In some cases, however, visual imagery and visual perception do not parallel each other. Some cases of visual agnosia have good visual imagery (e.g., they can draw objects from memory) despite being unable to recognize the same objects presented to them visually (e.g., Behrmann et al., 1994). For example, they may be able to draw a picture of a car from memory but not recognize line drawings of cars from vision. This imagery-perception dissociation can be accounted for by assuming good access to object structural descriptions top-down (i.e., from memory) but not bottom-up (i.e., from visual perception) (Figure 7.26). Similar findings were initially reported for HJA (Humphreys & Riddoch, 1987). However, a subsequent study on HJA some 16 years later suggests that caution is warranted in postulating a strong separation of vision and imagery (Riddoch et al., 1999). Although HJA could initially draw accurately from memory, this ability receded over time (but his memory, in general, remained intact). Presumably, visual input is needed to maintain the structural descriptions over longer periods of time.

Within the general population, there is a small proportion of people who do not report having visual imagery but have essentially normal abilities in visual perception (and no known cause of this lack of imagery). This is termed **aphantasia** (Zeman et al., 2015). For most people, imagining a stimulus (an oriented set of lines) can prime visual detection of that stimulus but this is reduced in people with aphantasia (Keogh & Pearson, 2018). This is consistent with the view that their imagery is less like visual perception than for other people. When aphantasics try to imagine known faces and places, there is less fMRI activity in the visual ventral stream in regions linked to perceiving these stimuli (Fulford et al., 2018). This is consistent with the view that these regions are shared between perception and imagery but can differ in their ease of accessibility from the top-down (in aphantasia) or bottom-up (in agnosia arising from brain-damage).

KEY TERM

Aphantasia
An inability to create mental images (e.g., unable to see with the minds eye).

SUMMARY AND KEY POINTS OF THE CHAPTER

- The primary visual cortex (V1) contains a spatial map based on the retinal image and detects edges and boundaries within the visual scene.
- The primary visual cortex may be necessary for conscious awareness of vision. Damage to this area can lead to a condition called blindsight, in which conscious experiences of vision are abolished, although some visual processing in the "blind" region is still computed by routes that bypass V1.
- Later visual regions are specialized for analyzing particular visual attributes such as color (area V4) and motion (area V5/MT).
- The ability to recognize objects from a wide variety of views (object constancy) may arise from matching visual features to a stored representation of objects or from mentally rotating the seen object to a standard viewpoint. Basic categorical recognition of objects implicates inferotemporal processing, whereas recognizing the orientation may involve the parietal lobes.
- The processing of faces relative to other objects may, to some degree, utilize different neural substrates and cognitive resources. Faces may make more demands on holistic processes and typically require individuation of particular exemplars. It is also possible that faces are special because they are an evolutionarily salient category.
- Mental imagery utilizes many of the same resources as actually perceiving, and like vision itself, different types of image (e.g., of color, objects, lines) may have different neural substrates.

EXAMPLE ESSAY QUESTIONS

- What is "blindsight"? What can studying blindsight tell us about the normal visual system?
- To what extent is the primary visual cortex (V1) necessary for visual perception?
- One function of the visual system is to extract constant properties of a stimulus independently from moment-to-moment fluctuations in viewing conditions. Explain how

the brain achieves this, using the examples of color constancy and object constancy.
- Are faces "special"? If so, why?
- To what extent is visually imagining like visually perceiving?

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Visit the Instructor & Student Resources website at routledgelearning.com/wardcognitiveneuroscience for:

- Videos including an interview with key psychologists Hubel and Wiesel, BBC documentary *Brain Story – The Mind's Eye*, a patient's experience with visual agnosia, and a lecture with author Jamie Ward on *The Seeing Brain*
- Multiple-choice questions and interactive flashcards to test your knowledge

CHAPTER 8

The hearing brain

CONTENTS

Sound originates from the motion or vibration of an object; for example, the vibration of the vocal cords, the plucking of a violin string, or the passing of an overhead aircraft. This manifests itself in the surrounding medium, normally air, as changes in pressure in which molecules are alternately squeezed together and stretched apart. The human auditory system is capable of detecting a huge range of changes in air pressure, from around 0.00002 to more than 100 Pascals. However, the role of the hearing brain is not merely to detect such changes. As with vision and other perceptual systems, the goal of hearing is not to create a literal depiction of the outside world, but rather to construct an internal model of the world that can be interpreted and acted upon (Figure 8.1). This model is constructed not only from ongoing sensory information but also from previous sensory experiences. In vision, a tomato will not be perceived to change color when it is moved from indoor lighting to outdoor lighting (even if the wavelength reflected from it has changed). Hearing operates on the same principles. The hearing brain is also concerned with extracting "constancy" out of an infinitely varying array of sensory input, and it will actively interpret

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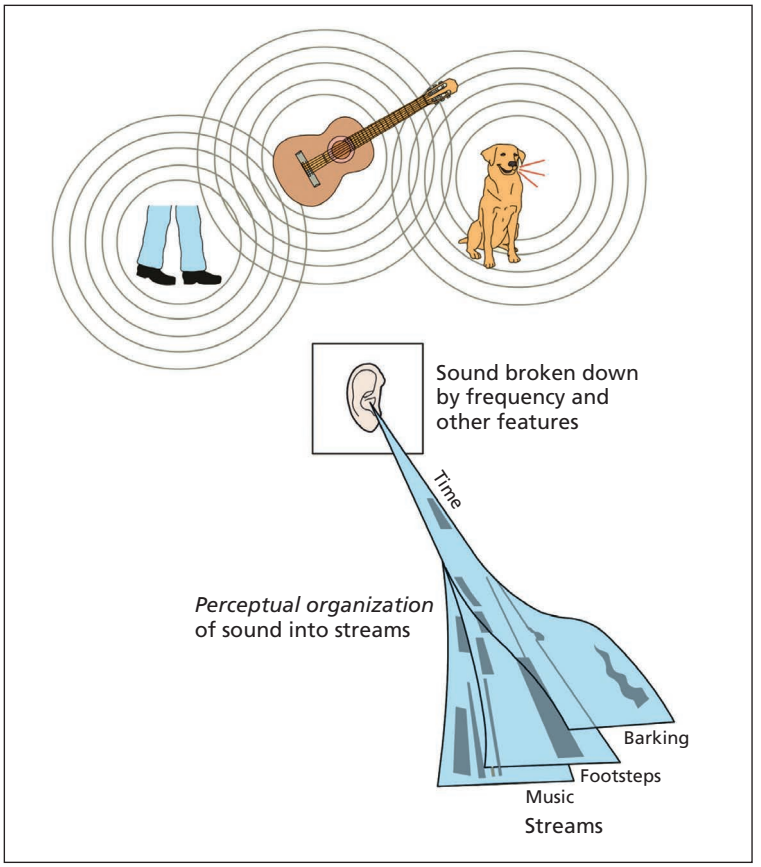

FIGURE 8.1: In our noisy environments, our ears often encounter several sounds at once. But it is the job of the brain (not the ears!) to figure out how many different sound sources (or "streams") there are and what they correspond to. This will depend both on the incoming sensory information and learned knowledge about sounds (e.g., melodies of music, the pitch range of voices).

the sensory input. For example, we recognize a familiar tune when heard in a different key, and we can recognize a familiar voice in a wide range of acoustic environments (in person, on the telephone, shouting over a megaphone). The hearing brain also uses stored knowledge to supplement the auditory input. If one is listening to a familiar song, such as The Rolling Stones' "Satisfaction," but there are gaps of 2–5 sec in the song ("I can't get no _____"), then auditory cortical areas are more active during the gaps, relative to unfamiliar songs (Kraemer et al., 2005). Our musical and lyrical knowledge can fill in silent gaps in heard songs (or almost silent, given that there is the scanner background noise).

One difference that does exist between the auditory and visual senses is their sensitivity to temporal and spatial information. The auditory system is exquisitely tuned to detect temporal information, such as rapid changes in frequency that characterize certain speech sounds, and in grouping information together over time, such as in extracting melody from music. The different time intervals associated with "dots" and "dashes" in Morse code are much easier to process when heard than seen (Saenz & Koch, 2008). In contrast, it is generally much easier to locate an object in space with vision than with hearing (Bertelson & Aschersleben, 1998).

This chapter will start by considering how sounds are processed by the early auditory system up to the primary and secondary auditory cortex. It will then go on to consider in more detail how the brain extracts features from the auditory scene, and divides up the auditory world into different streams (e.g., corresponding to different sound sources), and different kinds of information (e.g., "what" versus "where"). The final part of the chapter will consider auditory perception for three different classes of stimuli: music, voices, and speech.

ARE YOU A YANNY OR A LAUREL?

This internet meme has been described as a hearing equivalent of "The Dress." A high-school student went to the website Vocabulary.com to look up the sound of the word "Laurel" but was hearing it as "Yanny." A social media poll revealed that people were evenly divided in the way they perceived it, and their perceptions were also very reliable across multiple hearings. What is going on here? Firstly, these sounds are not as different as you might believe. Recordings of "Yanny" and "Laurel" look visually similar on a spectrogram (Figure 8.2). As with most complex sounds, such as speech, this sound consists of both high frequency and low frequency elements (related to high and low pitch). Within participants, it is possible to manipulate the percept by playing the sound at an overall lower pitch (favoring Yanny) or higher pitch (favoring Laurel). Between participants, some people might reliably weight the higher versus lower elements of the sound more in their judgment. Men, relative to women, are more likely to hear "Laurel," and the same is true of musicians versus non-musicians (Pressnitzer et al., 2018). The key point is that auditory perception is a process of interpretation rather that passive reception.

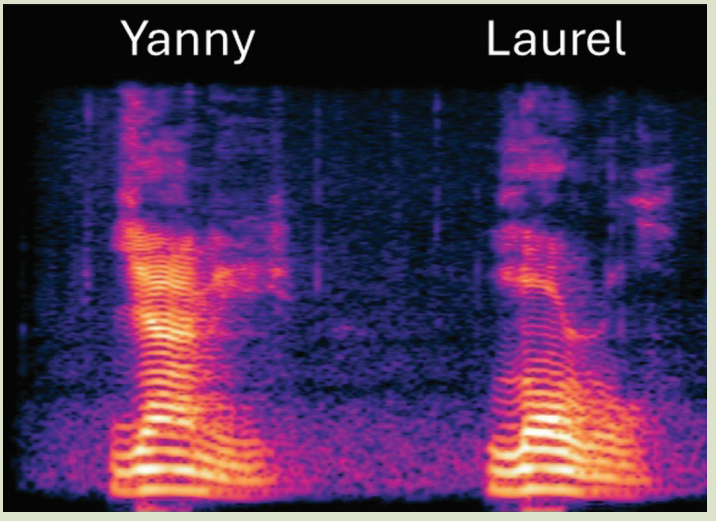

FIGURE 8.2: Spectrogram visualizations of the author saying "Yanny" and "Laurel."

THE NATURE OF SOUND

One of the simplest sounds has a sinusoid waveform (when pressure change is plotted against time), and these sounds are termed **pure tones**. Pure tones have a characteristic **pitch** that is related to the frequency of the sound wave (measured in Hertz, i.e., vibrations per second). The human auditory system responds to sound frequencies between 20 Hz and 20,000 Hz. The intensity of the sound (i.e., its amplitude when considered as a sine wave) is related to the subjective experience of **loudness** (measured in decibels). In perception, it is crucial to make a distinction between the physical properties of a stimulus and their perceived characteristics. Thus, in vision, there is a close relationship between the wavelength of light (a physical property) and color (a psychological property), but the two things are not the same. It is possible to see color without its associated wavelength, as in afterimages, and it is possible to process wavelength without perceiving color, as in cerebral achromatopsia. Similarly, in hearing, although pitch is related to the frequency of sounds and loudness is related to the intensity (or amplitude) of sounds, pitch and loudness are regarded as psychological features of sounds, whereas frequency and intensity are physical properties. For example, the pitch of a low-frequency sound appears to get lower if it is made louder and the pitch of a high-frequency sound appears to get higher if it is made louder (Stevens, 1935). Even though amplitude and frequency might be independent physical properties of sound waves, the subjective properties most closely associated with them (pitch and loudness) are not processed by the brain in a completely independent way.

In everyday life, pure tones are seldom heard. However, many sounds can be described in terms of combinations of superimposed pure tone sinusoids of different frequencies, intensities, and phases. For example, musical notes typically contain a series of regularly spaced sinusoids. Thus, a piano note of 220 Hz can be described in terms of sinusoids at 220 Hz, 440 Hz, 660 Hz, and so on (Figure 8.3). The lowest component (in this example 220 Hz), termed the **fundamental frequency** (f0), typically determines the perceived pitch of a musical note. However, if the fundamental frequency is missing from the series (e.g., a tone made up of 440 Hz, 660 Hz, 880 Hz, etc.), then the pitch is still perceived as equivalent to 220 Hz. This is termed the **missing fundamental phenomenon** and is an example of pitch constancy, that is, two notes with completely different physical characteristics can have the same perceived pitch. For example, a single note of 220 Hz can be perceived identically to a series of sinusoids at 440 Hz, 660 Hz, 880 Hz, etc. White noise can be thought of as an infinite sum of sinusoids of every frequency.

The relative intensity levels of the different sinusoid components of musical sounds are important for discriminating between the

ONLINE RESOURCES

Try the Yanny/Laurel illusion for yourself! Also, note the similar "Green needle" versus "Brain storm" debate. What do you hear? Try it on your friends. Scan the QR code or visit routledgelearning.com/wardcognitive neuroscience.

KEY TERMS

Pure tones
Sounds with a sinusoid waveform (when pressure change is plotted against time).

Pitch
The perceived property of sounds that enables them to be ordered from low to high.

Loudness
The perceived intensity of the sound.

Fundamental frequency
The lowest frequency component of a complex sound that determines the perceived pitch.

Missing fundamental phenomenon
If the fundamental frequency of a complex sound is removed, then the pitch is not perceived to change (the brain reinstates it).

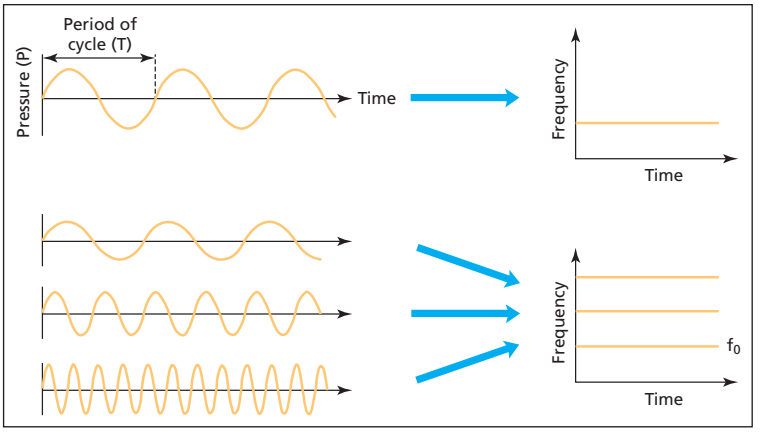

FIGURE 8.3: A pure tone (top) consists of sinusoidally varying pressure. Many naturally occurring sounds, such as musical tones (bottom), consist of a regular series of sinusoids of different frequencies. The perceived pitch is related to the lowest frequency in the series (the fundamental frequency, f0).

same notes played on different musical instruments, that is, **timbre** (pronounced "tamber"). Timbre, like pitch, is a psychological characteristic of a sound.

FROM EAR TO BRAIN

The ear contains three main parts: the outer, middle, and inner ear, as shown in Figure 8.4. The outer ear contains the pinna (pinnae in plural), or earlobes, and the auditory canal. Reflections of the sound wave within the folds of the pinna and within the auditory canal can amplify certain sounds and are important for locating a sound source. The middle ear converts airborne vibrations to liquid-borne vibrations with minimal loss of energy. A series of three tiny bones (malleus, incus, and stapes; also called hammer, anvil, and stirrup) transfers the mechanical pressure on the eardrum, at the end of the airborne auditory canal, to a smaller membrane, called the oval window, in the fluid-filled **cochlea**. The inner ear contains chambers that are important both for the senses of hearing (the cochlea) and balance (including the semicircular canals). The cochlea converts liquid-borne sound into neural impulses. A membrane within the cochlea, termed the **basilar membrane**, contains tiny hair cells linked to receptors. Sound induces mechanical movement of the basilar membrane and the hair cells on it. These movements induce a flow of ions through stretch-sensitive ion channels that initiates neural activity (release of neurotransmitters). The basilar membrane is not uniform but has different mechanical properties at either end (e.g., Von Bekesy, 1960). The end nearest the oval window is narrower and stiffer and shows a maximal deflection to high-frequency sounds. The end nearest the center of its spiral shape is wider and more elastic and shows a maximal deflection to low-frequency sounds. As such, different parts of the membrane are

KEY TERMS

Timbre
The perceptual quality of a sound enables us to distinguish between different musical instruments.

Cochlea
Part of the inner ear that converts liquid-borne sound into neural impulses.

Basilar membrane
A membrane within the cochlea containing tiny hair cells linked to neural receptors.

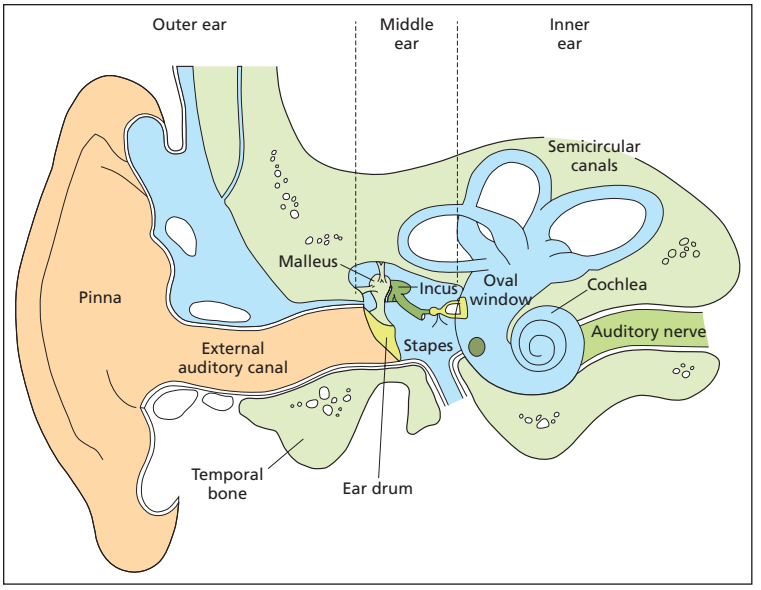

FIGURE 8.4: The structure of the outer, middle, and inner ear.

sensitive to different frequencies of sound. But note that sounds originating from different parts of space do not stimulate different parts of the membrane (as occurs in the analogous scenario of light stimulating photoreceptors in the eye). The location of sound sources needs to be inferred from other kinds of information (e.g., differences between the signals in the ears).

There are four or five synapses in the auditory pathway from the ear to the brain, starting with projections from the auditory nerve to the cochlear nuclei in the brainstem, and ending with projections from the medial geniculate nucleus to the **primary auditory cortex**, also called A1 or the "core" region (the main cortical area to receive auditory-based thalamic input). This is shown in Figure 8.5. The primary auditory cortex is located in Heschl's gyrus in the temporal lobes and is surrounded by adjacent secondary auditory cortical areas called the **belt** and **parabelt regions** (Kaas et al., 1999). These secondary regions also receive some input from the medial geniculate nucleus and, hence, damage to the primary auditory cortex does not produce complete deafness but does lead to problems in identifying and locating sounds (Musiek et al., 2007). This ascending pathway is not a passive transmission of information from the ear but, rather, is involved in the active extraction and synthesis of information in the auditory signal. For example, while the cochlear nucleus has 90,000 neurons, the medial geniculate nucleus has 500,000, and the auditory cortex has 100,000,000 (Worden, 1971). In addition, there are descending, top-down, pathways that go as far back as the cochlea itself (Rasmussen, 1953) and may be important in auditory attention.

KEY TERMS

Primary auditory cortex
The main cortical area to receive auditory-based thalamic input.

Belt region
Part of the secondary auditory cortex, with many projections from the primary auditory cortex.

Parabelt region
Part of the secondary auditory cortex, receiving projections from the adjacent belt region.

The early auditory system can be said to have a **tonotopic organization**. Just as different parts of the basilar membrane respond maximally to different sound frequencies, neurons within the auditory nerve respond maximally to certain sound frequencies more than others. Moreover, the nerve bundle is orderly such that neurons responding to higher frequencies are located on the periphery and those responding to lower frequencies more centrally (Kiang et al., 1965). To some extent, this organization is carried upwards to the early cortical stages. In both humans (Formisano et al., 2003) and other animals (Merzenich et al., 1973) there is evidence that the central region of the primary auditory cortex responds to lower frequencies and the outer regions, on both sides, to higher frequencies (see Figure 8.6).

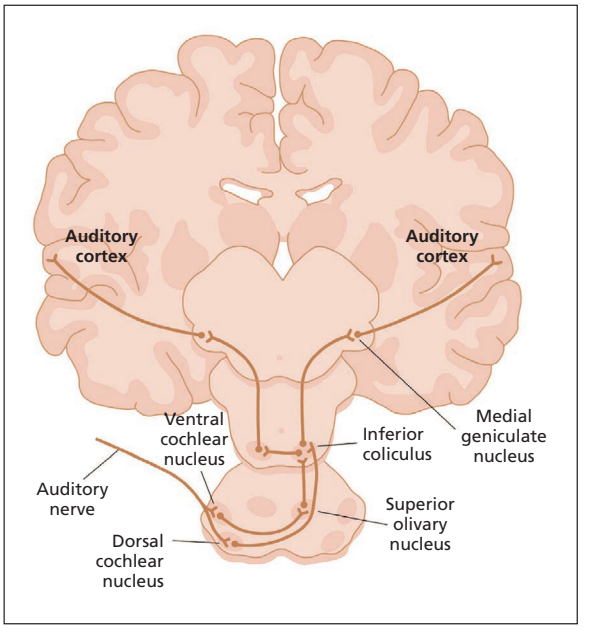

FIGURE 8.5: The ascending auditory pathway is not a passive transmission of information from the ear but, rather, is involved in the active extraction and synthesis of information in the auditory signal.

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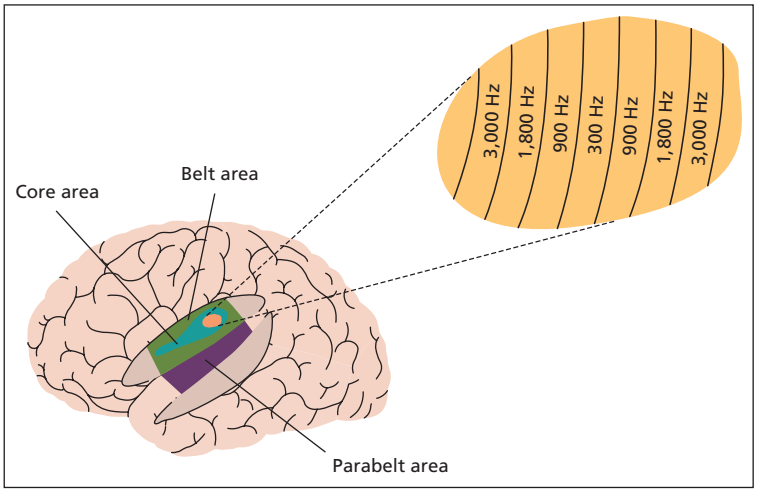

FIGURE 8.6: The primary auditory cortex lies on the medial surface of both the left and right temporal lobes and is organized tonotopically (i.e., different regions process different frequencies). It is surrounded by the secondary auditory cortex (termed belt and parabelt) that processes more complex aspects of the sound and provides the starting point for separate "what" and "where" routes.

Adapted from Goldstein (2012).

KEY TERM

Tonotopic organization
The principle that sounds close to each other in frequency are represented by neurons that are spatially close to each other in the brain.

DOING HEARING RESEARCH IN A NOISY MRI SCANNER

The noise from an MRI scanner is significant (up to 130 dB, i.e., similar to a jet engine take-off). The scanner noise may not only mask the auditory stimulus of importance; it could also change the nature of the auditory task by requiring attentive strategies to actively filter out the background noise. One solution that is now commonly used is to use so-called **sparse scanning** (Hall et al., 1999). In this method, scanning is temporarily suspended for a few seconds so that an auditory stimulus can be displayed against a silent background and then scanning restarts. This method is possible because of the slow time it takes for the hemodynamic response function to reach a peak (about 6 sec after stimulus onset).

KEY TERM

Sparse scanning
In fMRI, a short break in scanning to enable sounds to be presented in relative silence.

COMPARISONS BETWEEN THE AUDITORY AND VISUAL SYSTEMS

	Auditory system	Visual system
Thalamocortical route	Medial geniculate nucleus projects to primary auditory cortex	Lateral geniculate nucleus projects to primary visual cortex
Organizing principle of early neural processing	Tonotopic organization (orderly mapping between sound frequency and position on cortex)	Retinotopic organization (orderly mapping between position on retina and position on cortex)
Temporal and spatial sensitivity	Temporal > Spatial	Spatial > Temporal
Functional specialization of feature processing	Less well documented in the auditory domain	Well documented for color and movement
Higher-order context-dependent pathways	Evidence for separate auditory pathways for "what" versus "where"/"how"	Evidence for separate visual pathways for "what" versus "where"/"how"

BASIC PROCESSING OF AUDITORY INFORMATION

Beyond the early auditory cortical areas, there are many other routes and regions of the brain involved in auditory processing. The precise network of regions used depends on the stimulus content (e.g., human speech, voices, music, environmental noises) and the current context (e.g., whether one needs to understand speech, identify a speaker, or locate a sound source). These will be considered in the next sections.

Feature processing in the auditory cortex

Just as visual perception involves the processing of different features (color, shape, movement, texture), so too does auditory perception,

although the features differ (e.g., pitch, loudness, tempo). As with vision, there is some evidence of hierarchical processing of auditory feature information such that earlier cortical regions (e.g., the "core" region containing the primary auditory cortex) codes for more simple features and later cortical regions (e.g., the belt and parabelt) codes more complex information that could be thought of, to some extent, as conjunctions of simple features. Unlike vision, the evidence for modular-like organization of auditory features is less well established. But there is some evidence for a potential pitch region that responds to the psychological variable of pitch (i.e., how the note is perceived) as opposed to the physical properties of the sound (such as the frequency). This region, outside of the primary auditory cortex, responds to perceived pitch, as in the missing fundamental illusion, rather than actual frequency (Bendor & Wang, 2005).

Kaas et al. (1999) present a summary of how more complex auditory features are constructed in a hierarchical fashion from core → belt → parabelt regions. Single-cell recordings in primates show that the neurons in the core region respond to narrowly defined frequencies (e.g., responding maximally to a pure tone of 200 Hz), whereas cells in the belt region respond to a broader band of frequencies (e.g., responding to noise between 200 Hz and 300 Hz; Kosaki et al., 1997). This is consistent with the view that the neurons in the belt region sum together activity from many frequency-selective neurons in the core region; for example, by summing together activity from neurons tuned to respond to 200 Hz, 205 Hz, 210 Hz, 215 Hz, and so on to 300 Hz. This can be considered analogous to the way that simple cells in vision sum together information from center-surround cells (see Chapter 7).

Cells have been documented in the primary auditory cortex possessing something akin to center-surround properties (Tian et al., 2013). Recall that, in vision, on-off center-surround cells respond when a light is projected ON to the *center* of the receptive field and also respond when a projected light is switched OFF the *surround* of the receptive field. In hearing, the response properties are defined according to the range of frequencies that a neuron responds to (rather than spatial position), but a similar principle applies. For instance, a neuron that responds when a sound of 3–6 kHz is ON may also respond when a sound of 6–9 kHz (i.e., an adjacent frequency band) is switched OFF.

A hierarchy of auditory processing is observed in humans using fMRI, with core regions responding to pure tones and the surrounding belt and parabelt regions responding to noise bands and vocalizations, respectively (Chevillet et al., 2011). Vocalizations are characterized by sudden shifts in frequency, such as abrupt onsets in speech (e.g., the /p/ phoneme), or warbling or twitter calls in other species. Indeed, some neurons do not respond to fixed frequencies but only to changes in frequency and even the direction of change of frequency (Kajikawa et al., 2008; Whitfield & Evans, 1965). This could be considered analogous to complex cells in vision, which respond to movement and movement direction.

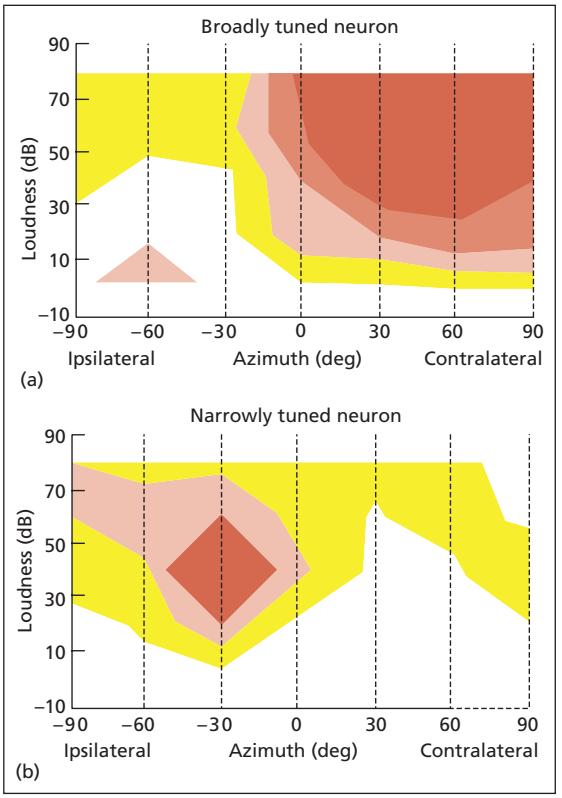

FIGURE 8.7: The density of shading represents the responsiveness of two different neurons in the auditory cortex to sounds of different loudness levels presented in different regions of space. Neuron (a) responds to sounds over a broad range of loudness level and in various parts of space, whereas neuron (b) is more finely tuned to a particular loudness level and a particular part of space.

From Clarey et al. (1994). Reprinted with permission of APS.

Neurons of the auditory cortex do not just respond to frequency-related information; they also respond to particular loudness levels and particular spatial locations. Clarey et al. (1994) recorded from neurons in the cat primary auditory cortex using noise bursts but varying loudness and sound location. Some neurons respond only to particular loudness levels, and some neurons respond only to particular locations (typically contralaterally, so sounds presented on the left of space are more strongly processed in the right auditory cortex and vice versa). More than a third of neurons respond to particular loudness levels *and* particular locations (see Figure 8.7); for example, a neuron may produce a maximal response both if the sound is between 30 and 50 dB and if it is located between 20 and 40 degrees on a particular side of space.

"What" versus "where"

Within the auditory cortical areas, there is some degree of specialization for "what" versus "where." That is, some neurons/regions are relatively specialized for coding the content of the sound (irrespective of where it is coming from), and other neurons/regions are relatively specialized for coding where the sound is coming from (irrespective of what is heard). Rauschecker and Tian (2000) found that neural responses in the anterior belt region showed a high degree of specialization for monkey calls (irrespective of their location), whereas the posterior belt region showed greatest spatial selectivity. They speculated that this may form the starting point for two routes: a dorsal route involving the parietal lobes that is concerned with locating sounds, and a ventral route along the temporal lobes concerned with identifying sounds. Functional imaging evidence from humans is largely consistent with this view (Barrett & Hall, 2006). For sounds that can be reproduced (e.g., speech in humans), one additional suggestion is that the auditory dorsal route acts as a "how" route – that is, the auditory signal interfaces with motor representations in the parietal and frontal cortex rather than spatial ones. Evidence from structural and functional imaging suggests that this dorsal route may (at least partially) segregate into separate "where" and "how" streams rather than existing as a single stream with a dual how/where function (Isenberg et al., 2012).

There are two broad solutions for identifying where a sound is located:

1. *Inter-aural differences*. If a sound is lateralized, it will tend to arrive at one ear before the other (**inter-aural time difference**) and will be less intense at the farthest ear because it lies in the "shadow" of the head (**inter-aural intensity difference**) – see Figure 8.8. Frequency-selective neurons in the core and belt regions adjust their responsiveness according to the inter-aural loudness differences and inter-aural time differences (Brugge & Merzenich, 1973). For example, a neuron that is selective for a particular frequency may be more responsive, that is, generate more action potentials, when the left ear receives the sound slightly before the right ear but may reduce its responsiveness if the right ear receives the sound first.
2. *Distortions of the sound wave by the head and pinnae*. To test the role of the earlobes (pinnae) in sound localization, Batteau (1967) placed microphones into the "ear canal" of casts of actual pinnae while playing sounds to these artificial ears from different locations. When participants listen to these recordings, using headphones (i.e., so the sound isn't distorted by their own pinnae), they are able to localize the sounds. Whereas inter-aural differences only provide information about the left–right (or azimuthal) location of a sound, distortions of the auditory input by the pinnae can be used to locate sounds in both the left–right direction and the top–bottom direction (Batteau, 1967). Participants struggled to locate sounds from recordings taken without the artificial ears attached. Moreover, performance is improved if sounds are recorded from participants' own ear shapes rather than a generic ear (Wenzel et al., 1993). The brain develops an internal model of how sounds get distorted by the unique shape of one's own ears and head (called a **head-related transfer function**, HRTF), and it is able to use this knowledge to infer the likely location. Griffiths and Warren (2002) propose that a region called the **planum temporale**, lying posterior to the primary auditory cortex, is involved in integrating the sensory input with the learned head-related transfer function for different parts of space (Figure 8.9). In fMRI, this region responds more to sounds that appear to be subjectively located outside the head rather than the same sounds perceived to be internal, as occurs when listening to most sounds played through headphones (Hunter et al., 2003).

The computations described previously can be used to locate sounds relative to the head (i.e., an egocentric coding of space). However, to determine the actual location of the sound source (i.e., in allocentric space), one also needs to know the current orientation and tilt of the head. A sound that is 10 degrees to the left of the head could actually be directly in front of the person if the head happens to be oriented at 10 degrees to the right. As such,

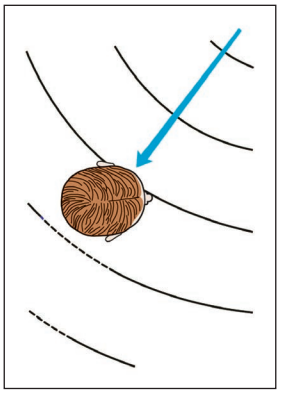

FIGURE 8.8: The sound arrives at the left ear first (inter-aural time difference) and is more intense in the incoming ear (inter-aural intensity difference).

KEY TERMS

Inter-aural time difference
The difference in timing between a sound arriving in each ear (used to localize sounds).

Inter-aural intensity difference
The difference in loudness between a sound arriving in each ear (used to localize sounds).

Head-related transfer function
An internal model of sounds get distorted by the unique shape of one's own ears and head.

Planum temporale
A part of the auditory cortex (posterior to the primary auditory cortex) that integrates auditory information with non-auditory information, for example, to enable sounds to be separated in space.

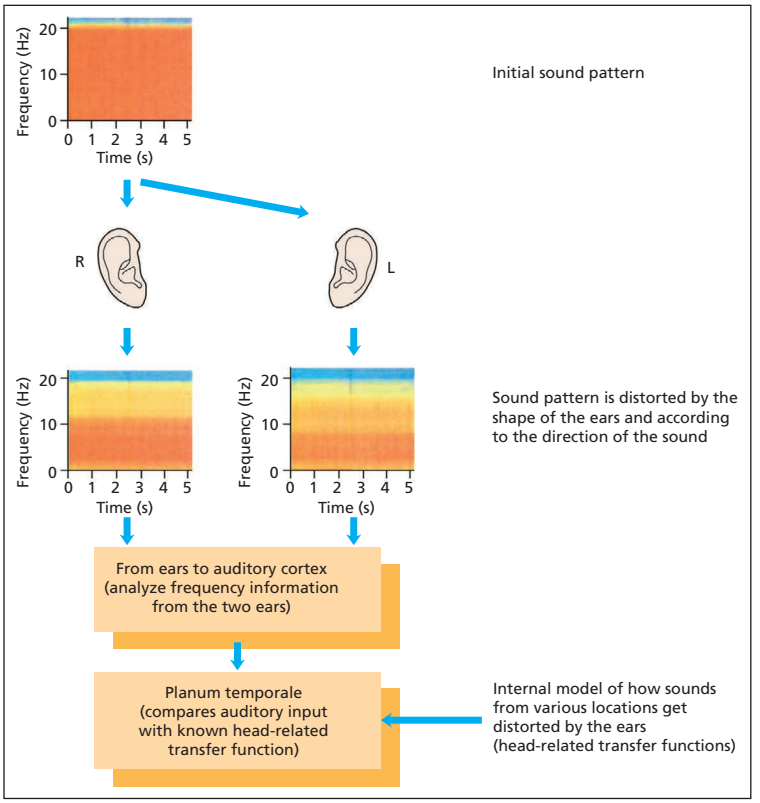

FIGURE 8.9: The shape of the ears distorts incoming sounds in predictable ways that depend on the location of the sound. The brain contains an internal model of how the sounds get distorted (head-related transfer function), and it can link the model with the auditory input to infer the location of a sound.

Adapted from Griffiths and Warren (2002).

auditory information needs to be combined with bodily postural information. Evidence from EEG suggests that information about the orientation of the head relative to the body affects auditory processing within 200 ms (Schechtman et al., 2012). Top-down information from the motor/proprioceptive system can therefore influence early auditory processing.

Auditory memory and auditory stream segregation

Visual objects generally extend through time and are available for reinspection. Auditory objects (e.g., a spoken word or musical phrase) tend not to hang around to be reinspected. Most models of hearing postulate an important role of a sensory memory store to integrate auditory information over brief time intervals (a few seconds). This auditory memory is assumed to be tapped by all kinds of heard material, that is, it should not be confused with the verbal short-term memory store that is considered speech-specific. Perhaps the best developed model of auditory memory is that proposed by Näätänen and colleagues (Näätänen et al., 2001), who regard the primary function of this memory system to lie in early

auditory stream segregation. Complex auditory scenes such as a cocktail party or an orchestral performance can be divided into different streams (or "objects") according to, say, their pitch, melody, instrumentation or location in space.

Much of the evidence in this area comes from studies of a human ERP component termed the **mismatch negativity (MMN)**. The mismatch negativity occurs when an auditory stimulus deviates from previously presented auditory stimuli (Näätänen et al., 1978). It occurs between 100 and 200 ms after the onset of the deviant sound. There is evidence that the MMN is generated anterior to the primary auditory cortex but may also involve an inferior frontal component; these regions may be linked to deviance detection and attentional orienting respectively (Tse & Penney, 2008). The simplest example is a sequence of tones in which one tone has a deviant pitch (e.g., A-A-A-A-B where A = 1,000 Hz, B > 1,000 Hz). This is illustrated in Figure 8.10. In one sense, the MMN can be considered as a "low-level" phenomenon, because it occurs in the absence of attention. It is found in some comatose patients several days before waking (Kane et al., 1993) and when the stimulus is presented to the unattended ear of healthy participants (Alho et al., 1994). However, the MMN is also found for more complex auditory patterns, suggesting a more sophisticated underlying mechanism. It is found if a descending tone sequence suddenly ascends in pitch or remains constant (Tervaniemi et al., 1994), or if the repetitive stimulus consists of varying pairs of *descending* tones, so there is no physical standard, and the deviant stimulus consists of a pair of *ascending* tones (Saarinen et al., 1992). Thus, the auditory memory must code rather abstract properties of the auditory stimuli. Schechtman et al. (2012) also showed that an MMN can be elicited by spatial deviants, suggesting that similar neural mechanisms underpin early stream segregation in both the frequency and spatial domain (a finding that is backed up by evidence from fMRI and MEG; Schadwinkel & Gutschalk, 2010).

Auditory stream segregation is unlikely to be limited to the auditory cortex. Parietal regions may be important too. Although the parietal cortex is seen as being an endpoint of the "where" pathway, it is to be noted that its role in auditory stream segregation is not solely spatial in nature but rather serving a more general role in binding and attention. Cusack (2005) used a perceptually ambiguous auditory stimulus of two alternating tones of different frequency that could either be interpreted as a single stream (like the "clip, clop, clip, clop" of a horse) or as two streams ("clip . . . clip" overlaid on "clop . . . clop").

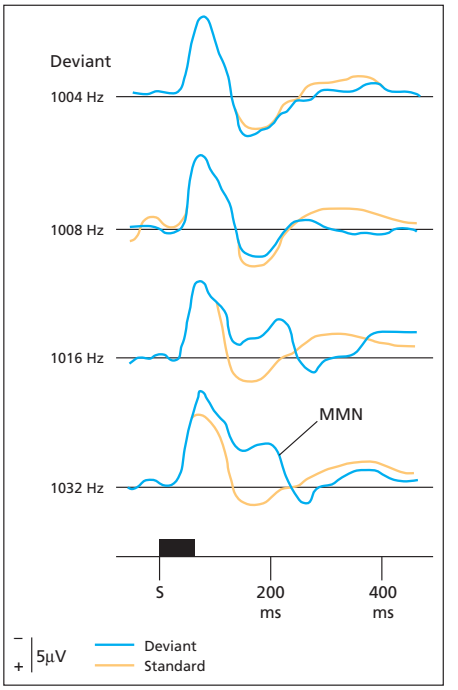

FIGURE 8.10: If a standard tone of 1,000 Hz is played repetitively (purple lines) but with an occasional deviant tone that is more than 1,000 Hz (green lines), then there is a distinct EEG event-related potential detected at the scalp that is termed the mismatch negativity, MMN. This has been attributed to an auditory memory component, and the MMN is also found for more complex auditory patterns.

Reprinted from Näätänen et al. (2001). ©2001, with permission from Elsevier.

KEY TERMS

Auditory stream segregation
The division of a complex auditory signal into different sources or auditory objects.

Mismatch negativity (MMN)
An ERP component that occurs when an auditory stimulus deviates from previously presented auditory stimuli.

FIGURE 8.11: Attending to one speaker in a crowded, noisy room (e.g., a cocktail party) requires integration of multiple pieces of information such as speaker characteristics (pitch of voice), spatial information (location), and visual information (mouth movements).

monkeybusinessimages/iStock

KEY TERM

Cocktail party problem
The problem of attending to a single auditory stream in the presence of competing streams (with different acoustic and spatial properties) – for instance, attending to one person's voice in a noisy room of other voices.

That is, the stimuli in the two conditions were physically identical but associated with different percepts. This contrasts with the MMN approach, which always uses perceptually different repeated and deviant sounds that may be easier to segregate at a sensory level. This manipulation found activity in the right intraparietal sulcus for two streams relative to one. This region has been implicated in binding different features together in vision (e.g., color and shape) and could possibly play a similar role in hearing. Indeed, patients with unilateral neglect (who typically have damage near this right parietal region) have difficulty in comparing auditory features if they are segregated into different auditory streams but not if they belong to the same stream (Cusack et al., 2000).

The parietal lobes are also likely to play an important role in solving the classical **cocktail party problem** in which a single stream (a speaker) must be attended among competing streams (with different acoustic and spatial properties) (Figure 8.11). Kerlin et al. (2010) used EEG to show that selectively attending to speech in a multi-talker environment is linked to increased power of low-frequency neural oscillations from the auditory cortex in addition to oscillatory changes over parietal sites in the alpha range. Alpha oscillations, at least in visual attention, have been linked to suppression of irrelevant information (Worden et al., 2000). Hill and Miller (2010) used fMRI to show that attending to a speaker, from a group of three, activates a frontoparietal network linked to attention. However, attending to the location of the speaker versus attending to the pitch of the speaker was linked to different biases within the network: specifically, there was greater activity in the intraparietal sulcus for speaker location but greater activity in the superior temporal sulcus (STS) when attending to speaker pitch. Visually attending to the relevant speaker's face, amongst other irrelevant speakers, increases activity in the auditory cortex (Golumbic et al., 2013).

Evaluation

The coding of auditory features in the primary and secondary auditory cortex is hierarchical, progressing from single-frequency tones to combinations of tones (occurring either simultaneously or sequentially in time). Although spatial information is present in the earliest neural responses, this is processed in more detail by a dorsal route (from the auditory cortex to the parietal cortex) that integrates auditory with non-auditory information. A separate ventral route responds more strongly to the content of the auditory stimulus (e.g., different vocalizations) and, in humans, is adapted for speech comprehension.

MUSIC PERCEPTION

Although music can rightfully be described as a form of art, this does not mean that it is purely a product of cultural learning. Many aspects of music perception have a biological basis and can be said to be "innate" in the same way as some argue language to be innate (Peretz, 2006). Namely, it is a universal phenomenon (all known human cultures, past and present, have had it), and it emerges early in life without formal training (but with exposure to an appropriate environment). At this point, it is important to emphasize a distinction between music perception and music production. Music production typically requires many years of formal training: although it need not, as in singing or tapping/clapping a rhythm. In contrast, all of us, with the possible exception of those who are "tone deaf" (see later), are able to perceive and appreciate music and are avid consumers of music.

Music can be said to have a number of essential features (Dowling & Harwood, 1986). First, musical systems tend to be based on a discrete set of pitch levels. The infinite set of different pitches that the brain perceives become parsed into a finite set of musical notes. For example, the western musical scale is made up of seven repeating notes (A to G, forming an octave when the first note is repeated), with intermediate semi-tones (the flats and sharps). Second, these different notes are combined to form perceptible groups and patterns. The way that these notes are grouped together is not arbitrary but depends on certain properties of the auditory system, such as those involved in auditory stream segregation. For example, notes that are similar in pitch or have similar durations may be grouped together. Some notes when played together "sound right" (consonance) or clash (dissonance), and this may depend on the physical relationship between the notes. For example, two notes that are double in fundamental frequency (e.g., 220 Hz and 440 Hz) have the lowest dissonance, and this has a special status in musical systems. In the Western musical system, this doubling corresponds to the same note an octave apart. Neural responses to consonance/dissonance emerge as early as the inferior colliculus in the brainstem (Bidelman & Krishnan, 2009).

Is the right hemisphere to music as the left hemisphere is to language? Although this hypothesis is interesting, it is also misleading as neither music nor language can be considered as single faculties. Instead, one proposal is that there are relative differences in hemispheric specializations for timing (left-hemispheric dominant) versus pitch-related information (right-hemispheric dominant) (Poeppel, 2003). Both music and speech depend on both of these; for instance, music consists of both rhythm (time-based) and melody (pitch-based). In support of this, Alcock et al. (2000b) report that pitch abilities are more affected by right-hemispheric lesions, but timing abilities are more affected by left-hemispheric lesions.

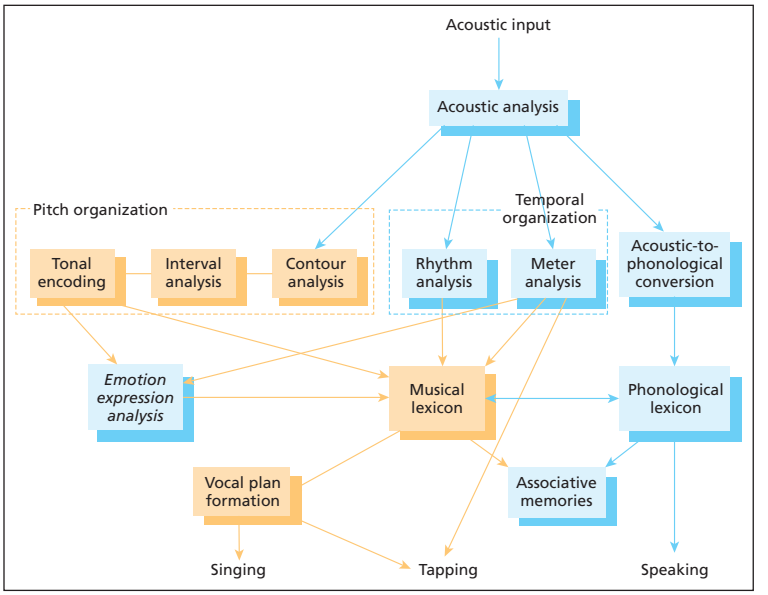

FIGURE 8.12: The model of musical cognition by Peretz and Coltheart (2003) contains separate processes for the lyrics versus melody and rhythm of music, as well as a further subdivision between processes for temporal organization (such as rhythm) and pitch-based organization (including melody).

From Peretz and Coltheart (2003). Reproduced with permission from Springer Nature.

Peretz and Coltheart (2003) outlined a basic cognitive model of music processing that emphasizes different components of musical processing. This is shown in Figure 8.12. The first distinction that they make is between processes that are shared between music and speech (shown in Figure 8.12 in blue) and those that are potentially specific to music (shown in orange). Thus, listening to someone singing "Happy Birthday" would evoke at least two sets of mechanisms: one concerned with the words and one concerned with the music. Within the domain of music, they then make a distinction between *pitch organization* (which includes pitch relations between notes) and *temporal organization*, including rhythm (the tempo of beats) and meter (repeating accentuated beats). Much of the evidence for this model has come from people with an acquired or congenital **amusia**.

KEY TERM

Amusia
An auditory agnosia in which music perception is affected more than the perception of other sounds.

Memory for tunes

Some brain-damaged patients are unable to recognize previously familiar melodies despite being able to recognize songs from spoken lyrics and being able to recognize voices and environmental sounds. For example, case CN was a non-musician who suffered bilateral temporal lobe damage (Peretz, 1996). Although she had some difficulties with pitch perception, her most profound difficulty was in identifying previously familiar tunes, and as such, her damage was attributed to a memory component of music (the "musical lexicon" in the previous model). Subsequent studies show that CN can identify intonation from speech, which requires analysis of pitch contours but not knowledge of tunes (Patel et al., 1998). In contrast to CN, some brain-damaged patients can lose the ability to recognize spoken words but are still able to recognize tunes (Mendez, 2001).

There is evidence that memory for familiar tunes is stored as part of semantic memory rather than episodic memory (although the latter may be used for recently learned tunes). Patients with semantic dementia, who have general impairments in semantic memory, have difficulty in recognizing previously familiar tunes. and the degree of impairment is linked to the amount of damage in the right anterior temporal lobes (Hsieh et al., 2011). By contrast, patients with Alzheimer's disease (which is characterized by a more profound deficit in episodic memory) tend to have only mild impairments (Hsieh et al., 2011). In neurotypical participants, imagining a familiar tune from memory relative to perceiving it involves functional connectivity between prefrontal and right anterior temporal regions (Herholz et al., 2012).

Rhythm

Disorders of rhythm can occur independently of disorders of pitch. Di Pietro et al. (2004) report a case of acquired amusia who could process pitch-based melody but could not identify rhythm from auditory input. He could do so from visual input, suggesting the problem wasn't in general time perception. Members of the KE family with a congenital speech disorder (see Chapter 6) also have problems in rhythm production and rhythm perception but perform as well as controls in pitch-based melody production and melody perception (Alcock et al., 2000a). The KE family is known to have structural abnormalities within the basal ganglia.

Evidence from functional imaging of normal listeners implicates interactions between the auditory system and the motor system in both rhythm perception and production. Passive listening to regular rhythms, relative to irregular ones, is linked to activity in the premotor cortex, supplementary motor area, and the cerebellum (Bengtsson et al., 2009). Tapping to a rhythm in which the beat varies in its audibility is linked to connectivity differences between auditory (posterior superior temporal) and premotor regions – with louder beats linked to stronger audio-motor functional connectivity (Chen et al., 2006). Activity in the basal ganglia is greatest when participants have to maintain a beat relative to the initial finding of the beat (Grahn & Rowe, 2013).

Pitch

Some people have good perception and production of rhythm but are impaired on pitch-based aspects of music. One such group are people who are said to be **tone deaf** or have **congenital amusia**, because there is no known neurological cause such as brain damage. This can occur in up to 4 percent of the population and is not associated with difficulties in other domains, such as general intelligence (Ayotte et al., 2002). It is associated with right-hemisphere abnormalities in white and gray matter density, both in

ONLINE RESOURCES

To watch the famous neurologist Oliver Sacks discussing music and the brain, visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience) and to test your own rhythm and pitch abilities go to testable.org/ward.

KEY TERM

Tone-deafness (or congenital amusia)
A developmental difficulty in perceiving pitch relationships.

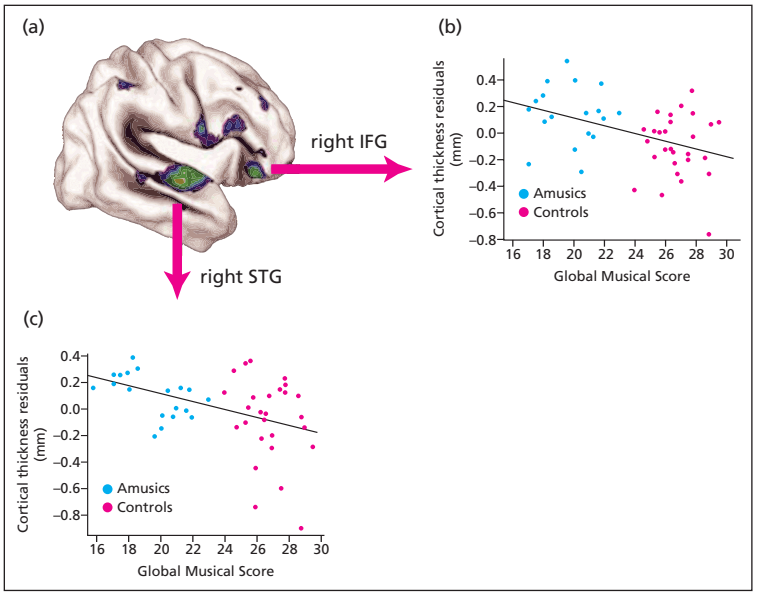

FIGURE 8.13: A right-hemisphere frontotemporal network is linked to structural abnormalities in congenital amusia. Increased gray matter is correlated with lower combined scores on a battery of six tests of musical cognition.

From Hyde et al. (2007). Copyright 2007 Society for Neuroscience.

the right auditory cortex and the right inferior frontal gyrus (Hyde et al., 2007), as shown in Figure 8.13. Hyde and Peretz (2004) presented participants with a series of five notes in which the fourth note was either out of pitch or out of time. Tone-deaf participants could detect the timing but not the pitch violations.

Another line of research has examined whether the pitch processing difficulties in congenital amusia are selective to music or affect pitch processing of other sounds, notably in speech. In tests involving fine-grained discriminations of syllables varying in pitch, there is evidence of impairment, but it is not as severe as for musical sounds (Tillmann et al., 2011). Similarly, they have difficulty in discriminating pitch shifts in sentences but – interestingly – are able to imitate pitch shifts during sentence repetition (Hutchins & Peretz, 2012). This is consistent with separate pathways for translating sounds into motor commands (intact) versus extracting higher-level perceptual features (impaired). In most Western languages, shifts in pitch are related to **prosody** (e.g., adding emphasis) and intonation (at the sentence-level) rather than comprehension. By contrast, many eastern languages are tonal in nature which means that, say, a rising or falling pitch could denote completely different words. Congenital amusia is also found in speakers of Mandarin Chinese, and many of these people also have difficulties in discriminating lexical tones as well as the pitch of musical sounds (Nan et al., 2010). Zatorre and Baum (2012) argue that while music and speech share common mechanisms in pitch processing, there are important differences too. In speech, pitch is processed on a continuous scale, and *relative* changes in pitch are important (e.g., a rise in pitch may imply a question, but the rise does not have to be of a fixed amount). In music, pitch is arranged into discrete notes and a small change

KEY TERM

Prosody
Changes in the stress pattern of speech (e.g., to add emphasis), the rhythm of speech, or the intonation (e.g., rising/falling pitch to indicate questioning or sarcasm).

of the pitch of a note in a melody can be perceived as "wrong" even if the relative pitch contour of the music is the same. Zatorre and Baum (2012) argue that there are separate neural substrates for coarse pitch changes (more important for speech) and fine-grained pitch changes (more important for music). They claim that the latter is more dependent on the right-hemisphere network, and this tends to be selectively impaired in congenital amusia.

Melody and musical syntax

The model of Peretz and Coltheart (2003) contains different stages of pitch processing in music that are concerned with the general up–down structure (contour analysis), the precise relationship between successive notes (interval analysis), and finally, the construction of **melody** (tonal encoding). In most music, the melody follows certain regularities in which only some notes are "allowed." Determining the set of possible notes for a given melody is what Peretz and Coltheart mean by tonal encoding. As well as allowing certain notes and not others, some notes are more probable at certain points in the melody than others. This rule-like aspect of music has been referred to as musical syntax, drawing an analogy with language (Koelsch & Siebel, 2005). Whereas both random pitch sequences and tonal melodies activate the bilateral auditory cortex and surrounding temporal regions (Patterson et al., 2002), musical syntactic deviations are associated with activation of inferior frontal regions (Maess et al., 2001). This tends to be bilateral and stronger on the right but includes Broca's area on the left, which has, historically, been considered as specific to language. Brain lesions in this area disrupt an event-related potential component measured using EEG (the ERAN, Early Right Anterior Negativity) that is linked to processing of musical syntactic deviations (Sammler et al., 2011). This may not be the only region that processes musical syntax. Intracranial electrophysiological recordings also highlight the importance of left anterior superior temporal regions (the ventral "what" stream) in the processing of both musical and linguistic syntax in addition to the inferior frontal gyrus (Sammler et al., 2013).

KEY TERM

Melody
Patterns of pitch over time.

Timbre

One notable omission from the model of Peretz and Coltheart (2003) is timbre. This perceptual quality of a sound enables us to distinguish between different musical instruments. The same note played on a cello and a saxophone will sound very different even if they are matched for pitch and loudness. Different instruments can be distinguished partly on the basis of how the note evolves over time (e.g., the attack and decay of the note) and partly on the basis of the relative intensity of the different frequency components of the note. Timbre perception is particularly affected by lesions of the right temporal lobe and can be dissociated from some aspects of pitch-related perception such as melody (Samson & Zatorre, 1994).

FIGURE 8.14: The music for movies such as *Jaws* and *Psycho* is designed to create a sense of fear. Would a patient with damage to the amygdala, who can't recognize fear from faces, be able to identify scary music?

Music and emotion

Music has a special ability to tap into our emotional processes. This may rely on certain musical conventions such as happy music tending to be a faster tempo than sad music; happy being in major keys, and sad being in minor keys; dissonance between notes to create tension; musical syntactic deviations to create "surprise"; and fast and regular to create scary music (think *Jaws*; Figure 8.14). A native African group, the Mafa, have been shown to be able to recognize happiness, sadness, and fear in Western music despite no cultural exposure to these musical styles (Fritz et al., 2009). Functional imaging shows that emotional music activates the same circuitry as other emotional stimuli and even the brain's reward circuitry (Blood & Zatorre, 2001; Koelsch et al., 2006). This suggests that music can be a powerful motivator like sex, food, and drugs, although the function of music, in evolutionary terms, remains unknown (see the Box). Patients with acquired difficulties in emotion processing, such as in recognizing fearful faces, may show comparable deficits in recognizing scary music (Gosselin et al., 2007).

WHAT IS THE FUNCTION OF MUSIC?

Unlike language, the function of music is less obvious. Music gives people a huge amount of enjoyment, but while humans prefer music over silence, the reverse is true of other primates (McDermott & Hauser, 2007). But enjoyment, in itself, does not explain its existence from a Darwinian point of view: namely, in what ways does music promote survival of our species? Darwin's (1871) own answer to this question is that human musical tendencies are derived from a system for attracting mates. Another answer to the problem is that music exists because it brings people together and creates social cohesion, both of which lead to survival benefits (Huron, 2001). A third suggestion, made in *The Singing Neanderthals* (Mithen, 2005), is that music is a precursor to language. Steven Pinker (1997) takes the contrary view by arguing that language was the precursor to music (rather than music the precursor to language) and that music, while being immensely enjoyable, does not have an adaptive function. As he puts it: "Music is auditory cheesecake. It just happens to tickle several important parts of the brain in a highly pleasurable way, as cheesecake tickles the palate." Although it is hard to establish the direction of cause and effect, there is now evidence of a close link between the structure

of speech and music. For instance, it is suggested that the cross-cultural tendency to have around 12 discrete notes in a musical scale derives from the number of formants in spoken vowels (Schwartz et al., 2003), and that major/minor musical modes reflect emotional prosody in human vocalization (Bowling et al., 2012). Although other primates do not show a preference for *human* music over silence (McDermott & Hauser, 2007), they do show a preference for music when it is derived from the structure of their own vocalizations (Snowdon & Teie, 2010).

VOICE PERCEPTION

Voices, like faces, convey a large amount of socially relevant information about the people around us. It is possible to infer someone's sex, size, age, and mood from their voice. Physical changes related to sex, size, and age affect the vocal apparatus in systematic ways. Larger bodies have longer vocal tracts, and this leads to greater dispersion of certain frequencies (the formants found, for example, in human vowels and dog growls are more dispersed in larger animals). Adult men have larger vocal folds (17–25 mm) than adult women (12.5–17.5 mm), resulting in a lower-pitched male voice. One can also infer the current emotional state (angry, sad, etc.) from a voice even in an unfamiliar language (Scherer et al., 2001). Familiar people can also be recognized from their voice, but this is generally more difficult than recognizing them from their face (Hanley et al., 1998). Individual differences in the shape and size of the vocal apparatus (teeth, lips, etc.) and resonators (e.g., nasal cavity), together with learned speaking style (e.g., accent), create a unique voice signature. Similarly to models of face perception, it has been suggested that there are multiple parallel routes for processing a voice: one route is involved in recognizing speaker identity, one in extracting affective information, and one in extracting speech content (Belin et al., 2011).

Belin et al. (2000) claimed to have identified a voice-selective area in the human brain. They found three regions in the bilateral superior temporal sulcus that respond to vocal sounds (speech and non-speech such as laughs) more than non-vocal sounds of comparable acoustic complexity, and including other sounds produced by humans such as clapping. Further research has suggested that these different regions may be sensitive to different aspects of voice. In particular, the right superior temporal region anterior to the auditory cortex (i.e., in the auditory "what" pathway) appears to be important for speaker identity, as shown in Figure 8.15 (Belin & Zatorre, 2003; Warren et al., 2006). TMS over this region disrupts the ability to detect the presence of a briefly heard voice, but not loudness judgments of the same stimuli (Bestelmeyer et al., 2011). An fMRI study with macaque monkeys

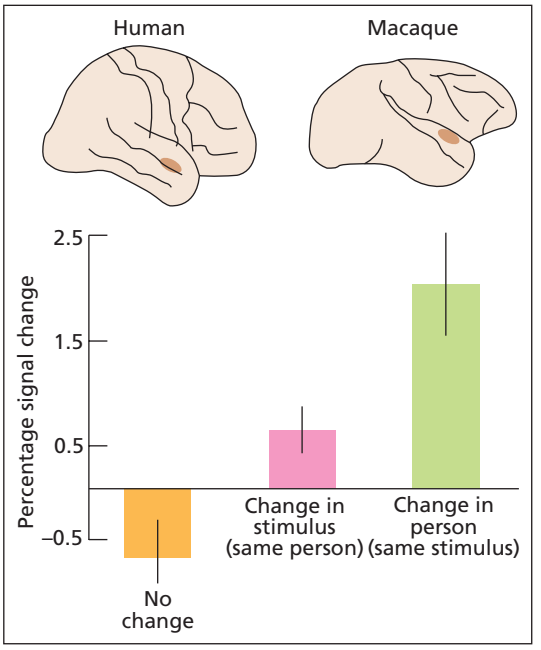

FIGURE 8.15: Approximate location of the voice-selective region in the right temporal lobe of humans (left) and macaques (right). This region responds more, in terms of fMRI BOLD signal, when the speaker changes (but the syllable/vocalization is the same) than when the syllable/vocalization changes (but the speaker is the same).

has identified a homologous region that not only responds to vocalizations from their own species but is also affected by changes in identity between different vocalizers (Petkov et al., 2008).

One case study, of developmental origin, was unable to identify familiar voices of personal acquaintances or famous people despite being able to recognize their faces and despite being able to extract other important information from their voices including their sex and emotional state (Garrido et al., 2009). Interestingly, fMRI of healthy participants shows that identifying a speaker from his or her voice activates face-selective regions but identifying the content of their speech does not (Von Kriegstein et al., 2005). Thus, although face and voice information are theoretically separable, the two are often activated together when the person is known.

SPEECH PERCEPTION

At what stage of processing, if any, does the brain treat speech sounds differently from other kinds of auditory stimuli? This question often reduces to identifying the stage in speech processing that is left lateralized. Wernicke (1848–1905), one of the earliest researchers to consider this question, believed that *auditory* speech processing was bilateral but that the left advantage arose through connections with the left motor–speech system (cited in Hickok & Poeppel, 2004). Functional imaging studies have shown that the primary auditory cortex of both left and right hemispheres responds equally to speech and other types of auditory stimuli (Binder et al., 2000). This suggests divergence at a later cortical stage. Beyond the auditory cortex, humans begin to show a greater left-hemisphere responsiveness for speech relative to non-speech along the so-called "what" route of the temporal lobes. For example, Scott et al. (2000) report increased activity in a left temporal region in intelligible relative to unintelligible speech of comparable acoustic complexity. The right-hemisphere homologue did not show this preference but was more responsive to dynamic pitch variation. This is consistent with the notion that the left hemisphere is specialized for processing rapid temporal change, and the right hemisphere extracts more melodic aspects (Zatorre et al., 2002). Moreover, a specific type of acquired auditory agnosia called **pure word deafness** is found following damage to the left hemisphere (Takahashi et al., 1992). These patients are able to identify environmental sounds and music

KEY TERM

Pure word deafness
Type of auditory agnosia in which patients are able to identify environmental sounds and music but not speech.

but not speech. The patients are able to produce speech but heard speech appears to be "too fast" or "distorted."

The nature of the speech signal

To appreciate the difficulties faced by the auditory system during speech perception, consider a typical **spectrogram** for the sentence "Joe took father's shoe bench out" shown in Figure 8.17. A spectrogram plots how the frequency of sound (on the vertical y-axis) changes over time (on the horizontal x-axis) with the intensity of the sound represented by the level of darkness. The first thing to notice is that, although there are gaps in the spectrogram, these typically correspond to the articulation of certain consonants (e.g., "t," "b," "f") rather than gaps occurring between words. Although we are used to seeing gaps between words in written language, they do not exist in speech (one famous example being "I scream" versus "ice-cream," which have the same sound). Thus, segmenting the speech stream into words will rely on stored knowledge of possible words as well as some auditory cues (e.g., stress patterns).

Another difficulty is that the same words can have very different acoustic properties depending on the person producing them. Male and female speakers have different pitch ranges, and speakers have different accents, talking speeds and so on. This is the familiar problem of extracting constant information from sensory input that can vary infinitely.

Looking again at the spectrogram, it appears as if some speech sounds have very different characteristics from others. The basic segments of speech are called phonemes and, perhaps surprisingly, fewer than 100 phonemes describe all the languages of the world. The International Phonetic Alphabet (IPA) contains one written symbol for each phoneme; English contains around 44 phonemes. It is important not to confuse phonemes with letters. For example, the TH and SH in "thin" and "shin" are single phonemes (θ and ʃ in

KEY TERM

Spectrogram
Plots the frequency of sound (on the y-axis) over time (on the x-axis) with the intensity of the sound represented by how dark it is.

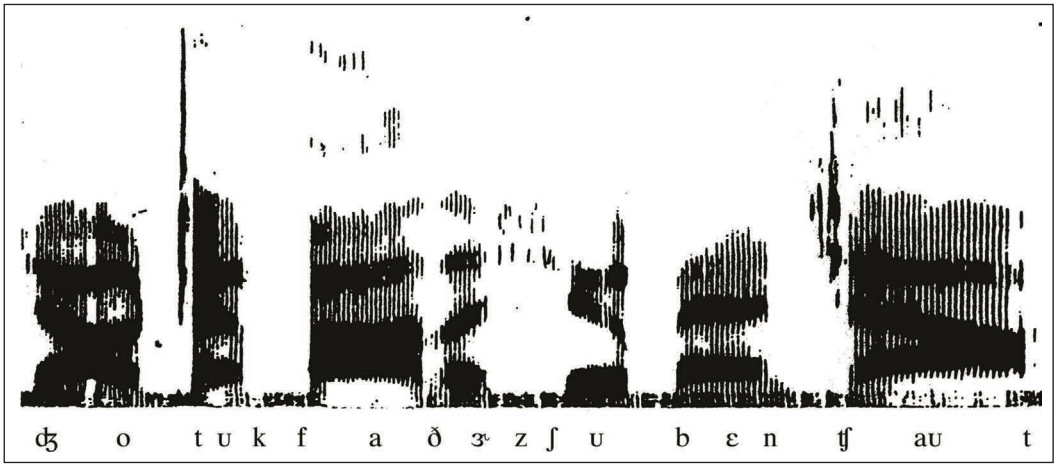

FIGURE 8.16: In the spectrogram, time is plotted along the x-axis and frequency along the y-axis, with intensity represented by darkness. There are no gaps between words but certain consonants (e.g., "b") block the flow of air and produce gaps. Vowels are represented by bands of horizontal stripes (called formants). The spectrogram represents "Joe took father's shoe bench out."

From Tartter (1986). © Vivien Tartter. Reprinted with kind permission of the author.

IPA) that are typically represented by two letters. Phonemes are more formally defined as minimal contrastive units of spoken language. To understand what this means, hold your hand very close to your mouth and say the words "pin" and "peg." Did you notice that the "p" sound of pin was more associated with an outward expulsion of air (called aspiration)? These are two **allophones** of the single "p" phoneme. Although they are physically different, the difference is irrelevant for recognizing the words. In some languages, the presence or absence of aspiration may signify a change in meaning. In Thai, "paa" aspirated means "to split," whereas "paa" unaspirated means "forest." These are separate phonemes in Thai, but allophonic variants in English.

The different acoustic properties of phonemes can be related back to the way they are articulated. Vowels are produced with a relative free flow of air, modified by the shape (high, middle, low) and position (front, center, back) of the tongue. In the spectrogram, this free flow is represented as a series of horizontal stripes (called **formants**). Consonants typically place more constriction on the flow of air, sometimes blocking it completely as in phonemes such as "b" and "d." Other consonants differ by **voicing**. Hold your voice box when saying "zzzz" compared with "ssss." In the first instance, you should feel your vocal cords vibrating. On a spectrogram, this can be seen as a series of closely spaced vertical lines.

One way in which the brain deals with variability in the acoustic input is by using categorical perception. Categorical perception refers to the fact that continuous changes in the input are mapped onto discrete percepts. For example, the syllables "da" and "ta" are identical except that the phoneme "t" is unvoiced ("d" and "a" are voiced). It is possible to experimentally manipulate the onset of voicing along a continuum from 0 ms (perceived as "da") to 80 ms (perceived as "ta"). But what happens at intermediate values such as 30 ms? Is a third type of sound perceived? No, listeners will always perceive it as one phoneme or the other, albeit to varying degrees of certainty (Eimas, 1963). Intracranial electrophysiological recordings in humans undergoing surgery have found regions in the left superior temporal gyrus, outside the primary auditory cortex, that show categorical (all or nothing) responses to different phonemes (Chang et al., 2010). Categorical perception also provides one way of dealing with variability in the acoustic signal due to **co-articulation**. Co-articulation refers to the fact that the production of a phoneme (and, hence, the sound of that phoneme) is influenced by the preceding and proceeding phonemes.

The motor theory of speech perception

It has already been suggested that speech perception involves matching an infinitely varying acoustic signal to a finite number of stored representations in the brain, thus giving rise to categorical perception. But what is the nature of these stored representations

KEY TERMS

Allophones
Different spoken/acoustic renditions of the same phoneme.

Formants
Horizontal stripes on the spectrogram produced with a relative free flow of air (e.g., by vowels).

Voicing
Vibration of the vocal cords that characterizes the production of some consonants.

Co-articulation
The production of one phoneme is influenced by the preceding and proceeding phonemes.

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and how exactly does this process occur? One possibility is that the auditory signal is matched onto motor representations for producing one's own speech rather than matching to an acoustic template. This is the motor theory of speech perception (Liberman & Mattingly, 1985; Liberman & Whalen, 2000). In this account, phonemes are recognized by inferring the articulatory movements that would have been necessary to produce these sounds. The motor commands must be abstract insofar as one can understand speech without literally having to echo it back.

The motor theory of speech perception has enjoyed a renaissance in recent years owing to the discovery of mirror neurons in the premotor and inferior frontal cortices (including parts of Broca's area). These neurons respond when the subject makes a gesture (e.g., a movement of the hands or mouth). That is, they have motor properties, but they can also respond to the sight and sound of gestures in other people, so they have perceptual properties too (Rizzolatti & Craighero, 2004). One claim is that human language evolved from initially relying on hand-based gestures (i.e., a visuo-motor language like modern sign language) to ultimately involving vocalized gestures (i.e., speech, a predominantly audio-motor language) (Corballis, 2002; Rizzolatti & Arbib, 1998).

The strongest form of the motor theory of speech perception would predict that damage to these motor/mirror regions in humans would result in severe difficulties in speech perception (as well as speech production). However, this is not the case. Patients with lesions in this area have the mildest of impairments in speech perception as assessed by tasks such as syllable discrimination (Hickok et al., 2011). This suggests that auditory-related regions alone can support efficient perception of speech sounds. But there is evidence, nonetheless, that motor representations may make some contribution to speech perception. Virtual lesions using TMS suggest that the premotor region only contributes to speech perception when the auditory signal is hard to disambiguate (D'Ausilio et al., 2012). Similarly, there is evidence from fMRI that the motor/mirror system tends to be more activated when a phoneme (presented against noise) is perceived correctly relative to when it is misperceived (Callan et al., 2010). The pattern of activity in these regions is consistent with a categorical judgment being made when presented with a blend between a "ba" and a "da" syllable (Lee et al., 2012). That is, motor representations of speech may be important when the auditory signal is uncertain. In such cases the motor system appears to make contact with the auditory system via the dorsal, rather than ventral, auditory route (Chevillet et al., 2013).

Motor representations may also be important for perceptual learning. Listening to phonemes belonging to another language is not sufficient to bring them under the jurisdiction of the left-hemisphere auditory-motor system – one also needs to produce

these phonemes as part of one's own learned language(s) in order to trigger left-lateralized speech perception (Best & Avery, 1999).

If left-hemisphere motor representations are important for phonemic aspects of speech perception, then the right-hemisphere equivalents may be important for prosody. fMRI studies of prosodic discrimination (distinguishing a statement from a question) activates a number of right-hemisphere regions, and TMS over the right premotor cortex disrupts the ability to make this discrimination (Sammler et al., 2015).

Auditory ventral and dorsal routes for "what" and "how"

The general distinction between an auditory ventral route ("what") and an auditory dorsal route ("where") was introduced earlier in the chapter. One further claim is that, for speech sounds, there is a further branch within the dorsal pathway that comprises a "how" route that links speech sounds with motor representations for producing speech (Hickok & Poeppel, 2004; Rauschecker & Scott,

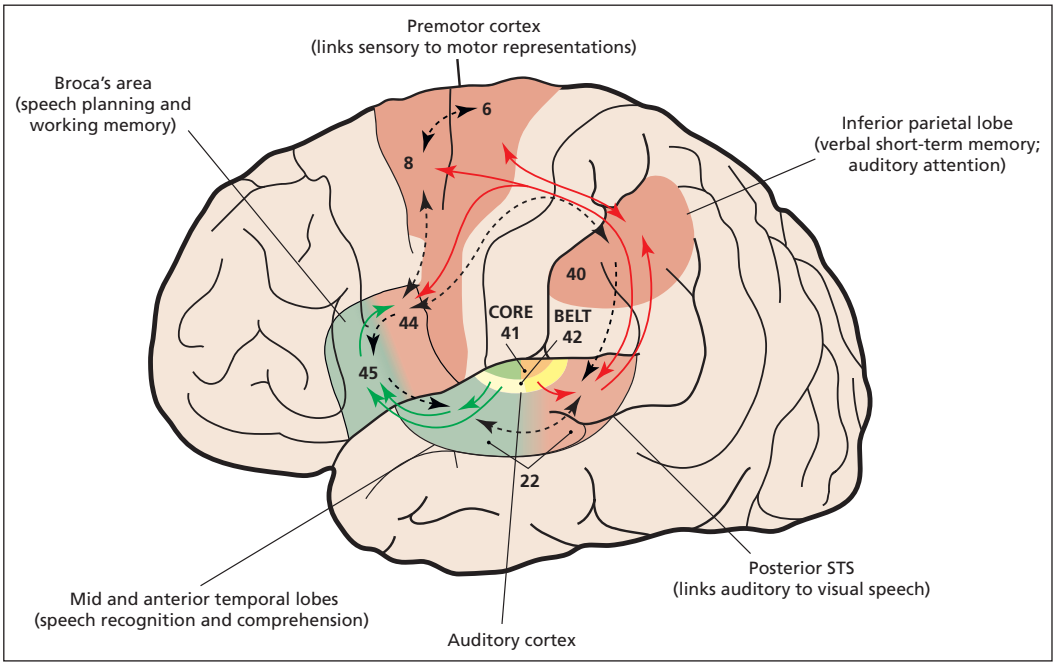

FIGURE 8.17: There may be two routes for perceiving and repeating speech: one that is based on lexical-semantic processing and one that is based on auditory-motor correspondence. These have been termed the ventral "what" route (green) and the dorsal "how" route (red), respectively. The numbers on the figure refer to Brodmann's areas.

Adapted from Bornkessel-Schlesewsky et al. (2015).

2009). This is shown in Figure 8.18 with the dorsal route in red and ventral route in green.

The "what" stream runs anteriorly along the temporal lobe and the more speech-like (or intelligible) the auditory stimulus is, then the more anterior the activity tends to be when measured with fMRI (Scott & Wise, 2004). Chapter 12 considers in detail the neural basis for linguistic aspects of speech processing (i.e., word recognition, semantics, syntax). The "how" stream runs posteriorly along the superior temporal lobe and the inferior parietal lobe (including the angular gyrus). The parietal and frontal parts of this pathway are assumed to be connected by the white matter tract

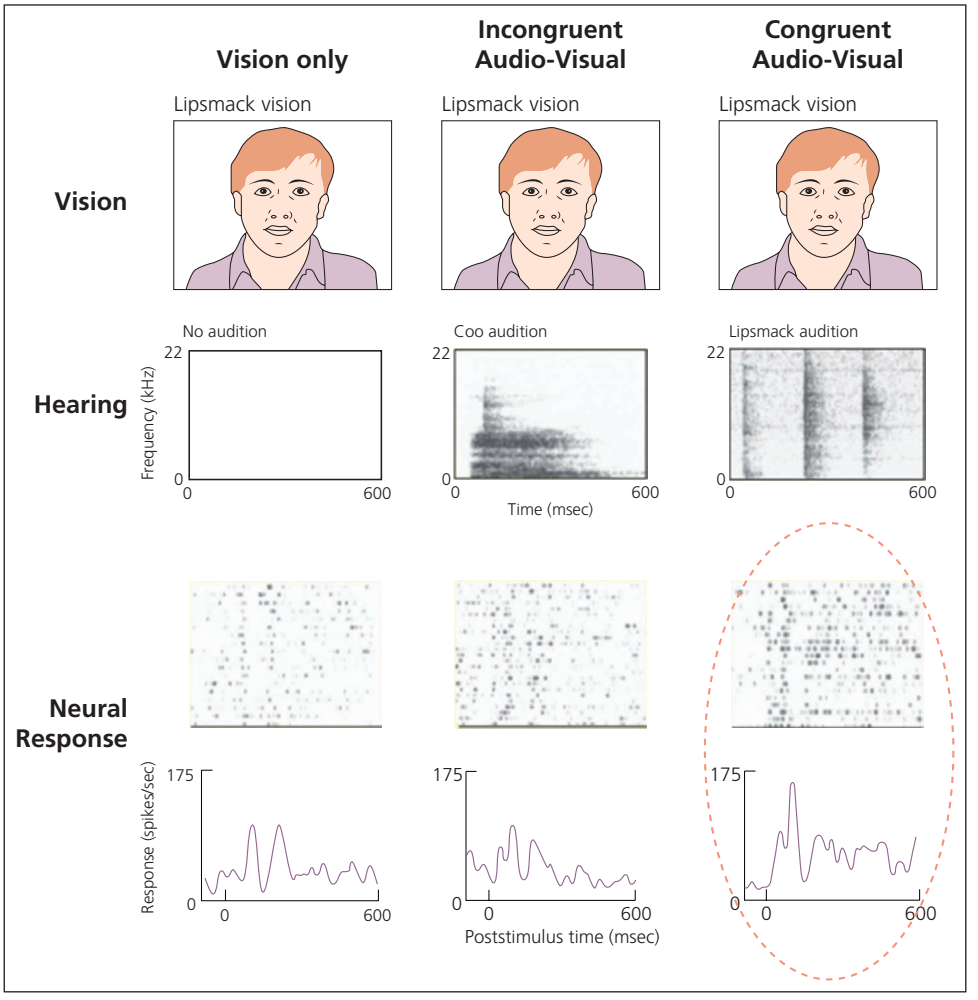

FIGURE 8.18: Single-cell recordings in the monkey posterior STS show increased firing when the same vocalization is both seen and heard. This suggests that the region is not a purely visual one, but integrates across hearing and vision.

From Barraclough et al. (2005). © 2005 by the Massachusetts Institute of Technology. Reproduced with permission.

KEY TERMS

Arcuate fasciculus
A white matter bundle that connects the temporoparietal region to the frontal lobes.

McGurk illusion
An auditory percept derived from a fusion of mismatching heard speech and seen speech.

known as the **arcuate fasciculus**. The posterior STS region is a multisensory region that is known to respond to the sight of speech as well as to hearing speech sounds (Calvert et al., 2001). Single-cell recordings from monkeys in this region show neurons that respond to both the sight and sound of the same vocalization (Barraclough et al., 2005), as shown in Figure 8.19. That is, the representation in the posterior STS could be regarded as the perceptual equivalent of a speech gesture. This can be contrasted with representations in the premotor cortex, which are both perceptual and motoric in nature (Kohler et al., 2002).

The function of the "what" pathway is universally agreed upon: that is, it is involved in processing the meaningful content of speech (and, in parallel, the identity of the speaker). The function of the "how" pathway is less clearly agreed upon. As already noted, some have argued that the "how" route is important for speech perception. This view is controversial (Lotto et al., 2009). Another suggestion, not commonly held, is that the "how" route functions to regulate turn-taking during a conversation (Scott et al., 2009). A more generally agreed-upon function of the "how" route is that it is involved in the learning and memory of auditory-verbal material. This may include both the long-term learning of novel phonemes and words, and the short-term retention (or "rehearsal") of verbal material. In terms of longer-term learning, activity in the left angular gyrus and left inferior frontal region is linked to learning to understand degraded speech (Eisner et al., 2010). The posterior STS and left inferior frontal gyrus also shows decreasing BOLD activity (i.e., less neural effort over time) when learning auditory nonwords via silent rehearsal (Rauschecker et al., 2008). Hickok and Poeppel (2004) have suggested that the how route may be the neuroanatomical basis for the phonological loop (or articulatory loop) proposed by Baddeley and Hitch (1974; Baddeley et al., 1984). This system is a short-term memory store for verbal material, and the information in the store is refreshed by subvocal articulation, as in the example of retaining a phone number between hearing it and dialing. Indeed, left parietal regions have been implicated in implementing a phonological memory store in both human neuropsychology and functional imaging (Buchsbaum et al., 2011).

Repetition of speech places significant demands on verbal working memory and, as such, seems to depend heavily on the "how" route. Of course, the ventral "what" route can support repetition of single words and perhaps certain meaningful phrases, but *verbatim* repetition of longer sequences and repetition of meaningless material will depend on the "how" route. Lesions along the "how" pathway, particularly in the posterior STS and angular gyrus, tend to result in deficits in repetition but good auditory comprehension (Baldo et al., 2012; Kuemmerer et al., 2013). Inter-individual differences in the ability to repeat complex auditory nonwords are linked to the functional connectivity between the angular gyrus (involved in short-term memory) and the hippocampus (involved in long-term learning) (McGettigan et al., 2011).

HEARING LIPS AND SEEING VOICES – THE MCGURK ILLUSION

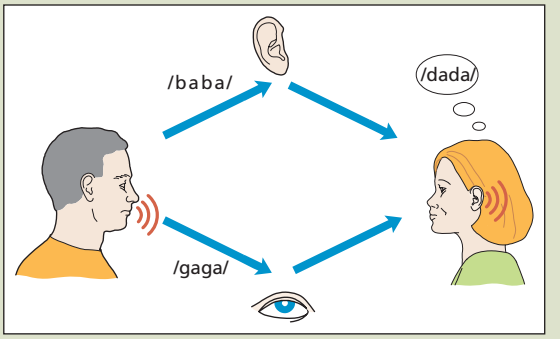

FIGURE 8.19: In the McGurk illusion, the listener perceives a different syllable from that produced because of a mismatch between hearing and vision. At what stage in the auditory pathway might this illusion arise?

Reprinted from Calvert et al. (2000). © 2000, with permission from Elsevier.

Although we may not think of ourselves as good lip-readers, we all are capable of using this visual information to supplement what we hear. Visual cues from lip-reading are particularly important when the auditory input becomes less reliable, such as in noisy settings (Sumby & Pollack, 1954) or in people who are hearing impaired (Grant et al., 1998). Normally it is advantageous to combine information from two or more different senses. However, if the information contained in the two senses is discrepant, then the brain may generate a misperception or illusion based on its "best guess" solution. One striking example of this is the so-called **McGurk illusion** (McGurk & MacDonald, 1976). To create the illusion, one needs to dub together a separate auditory stream saying one thing (e.g., "baba") with visual lip movements saying another thing (e.g., "gaga"), as shown in Figure 8.20. Participants often subjectively report hearing a third syllable – in this example, it is "dada." Close your eyes and you hear the correct auditory stimulus ("baba"); open them again and you hear the illusory stimulus ("dada"). At what point in the auditory or speech perception pathway does the illusion arise? At present there are two main candidates. One proposal is that the illusion arises from the *multisensory perception* of speech. The left (posterior) superior temporal region is known to respond to speech and the sight of meaningful lip movements. Applying TMS to this region temporarily reduces the susceptibility to the illusion (Beauchamp et al., 2010), and people who are particularly prone to perceiving the illusion (relative to those who are not) show greater activity in this region to mismatching audiovisual stimuli during fMRI (Nath & Beauchamp, 2012). An alternative proposal is that the illusion arises from activating the *motor system* for speech production (including inferior frontal cortex/premotor regions and the insula). Skipper et al. (2007) found, using fMRI, that an illusory "da" stimulus (made up of auditory "ba" and visual "ga") resembles a real "da" stimulus (made up of auditory "da" and visual "da") in motor regions. Other research suggests that these regions are involved in the categorical perception of ambiguous (audio-only) syllables (Lee et al., 2012). The different roles of these two regions (superior temporal sulcus compared with inferior frontal gyrus) and their relative importance in giving rise to the illusion require further clarification, but one suggestion is that it is the nature of the coupling between these regions that determines whether the illusion occurs (Keil et al., 2012).

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SUMMARY AND KEY POINTS OF THE CHAPTER

- As with visual perception, hearing involves extracting features (e.g., loudness, pitch) out of the sensory signal that may be useful for segregating the input into different "objects" (e.g., separating out speakers in a noisy room).
- Neurons within the (secondary) auditory cortex may have differing degrees of specialization for the content of the sound ("what") versus the location of the sound ("where"). This may be the starting point for an auditory dorsal/where pathway to the parietal lobes and a ventral/what pathway along the temporal lobes (predominantly left lateralized for speech).
- Music perception involves a number of different mechanisms, such as rhythm/timing, pitch perception, and melody (or pitch pattern perception). These different components have partially separate neural substrates as revealed by fMRI and lesion-based studies.
- There is some evidence for a specialized region in the (predominantly right) temporal lobe that is specialized for recognizing voices.
- Speech recognition involves extracting categorical information from sensory input that can vary infinitely (e.g., due to speaker differences in pitch, accent, articulation). This may be achieved via acoustic processing (matching the sounds onto stored auditory templates) and possibly via motor processing (matching the sounds onto stored articulation templates).
- Speech recognition (and speech repetition) may involve both a ventral what route (via semantics) and a dorsal how route for unfamiliar words and verbatim repetition (possibly corresponding to the use of the "articulatory loop").

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CHAPTER 9

The attending brain

CONTENTS

Attention is the process by which certain information is selected for further processing and other information is discarded. Attention is needed to avoid sensory overload. The brain does not have the capacity to fully process all the information it receives and nor would it be efficient for it to do so. As such, attention is often likened to a filter or a bottleneck in processing (Broadbent, 1958). There are some striking examples of this bottleneck in operation in the real world. Although we have a sense that our visual field is uniformly rich and expansive, research has shown that we often only attend to (and are aware of) a small proportion of it at any moment. If we were watching a game of basketball and a man in a gorilla costume walked between the players, surely we would be aware of it? But if our attention were drawn to one aspect of the game (such as counting the number of passes), then there is a high probability (50 percent) that you would not notice it (Simons & Chabris, 1999). This phenomenon is termed **inattentional blindness** (see Figure 9.1). A related phenomenon is **change blindness**, in which participants fail to notice the appearance/disappearance of objects between two alternating images separated with a brief blank screen (Rensink et al., 1997), as illustrated in Figure 9.2. Similarly, people fail to notice when a person serving you in a shop briefly disappears

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FIGURE 9.1: When concentrating on counting the passes in a basketball game, many people fail to notice the arrival of the gorilla! This study shows that our awareness of the details of a visual scene can be very limited, particularly if our attention is focused on a demanding task.

Simons, D. J., & Chabris, C. F. (1999). Gorillas in our midst: Sustained inattentional blindness for dynamic events. *Perception, 28*, 1059–1074. Figure provided by Daniel Simons. www.dansimons.com or www.theinvisiblegorilla.com

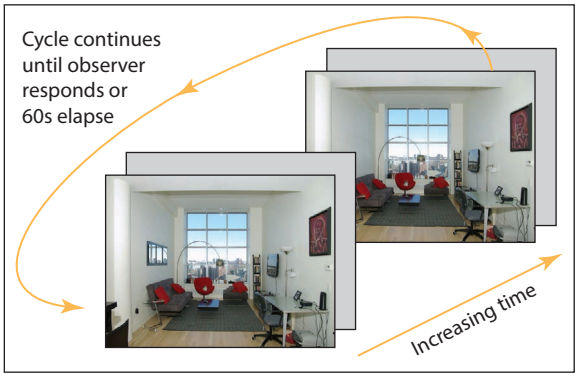

FIGURE 9.2: In change detection tasks, two different images alternate quickly (with a short blank in between). Participants often appear "blind" to changes in the image (here, the mirror on the wall) and this is linked to limitations in attentional capacity.

Images from Sareen, P, Ehinger, K. A., & Wolfe, J. M. (2016). CB database: A change blindness database for objects in natural indoor scenes. *Behavior Research Methods, 48*(4), 1343–1348.

from view and another person reappears to continue the interaction (Simons & Levin, 1998). Although both of these examples are metaphorically labeled as "blindness," they reflect the capacity limitations of our attentional systems rather than a fundamental limitation of vision. In all these examples we are perfectly capable of seeing the missed object when it is pointed out to us. Functional imaging suggests an involvement of parietal areas (lying outside the main visual system) in change detection (Beck et al., 2001). Nor are lapses of attention limited to vision. An auditory equivalent of inattentional blindness (called inattentional deafness) is that most people fail to notice a man saying "I am a gorilla! I am a gorilla! . . . [repeated for 19 seconds]" if they are attending to a different conversation (Dalton & Fraenkel, 2012).

Whereas perception is very much concerned with making sense of the external environment, attentional processes lie at the interface between the external environment and our internal states (goals, expectations, and so on). The extent to which attention is driven by the environment (our attention being grabbed, so-called bottom-up) or our goals (our attention being sustained, so-called top-down) can vary according to the circumstances. In most cases both forces are in operation, and attention can be construed as a cascade

KEY TERMS

Attention
The process by which certain information is selected for further processing and other information is discarded.

Inattentional blindness
A failure to be aware of a visual stimulus because attention is directed away from it.

Change blindness
A failure to notice the appearance/disappearance of objects between two alternating images.

of bottom-up and top-down influences in which selection takes place.

SPATIAL AND NONSPATIAL ATTENTIONAL PROCESS

In terms of visual attention, one of the most pervasive metaphors is to think about attention in terms of a spotlight (Figure 9.3). The spotlight may highlight a particular location in space (e.g., if that location contains a **salient** object). It may move from one location to another (e.g., when searching), and it may even zoom in or out (La Berge, 1983). The locus of the attentional spotlight need not necessarily be the same as the locus of eye fixation. It is possible, for example, to look straight ahead while focusing attention to the left or right when metaphorically "looking out of the corner of one's eyes." However, there is a natural tendency for attention and eye fixation to go together because visual acuity (discriminating fine detail) is greatest at the point of fixation. Moving the focus of attention is termed **orienting** and is conventionally divided into **covert orienting** (moving attention without moving the eyes or head) and **overt orienting** (moving the eyes or head along with the focus of attention). It is important not to take the spotlight metaphor too literally. For example, there is evidence to suggest that attention can be split between two nonadjacent locations without incorporating the middle locations (Awh & Pashler, 2000). The most useful aspects of the spotlight metaphor are to emphasize the notion of limited capacity (not everything is illuminated) and to emphasize the typically spatial characteristics of attention. However, there are nonspatial attentional processes too, as described later.

FIGURE 9.3: Attention has been likened to a spotlight that highlights certain information or a bottleneck in information processing. But how do we decide which information to select and which to ignore?

rvbox/iStock

Posner described a classic study to illustrate that attention operates on a spatial basis (Posner, 1980; Posner & Cohen, 1984). The participants were presented with three boxes on the screen in different positions: left, central, and right (see Figure 9.4). The task of the participant was simply to press a button when they detected a target in one of the boxes. On "catch trials" no target appeared. At a brief interval before the onset of the target, a cue would also appear in one of the locations such as an increase in luminance (a flash). The purpose of the cue was to summon attention to that location. On some trials the cue would be in the same box as the target, and on others it would not. As such, the cue is completely uninformative with regards to the later position of the target. When the cue precedes the target by up to 150 ms, participants are significantly faster at detecting the target at that location. The cue captures the attentional spotlight, and this facilitates subsequent

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Test yourself on change blindness and visual search by visiting the demonstration test library (www.testable.org/ward).

KEY TERMS

Salient
Any aspect of a stimulus that, for whatever reason, stands out from the rest.

Orienting
The movement of attention from one location to another.

Covert orienting
The movement of attention from one location to another without moving the eyes/body.

Overt orienting
The movement of attention accompanied by movement of the eyes or body.

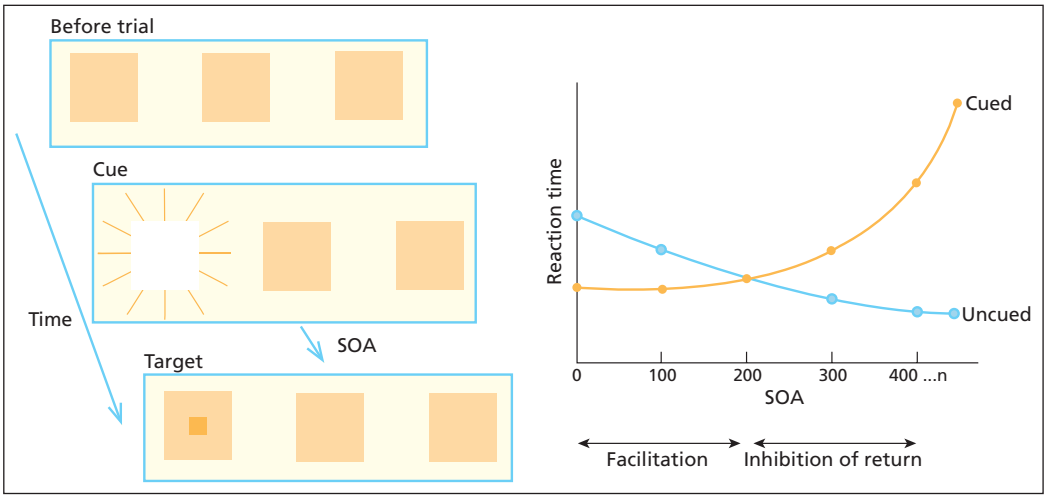

FIGURE 9.4: Participants initially fixate at the central box. A brief cue then appears as a brightening of one of the peripheral boxes. After a delay (called the "stimulus onset asynchrony," or SOA), the target then appears in the cued or uncued box. Participants are faster at detecting the target in the cued location if the target appears soon after the cue (facilitation) but are slower if the target appears much later (inhibition).

perceptual processing at that location. At longer delays (above 300 ms) the reverse pattern is found: participants are slower at detecting a target in the same location as the cue. This can be explained by assuming that the spotlight initially shifts to the cued location, but if the target does not appear, attention shifts to another location (called disengagement). There is a processing cost in terms of reaction time associated with going back to the previously attended location. This is called **inhibition of return**.

How does the spotlight know where to go? Who controls the spotlight? In the Posner spatial cueing task, the spotlight is attracted by a sudden change in the periphery. That is, attention is externally guided and bottom-up. This is referred to as **exogenous orienting**. However, it is also possible for attention to be guided, to some degree, by the goals of the perceiver. This is referred to as **endogenous orienting**. As an example of this, La Berge (1983) presented participants with words and varied the instructions. In one instance, they were asked to attend to the central letter, and on another occasion they were asked to attend to the whole word. When attending to the central letter, participants were faster at making judgments about that letter but not other letters in the word. In contrast, when asked to attend to the whole word they were faster at making judgments about all the letters. Thus, the attentional focus can be manipulated by the demands of the task (i.e., top-down). Another commonly used paradigm that uses endogenous attention is called **visual search** (Treisman, 1988). In visual search experiments, participants are asked to detect the presence or absence of a specified target object (e.g., the letter "F") in an array of other distracting objects (e.g., the letters "E" and "T"). As discussed in more detail later, visual search is a good example of a

KEY TERMS

Inhibition of return
A slowing of reaction time associated with going back to a previously attended location.

Exogenous orienting
Attention that is externally guided by a stimulus.

Endogenous orienting
Attention is guided by the goals of the perceiver.

Visual search
A task of detecting the presence or absence of a specified target object in an array of other distracting objects.

mix of bottom-up processing (perceptual identification of objects and features) and top-down processing (holding in mind the target and endogenously driven orienting of attention).

Examples of nonspatial attention mechanisms include object-based attention and time-based/temporal (not to be confused with temporal lobes) attentional processes. With regards to object-based attention, if two objects (e.g., a house and a face) are transparently superimposed in the same spatial location, then participants can still selectively attend to one or the other, as shown in the example in Figure 9.5. This has consequences for neural activity – the attended object is linked to a greater BOLD response in its corresponding brain region given that visual ventral stream contains regions that respond differently to places and faces (O'Craven et al., 1999). So attending to a face will activate the fusiform face area, and attending to a house will activate the parahippocampal place area even though both objects are in the same spatial location. It also has consequences for cognition: for instance, the previously unattended object will be responded to more slowly if it now becomes task-relevant (Tipper, 1985). With regards to Posner-style cueing tasks, research has shown that inhibition of return is partly related to the spatial location itself and partly related to the object that happens to occupy that location (Tipper et al., 1991). If the object moves, then the inhibition can also move with the object rather than remaining entirely at the initial location.

The best example of attention also operating in a temporal domain comes from the **attentional blink** (Dux & Marois, 2009; Raymond et al., 1992). In the attentional blink paradigm, a series of objects (e.g., letters) are presented in rapid succession (~10 per second) and in the same spatial location. The typical task is to report two targets that may appear anywhere within the stream which are referred to as T1 and T2 (e.g., letters among digits; or white letters among black) – see Figure 9.6. What is found is that participants are "blind" to the second target, T2, when it occurs soon after the first target, T1 (typically 2–3 items later). This is believed to reflect attention rather than perception because it is strongly modulated by the task. Namely, the effect is found when participants are instructed to attend to the first target but not when instructed to ignore it (Raymond et al., 1992).

FREE
INSTRUCTOR & STUDENT RESOURCES

ONLINE RESOURCES

Test yourself on the attentional blink and the Posner cueing task by visiting the demonstration test library (www.testable.org/ward).

KEY TERM

Attentional blink
An inability to report a target stimulus if it appears soon after another target stimulus.

FIGURE 9.5: Do you see a face or a house? The ability to voluntarily shift between these percepts is an example of object-based attention.

From Kanwisher and Wojciulik (2000). Reproduced with permission from Springer Nature.

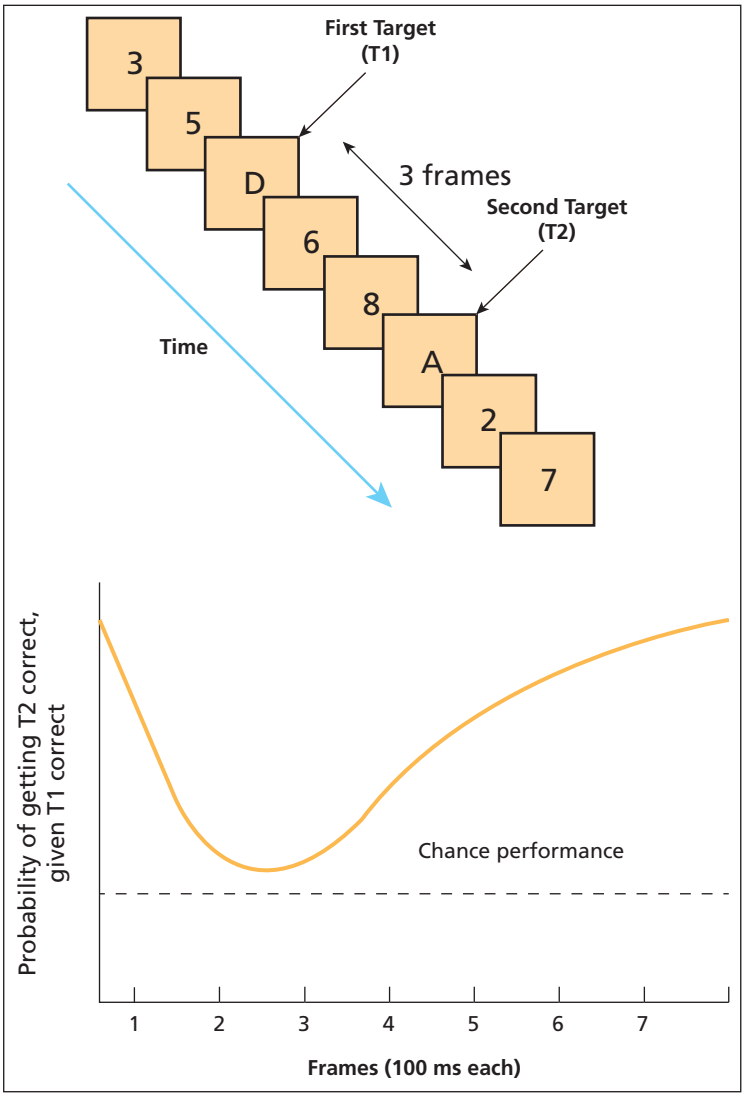

FIGURE 9.6: In the attentional blink paradigm, there is a fast presentation of stimuli, and participants are asked to report which targets they saw (e.g., reporting letters among digits, "D and A" being the correct answer in this example). Participants fail to report the second target when it appears soon after an initial target. The initial target (T1) may take over our limited attentional capacity, leading to an apparent "blindness" of a subsequent target (T2).

THE ROLE OF THE FRONTOPARIETAL NETWORK IN ATTENTION

This section considers the role of the parietal lobes (and to a lesser degree the frontal lobes) in attention. In general, various frontal and parietal regions tend to be co-activated in tasks requiring attention (i.e., they form a network along with the sensory systems that fall under the "spotlight"). However, there are differences in specialization within this network with frontal regions being more implicated in task selection and motor selection, and parietal regions acting as a hub that pulls together bottom-up (sensory) signals with top-down (goal-based) signals. The first part of this section considers mechanisms of spatial attention and how these relate to the notion of a "where" pathway. The second part of the

section considers hemispheric asymmetries in function considering both spatial and nonspatial attention processes.

The "where" pathway, salience maps, and orienting of attention

From early visual processing in the occipital cortex, two important pathways can be distinguished that are specialized for different types of information (Ungerleider & Mishkin, 1982). A ventral route (or "what" pathway) leading into the temporal lobes is concerned with identifying objects. In contrast, a dorsal route (or "where" pathway) leading into the parietal lobes is specialized for locating objects in space (Figure 9.7). The dorsal route has an important role to play in attention, spatial or otherwise. The dorsal route also guides action toward objects and some researchers also consider it a "how" pathway as well as a "where" pathway (Goodale & Milner, 1992). Analogous dorsal and ventral routes for hearing have also been proposed (e.g., Barrett & Hall, 2006).

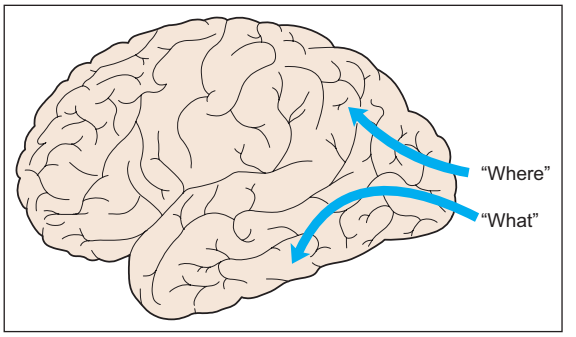

FIGURE 9.7: Later stages of visual processing are broadly divided into two routes: a "what" pathway (or ventral stream) is involved in object perception and memory, whereas a "where" pathway (or dorsal stream) is involved in attending to and acting upon objects.

Single-cell recordings from the monkey parietal lobe provide important insights into the neural mechanisms of spatial attention. Bisley and Goldberg (2010) summarize evidence that a region in the posterior parietal lobe, termed **lateral intraparietal area (LIP)**, is involved in attention. This region responds to external sensory stimuli (vision, sound) and is important for eliciting a particular kind of motor response (eye movements, termed **saccades**). Superficially, then, it could be labeled as a sensorimotor association region. However, a closer inspection of its response properties reveals how it may play an important role in attention. First, this region does not respond to most visual stimuli, but rather has a sparse response profile such that it tends to respond to stimuli that are unexpected (e.g., abrupt, unpredictable onsets) or relevant to the task. When searching for a target in an array of objects (e.g., a red triangle), LIP neurons tend to respond more strongly when the target lands in its receptive field than when a distractor (e.g., a blue square) does (Gottlieb et al., 1998). They also respond more when a target is linked to either a strong reward or strong punishment (Leathers & Olson, 2012). So its responsiveness isn't related just to sensory stimulation per se. Moreover, sudden changes in luminance are a salient stimulus to these neurons (Balan & Gottlieb, 2009), analogous to how luminance changes drive attention in the Posner cueing task. As such, neurons in this region have response characteristics associated with both exogenous and endogenous attention. It has been suggested that area LIP contains a **salience map** of space in which only the locations of the most behaviorally relevant stimuli are encoded (e.g., Itti &

KEY TERMS

Lateral intraparietal area (LIP)
Contains neurons that respond to salient stimuli in the environment and are used to plan eye movements.

Saccade
A fast, ballistic movement of the eyes.

Salience map
A spatial layout that emphasizes the most behaviorally relevant stimuli in the environment.

Koch, 2001). However, it also represents salience in a nonspatial way too, given that it responds strongly to task-relevant targets and rewards more broadly. This is clearly reminiscent of the bottleneck or spotlight metaphor of attention in cognitive models that selects only a subset of information in the environment.

In addition to representing the saliency of visual stimuli, neurons in LIP also respond to the current position of the eye (in fact, its responsiveness depends on the two sources of information being multiplied together; Bisley & Goldberg, 2010). This information can be used to plan a saccade – that is, overt orienting of attention. There is also evidence that they may support covert orienting. Lesioning LIP in one hemisphere leads to slower visual search in the contralateral (not ipsilateral) visual field even in the absence of overt orienting with saccades (Wardak et al., 2004).

Spatial attention to sounds is also associated with activity in LIP neurons, and this can also be used to plan saccades (Stricanne et al., 1996). Thus, this part of the brain is multisensory. In order to link sound and vision together on the same salience map, it requires the different senses to be spatially aligned or **remapped**. This is because the locations of sounds are coded relative to the angle of the head/ears, but the location of vision is coded (at least initially) relative to the angle of the eyes. Some neurons in LIP transform sound locations to be relative to the angle of the eyes so they can be used to plan saccades, instead of being located relative to the head/ears (Stricanne et al., 1996), as illustrated in Figure 9.8.

In humans, using fMRI, presenting an arrow (an endogenous cue for spatial orienting) is associated with brief activity in visual cortical regions followed by sustained activity in posterior parietal lobes (including the likely homologue of area LIP) and a frontal region called the **frontal eye field (FEF)** (Corbetta et al., 2000). This activity occurs irrespective of whether the required response is one of covert orienting of attention, a saccade, or a pointing response (Astafiev et al., 2003). That is, it reflects a general orienting of attention. It may also not be spatially specific as a similar region is implicated in orienting attention between spatially superimposed objects, as in the previous face-house example (Serences et al., 2004). Bressler et al. (2008) examined the functional connectivity among this network

KEY TERMS

Remapping
Adjusting one set of spatial coordinates to be aligned with a different coordinate system.

Frontal eye field (FEF)
Part of the frontal lobes responsible for voluntary movement of the eyes.

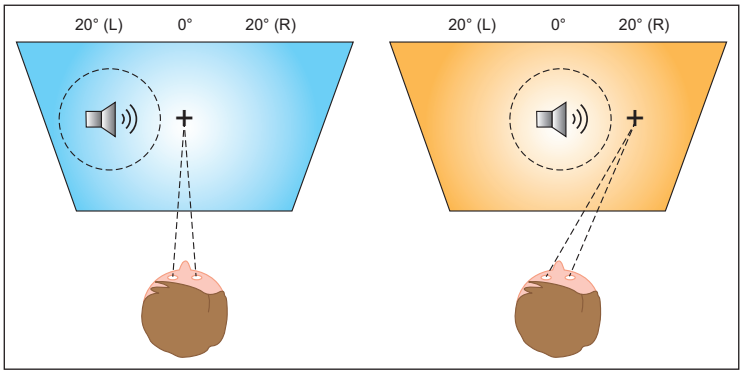

FIGURE 9.8: An example of an auditory neuron that responds to sounds that have been "remapped" into eye-centered coordinates. These neurons are found in brain regions such as LIP and the superior colliculus. This neuron responds to sounds about 20 degrees to the left of eye-gaze fixation irrespective of whether the sound source itself comes from the left (left figure) or center of space (right figure). This enables orienting of the eyes to sounds.

From Stein and Stanford (2008). Reproduced with permission from Springer Nature.

during presentation of a preparatory orienting stimulus (the spoken words "left" or "right") prior to a visual stimulus and concluded that, in this situation, the directionality of activation was top-down: that is, from frontal regions, to parietal regions, to the visual occipital cortex. In other situations the network may operate in reverse, such as when an exogenous sensory cue is presented. Using evidence from single-cell recordings from multiple regions, Siegel et al. (2015) trained macaques to attend to either color or motion and to respond to relevant features (e.g., direction of motion) with a saccade. In this case, there was bottom-up activity from the sensory cortex to LIP and prefrontal regions. The LIP and prefrontal regions accumulate evidence about the choice (i.e., relating to whether a saccade should be made to the left or right), which is simultaneously broadcast top-down to sensory regions. Neurons in the frontal eye fields transform the accumulated evidence into a discrete choice, that is, a saccadic motor response.

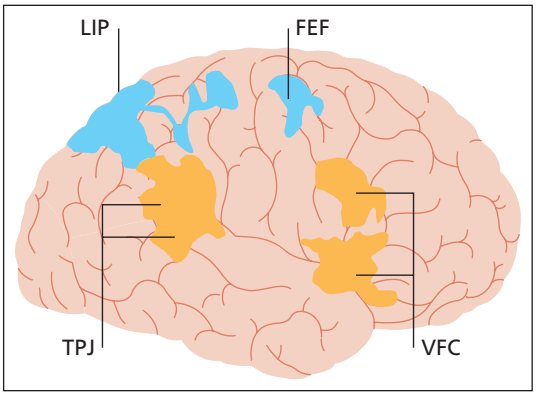

FIGURE 9.9: Corbetta and Shulman (2002) have suggested that there are two main attention-related circuits involving the parietal lobes: a dorso-dorsal circuit (involving LIP) that is involved in attentional orienting within a salience map and a more ventral circuit (involving the right temporoparietal junction, TPJ) that diverts attention away from its current focus.

According to Corbetta and Shulman (2002), this is only one of two major attentional networks involving frontoparietal networks (Figure 9.9). They suggest that the dorsal stream should be reconsidered as split into two: a dorso-dorsal branch and a ventro-dorsal branch (for a related proposal see Rizzolatti & Matelli, 2003). They conceptualize the role of the dorso-dorsal stream in attention as one of orienting within a salience map (as described previously) and involving the LIP and FEF. By contrast, they regard the more ventro-dorsal branch as a "circuit breaker" that interrupts ongoing cognitive activity to direct attention outside of the current focus of processing. This attentional disengagement mechanism is assumed to involve the temporoparietal region (and ventral prefrontal cortex) and is considered to be more strongly right lateralized. For instance, activity in this right temporoparietal region is found when detecting a target (but not when processing a spatial cue), whereas activity in the LIP region shows a strong response to the cue (Corbetta et al., 2000). Activity in the right temporoparietal region is enhanced when detecting an infrequent target, particularly if it is presented at an unattended location (Arrington et al., 2000). Downar et al. (2000) found that several frontal areas as well as the temporoparietal junction (TPJ) were activated when participants were monitoring for a stimulus change, independently of whether the change occurred in auditory, visual, or tactile stimuli.

Hemispheric differences in parietal lobe contributions to attention

Whereas early visual cortex has a complete separation between visual hemifields (left space projecting to right visual cortex, and

vice versa), the parietal lobes of the right and left hemispheres of humans represent the full visual field but do so in a graded fashion that favors the contralateral side of space (this is not necessarily true of macaques, Patel et al., 2015). So the right parietal lobe shows a maximal responsiveness to stimuli on the far left side, a moderate responsiveness to the middle, and a weaker response to the far right side. The left parietal lobe shows the reverse profile. One consequence of this is that damage to the parietal lobes in one hemisphere leads to left–right spatially graded deficits in attention. For instance, damage to the right parietal lobe would lead to less attentional resources allocated to the far left side, moderate attentional resources to the midline, and near-normal attentional abilities on the right. This disorder is called **hemispatial neglect**, in which patients fail to attend to stimuli on the opposite side of space to the lesion. Neglect is normally far more severe following right-hemisphere lesions, resulting in failure to attend to the left. This suggests that, in humans, there is likely to be a hemispheric asymmetry such that the right parietal lobe is more specialized for spatial attention than the left. Another possible way of conceptualizing this is that the right parietal lobe makes a larger contribution to the construction of a salience map than the left side, resulting in a normal bias for the left side of space to be salient (a phenomenon termed **pseudo-neglect**, see Box), and for the left side of space to be, therefore, particularly vulnerable to the effects of brain damage (neglect).

KEY TERMS

Hemispatial neglect
A failure to attend to stimuli on the opposite side of space to a brain lesion.

Pseudo-neglect
In a non-lesioned brain there is over-attention to the left side of space.

WHY DO ACTORS MAKE A HIDDEN ENTRANCE FROM STAGE RIGHT?

The right parietal lobes of humans are generally considered to have a more dominant role in spatial attention than its left hemisphere equivalent. One consequence of this is that right-hemisphere lesions have severe consequences for spatial attention, particularly for the left space (as in the condition of "neglect"). Another consequence of right-hemisphere spatial dominance is that, in a nonlesioned brain, there is *over-attention* to the left side of space (termed pseudo-neglect). For example, there is a general tendency for everyone to bisect lines more to the left of center (Bowers & Heilman, 1980). This phenomenon may explain why actors enter from stage right when they do not wish their entrance to be noticed (Dean, 1946). It may also explain why pictures are more likely to be given titles referring to objects on the left, and why the left side of pictures feels nearer than the right side of the same picture when flipped (Nelson & MacDonald, 1971). The light in paintings is more likely to be depicted as coming from the left side, and people are faster at judging the direction of illumination when the source of light appears to come from the left (Sun & Perona, 1998). Moreover, we are less likely to bump into objects on the left than the right (Nicholls et al., 2007). Thus, there is a pervasive leftwards attentional bias that exists even when equating for cross-cultural differences such as reading direction (Nicholls & Roberts, 2002) (Figure 9.10).

FIGURE 9.10: Which bar appears darker: the one on the top or the bottom? Most people perceive the bottom bar as being darker because of an attentional bias to the left caused by a right-hemisphere dominance for space/attention, even though the two images are identical mirror images.

Parietal lobe lesions can also result in nonspatial deficits of attention. Husain et al. (1997) found that neglect patients had an unusually long "blind" period in the attentional blink task in which stimuli were presented centrally. Again, this can be construed in terms of both hemispheres making a contribution to the normal detection of salient stimuli (in this case, the second target in a rapidly changing stream). When one hemisphere is damaged, the attentional capacity is depleted.

Mevorach and colleagues have proposed that the left and right parietal lobes have different roles in nonspatial attention: specifically, the right hemisphere is considered important for attending to a salient stimulus, and the left hemisphere is important for suppressing a non-salient stimulus or "ignoring the elephant in the room" (Mevorach et al., 2006; Mevorach et al., 2010). Their nonspatial manipulation of saliency involved making certain elements of the display easier to perceive (Figure 9.11). For instance, a figure composed of an "H" made up of small Ss

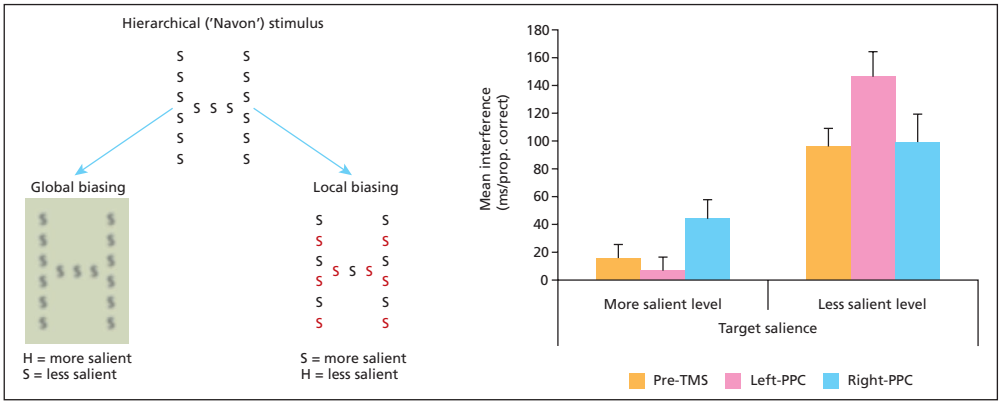

FIGURE 9.11: Having alternating colors makes local elements salient, but blurring the local elements makes the global shape more salient. TMS over the right posterior parietal cortex disrupts the ability to detect the more salient element (e.g., the local S in the right example, and the global "H" in the left example). TMS over the left posterior parietal cortex disrupts the ability to detect the less salient element (e.g., the global "H" in the right example, and the local S in the left example).

Graph from Mevorach et al. (2006). Reproduced with permission from Springer Nature.

ONLINE RESOURCES

To see a demonstration of the rubber hand illusion online scan the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

can be altered so that either the "H" is more salient (blurring the Ss) or the S is more salient (using alternating colors). fMRI shows that the *left* intraparietal sulcus is involved when the task is to focus on non-salient features (and ignore salient ones) – such as finding the local Ss in a blurred global "H" (Mevorach et al., 2006). Disruption of this region using TMS (but not the right-hemisphere region) interferes with the ability to do this task and disrupts the connectivity between this region and those in the occipital lobe that are presumably engaged in shape processing. By contrast, the *right* intraparietal cortex responds more when the task is to identify the salient features (and ignore the non-salient ones) and TMS to this region disrupts that task (Mevorach et al., 2006). What is presently unclear is how these sorts of nonspatial selection mechanisms relate to the spatially specific deficits seen in neglect. One possibility is that neglect comprises a variety of attention-related deficits, some that are spatially specific (the defining symptoms of neglect) and some that are not. Whatever the relationship to neglect, there is an emerging consensus that attention itself can be fractionated into different kinds of mechanisms (Riddoch et al., 2010).

SPATIAL ATTENTION ACROSS THE SENSES: VENTRILOQUIST AND RUBBER HAND ILLUSIONS

In ventriloquism, there is a conflict between the actual source of a sound (the ventriloquist) and the apparent source of the sound (the dummy). In this instance, the sound appears to come from the dummy because the dummy has associated lip movements, whereas the lip movements of the ventriloquist are suppressed. In other words, the spatial location of the visual cue "captures" the location of the sound.

Why is it that sound tends to be captured by the visual stimulus but not vice versa? One explanation is that the ability to locate things in space is more accurate with vision than audition, so when there is a mismatch between them, the brain may default to the visual location. Witkin et al. (1952) found that sound localization was impaired in the presence of a visual cue in a conflicting location. Driver and Spence (1994) found that people are able to repeat back a speech stream (or "shadow") more accurately when lip movements and the loudspeaker are on the same side of space than when they are on opposite sides.

In the brain, there are multisensory regions such as in the superior temporal sulcus and intraparietal sulcus that respond selectively to sound and vision when both occur at the same time or in the same location (Calvert, 2001). For instance, the superior temporal sulcus shows greater activity to synchronous audiovisual speech than asynchronous speech (Macaluso et al., 2004). However, when there is a *spatial* mismatch between the auditory and visual locations of synchronous speech the right inferior parietal lobe

is activated (Macaluso et al., 2004). This audiovisual spatial mismatch is found in the ventriloquist illusion and may involve the shifting or suppression of the sound location or, conversely, "grabbing" of spatial attention by the visual modality.

More bizarrely, there is an analogue of the ventriloquist effect in the tactile modality. Botvinick and Cohen (1998) placed participants' hand behind a hidden screen and placed a rubber hand on the visible side of the screen, as shown in Figure 9.12. Watching the rubber hand stroked with a paintbrush while their own (unseen) hand was stroked with a paintbrush could induce a kind of "out-of-body" experience. Participants report curious sensations such as "I felt as if the rubber hands were my hands." In this instance, there is a conflict between the seen location of the (rubber) hand and felt bodily location of the real hand: the conflict is resolved by visual capture of the tactile sensation.

FIGURE 9.12: In the rubber hand illusion, if the dummy hand (visible to the participant) and the real hand (which the participant cannot see) are stroked at the same time, then the participant reports ownership of the dummy hand, what would happen if the dummy hand were stabbed?

Evaluation

This section has taken core ideas relating to the concept of attention (e.g., filtering irrelevant information, the spotlight metaphor, links to eye movements) and explained how these may be implemented in the brain. The parietal lobes have a key role because they interface between regions involved in executive control (top-down aspects of attention) and regions involved in perceptual processing (bottom-up aspects of attention). One of the emerging trends in the literature on attention, which has been driven largely by neuroscience, is to consider attention in terms of separable but interacting component processes (e.g., orienting attention, disengaging attention, and so on). This is not surprising given that most other cognitive faculties (e.g., vision, memory) are now thought of in this way. However, it would be fair to say that there is less consensus over what the constituent components are (if any) in the attention domain. The next main section considers several specific models of attention that conform to the general principles discussed thus far.

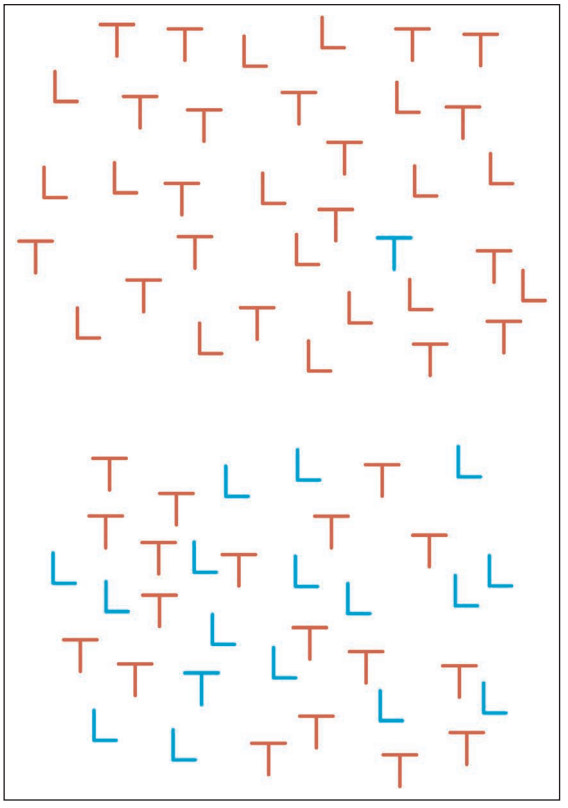

FIGURE 9.13: Try to find the blue "T" as quickly as possible. Why is one condition harder than the other? Feature integration theory assumes that basic features are coded in parallel but that focused attention requires serial search. When the letter differs from others by a single feature, such as color, it can be identified quickly by the initial stage of feature detection. When the letter differs from others by two or more features, attention is needed to serially search.

THEORIES OF ATTENTION

This section considers in more detail three influential theories in the attention literature: the feature integration theory proposed by Treisman and colleagues; biased competition theory proposed by Desimone, Duncan, and colleagues; and the premotor theory of Rizzolatti and colleagues.

Feature integration theory

Feature integration theory (FIT) is a model of how attention selects perceptual objects and binds the different features of those objects (e.g., color and shape) into a reportable experience. Most of the evidence for it (and against it) has come from the visual search paradigm. Look at the two arrays of letters in Figure 9.13. Your task is to try to find the blue "T" as quickly as possible.

Was the letter relatively easy to find in the first array, but hard to find in the second array? In the second case, did you feel as if you were searching each location in turn until you found it? In the first array, the target object (the blue "T") does not share any features with the distractor objects in the array (red Ts and red Ls). The object can therefore be found from a simple inspection of the perceptual mechanism that supports color detection.

According to FIT, perceptual features such as color and shape are coded in parallel and prior to attention (Treisman, 1988; Treisman & Gelade, 1980). If an object does not share features with other objects in the array, it appears to **pop out**. In the second array, the distractors are made up of the same features that define the object. Thus, the object cannot be detected by inspecting the color module alone (because some distractors are blue) or by inspecting the shape module alone (because some distractors are T-shaped). To detect the target, one needs to bring together information about several features (i.e., a conjunction of color and shape). FIT assumes that this occurs by allocating spatial attention to the location of candidate objects. If the object turns out not to be the target, then the "spotlight" inspects the next candidate and so on in a serial fashion.

Typical data from a visual search experiment such as the one conducted by Treisman and Gelade (1980) are in Figure 9.14. The

KEY TERM

Pop-out
The ability to detect an object among distractor objects in situations in which the number of distractors presented is unimportant.

dependent measure is the time taken to find the target (some arrays do not contain the target, but these data are not presented here). The variables manipulated were the number of distractors in the array and the type of distractor. When the target can only be found from a conjunction of features, there is a linearly increasing relationship between the number of distractors and time taken to complete the search. This is consistent with the notion that each candidate object must be serially inspected in turn. When a target can be found from only a single feature, it makes very little difference how many distractors are present, because it "pops out." If attention is not properly deployed, then individual features may incorrectly combine. These are referred to as **illusory conjunctions**. For example, if displays of colored letters are presented briefly so that serial search with focal attention cannot take place, then participants may incorrectly say that they had seen a red "H" when in fact they had been presented with a blue "H" and a red "E" (Treisman & Schmidt, 1982). This supports the conclusion arising from FIT that attention needs to be deployed to combine features of the same object correctly.

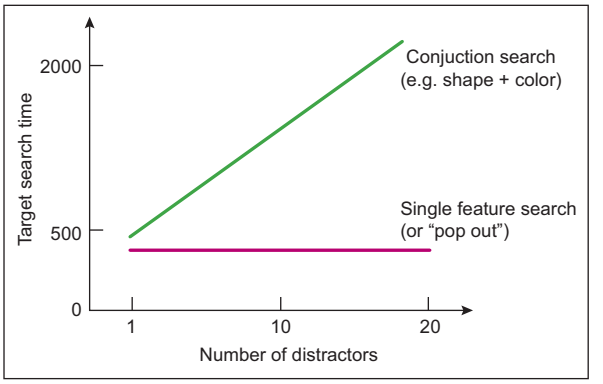

FIGURE 9.14: According to FIT, when a target is defined by a conjunction of features, search becomes slower when there are more items, because the items are searched serially. When a target is defined by a single feature, it may "pop out"; that is, the time taken to find it is not determined by the number of items in the array.

KEY TERM

Illusory conjunctions
A situation in which visual features of two different objects are incorrectly perceived as being associated with a single object.

TMS applied over the parietal lobe slows conjunction searches but not single-feature searches (Ashbridge et al., 1997, 1999), and functional imaging has demonstrated parietal involvement in conjunction, but not single-feature searches (Corbetta et al., 1995). Patients with parietal lesions often show a high level of illusory conjunction errors with brief presentation (Friedman-Hill et al., 1995).

One difficulty with FIT is that there is no a priori way to define what constitutes a "feature." Features tend to be defined in a post hoc manner according to whether they elicit pop-out. Duncan and Humphreys (1989) suggest that most of the data that FIT attempts to explain can also be explained in terms of how easy it is to perceptually group objects together rather than in terms of parallel feature perception followed by serial attention. They found that it is not just the similarity between the target and distractor that is important, but also the similarity between different types of distractor. This implies that there is some feature binding prior to attention, and this contradicts a basic assumption of FIT. Another issue is whether simple feature searches (e.g., a single blue letter among red letters) really occur without attention as assumed by FIT. An alternative position is that *all* visual search requires attention even in the case of pop-out stimuli. Wolfe (2003) argues that pop-out is not preattentive but is simply a stimulus-driven (exogenous) cue of attention.

KEY TERMS

Early selection
A theory of attention in which information is selected according to perceptual attributes.

Late selection
A theory of attention in which all incoming information is processed up to the level of meaning (semantics) before being selected for further processing.

Negative priming
If an ignored object suddenly becomes the attended object, then participants are slower at processing it.

Finally, FIT is an example of what has been termed an **early selection** model of attention. Recall that the main reason for having attentional mechanisms is to select some information for further processing, at the expense of other information. According to early selection theories, information is selected according to perceptual attributes (e.g., color or pitch). This can be contrasted with **late selection** theories that assume that all incoming information is processed up to the level of meaning (semantics) before being selected for further processing. One of the most frequently cited examples of late selection is the **negative priming** effect (Tipper, 1985). In Figure 9.15, participants must name the red object and ignore the blue one. If the ignored object on trial N suddenly becomes the attended object on trial N+1, then participants are slower at naming it (called negative priming). The effect can also be found if the critical object is from the same semantic category. This suggests that the ignored object was, in fact, processed meaningfully rather than being excluded purely on the basis of its color as would be expected by early selection theories such as FIT.

How can the evidence both for and against FIT be reconciled? The selection of objects for further processing may sometimes be early (i.e., based on perceptual features) and sometimes late (i.e., based on meaning), depending on the demands of the task. Lavie (1995) has shown that, when there is a high perceptual load (e.g., the large arrays typically used for visual search), then selection may be early, but in conditions of low load in which few objects are

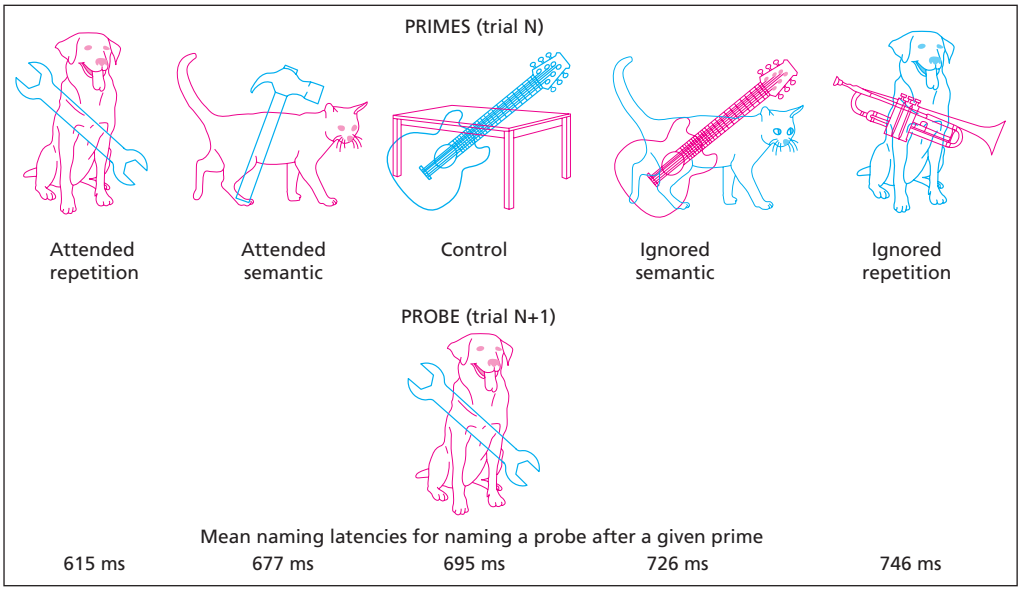

FIGURE 9.15: In this example, participants must name the red object and ignore the blue one. If an ignored object becomes an attended object on the subsequent trial, then there is a cost of processing, which is termed negative priming.

present (as in the negative priming task), there is a capacity for all objects to be processed meaningfully. This is consistent with late selection. In other words, late selection only occurs when the limited attentional capacity hasn't been exhausted by perceptual selection. Other findings have suggested that the process of feature binding may also operate at several levels (Humphreys et al., 2000), with some forms of binding occurring prior to attention. This could account for the distractor similarity effects of Duncan and Humphreys (1989).

Biased competition theory

The biased competition theory of Desimone and Duncan (1995) draws more heavily from neuroscience than from cognitive psychology. It explicitly rejects a spotlight metaphor of attention (inherent, for instance, in feature integration theory). Instead "attention is an emergent property of many neural mechanisms working to resolve competition for perceptual processing and control of behavior." By "emergent property" Desimone and Duncan imply that attention isn't a dedicated module in the brain, but rather a broad set of mechanisms for reducing many inputs to limited outcomes, and there is no clear division between attentive and preattentive stages. The biased competition theory has been extended and updated by others in light of more recent evidence (Beck & Kastner, 2009; Knudsen, 2007).

One assumption of the model is that competition occurs at multiple stages rather than at some fixed bottleneck – i.e., neither early nor late selection but something more dynamic. This competition occurs first within the visual ventral stream itself in terms of the processing of visual features (colors, motion, etc.) and objects. For instance, single-cell electrophysiology shows that when two stimuli are presented in a single receptive field (e.g., two color patches presented in the receptive field of a neuron in V4), the responsiveness of the neuron is less than the sum of its responsiveness to each stimulus in isolation (Luck et al., 1997). This is one way in which "competition" may be realized at the neural level (i.e., reduced neural responsiveness to multiple stimuli).

In humans, the BOLD response in areas of the visual ventral stream to multiple stimuli presented together is less than the sum of its parts as determined by a control condition involving sequential presentation (Kastner et al., 2001). This also depends on how spatially close together the different stimuli are. Brain regions containing neurons with small receptive fields (e.g., V1) are only disrupted by competitors that are close-by, but regions that have larger receptive fields (e.g., V4) are also disrupted by more distant competitors. As well as spatial proximity, the degree of competition depends on perceptual similarity of multiple stimuli within the field (Beck & Kastner, 2009). This may be the neural basis of early grouping effects and also pop-out. Certain perceptual representations may also tend to dominate in the competitive

process by virtue of being familiar (e.g., spotting your partner in a crowd) or by virtue of being recently seen, and so on. Again, this does not require a special mechanism as such: it just requires that there is bias in the way these stimuli are represented that facilitates their selection (e.g., neurons fire more when expected or frequently encountered). Selection may also be biased by top-down signals. When a receptive field contains an experimentally defined target and an irrelevant distractor, the magnitude of the neural response resembles that to the target alone, rather than the sum of target + distractor (Moran & Desimone, 1985). This suggests some filtering out of the distractor.

Another key assumption of this theory is that attention is not deployed serially, but rather perceptual competition occurs in parallel. Serial processing, by contrast, is assumed to arise from competition at the motor response level rather than perceptual processing (e.g., from the fact that it is only possible to fixate one location at a time; an idea that is linked closely to the premotor theory of attention discussed in the next section). Neurons recorded in monkey V4 during visual search tasks are activated in parallel (i.e., irrespective of whether it is being currently attended/fixated) whenever a target feature (e.g., color) falls in the receptive field (Bichot et al., 2005). This occurs for both simple feature (i.e., pop-out) and conjunction searches. However, there is also an enhanced response when the target is selected for a saccade suggesting that serial processing is linked to motor responses. Whereas feature integration theory assumes either parallel *or* serial search (depending on the nature of the targets), the biased competition theory suggests both kinds of mechanisms act together but at different levels in the selection hierarchy (perception = parallel, motor = serial).

KEY TERM

Extinction
In the context of attention, unawareness of a stimulus in the presence of competing stimuli.

The biased competition model also accounts for spatial and nonspatial attention within the same model. The differences between spatial and nonspatial attention were originally assumed to be due to different anatomical origins of the biasing signals rather than reflecting different mechanisms per se. The posterior parietal cortex was thought to be the origin of spatial biases (e.g., effects of arrows in orienting attention), and prefrontal cortex was thought to code task-related biases (find the blue X). However, other research has suggested that the same frontal and parietal regions support both spatial and nonspatial search cues (Egner et al., 2008).

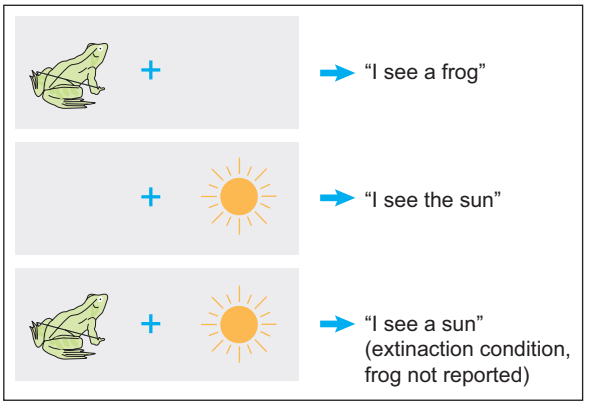

FIGURE 9.16: Patients with right parietal lobe lesions may fail to notice the stimulus on the left when two stimuli are briefly shown (called extinction), but notice it when it is shown in isolation. It suggests that attention depends on competition between stimuli.

The model also explains certain neuropsychological findings. Damage to the parietal lobe not only produces neglect; it may also lead to a symptom called **extinction** (Riddoch et al., 2010). When a single stimulus is presented briefly to either the left or the right of fixation, patients with parietal lesions tend to accurately report them. But

when presented with two stimuli at the same time, the patient may report seeing the object on the right but not the object on the left (in the case of right parietal damage) – see Figure 9.16. Thus the patient has not lost the ability to see the left side of space, nor have they lost the ability to attend to the left side of space per se. Instead it depends on competitive interactions between multiple objects (the presence of an object in the "good" hemifield strongly biases selection). Similarly, in the Posner cueing task, patients with right parietal lobe lesions are able to initially orient attention to either the left or right side of space as a result of a pre-stimulus flash of light on either the left or right. However, while they are able to shift attention from a cue on the left (their neglected side) to a target on the right (their "good" side), they are impaired in the reverse scenario (shifting from the "good" to neglected side) (Posner & Petersen, 1990). This can be explained by biased competition: it is harder to orient to the "bad" side following a salient visual stimulus on the "good" side.

The premotor theory of attention

The premotor theory of attention assumes that the orienting of attention is nothing more than the preparation of motor actions (Rizzolatti et al., 1987, 1994). As such, it is primarily a theory of spatial attention. The theory encompasses both overt orienting, in which actual movement occurs, and covert orienting. The latter is assumed to reflect a movement that is planned but not executed.

The initial evidence for the theory came from a spatial cueing task (Rizzolatti et al., 1987). The task used four spatial locations arranged left to right (1, 2, 3, and 4) and a centrally fixated square, as shown in Figure 9.17. Within the central square, a digit would appear that would indicate where a target was likely to appear (with 80 percent certainty). A flash would then appear in one of the four boxes, and the participant simply had to press a button as soon as it was detected. Participants were slower when the cue was misleading, forcing them to shift attention. However, they found that costs in response times were not only related to whether attention had to shift per se but also whether attention had to *reverse* in direction. So a shift of attention from position 2 (left) to position 1 (far left) had a small cost, whereas a shift from position 2 (left) to a rightward location (position 3) had a larger cost (and similarly a shift from 3 to 4 was less costly than from 3 to 2). The same results were also found for vertical alignments of the four positions so the findings do not relate to processing differences across hemispheres. The basic finding is hard to reconcile with a simple "spotlight" account, because the spotlight is moved the

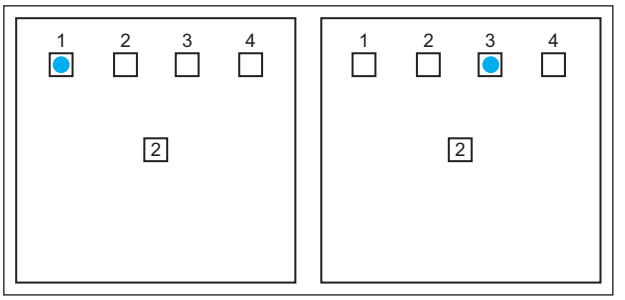

FIGURE 9.17: In the study of Rizzolatti et al. (1987), a centrally presented digit indicates where a target stimulus is likely to appear (in this case, position 2), but it may sometimes appear in an unattended location (as shown here, in positions 1 or 3). Although positions 1 and 3 are equidistant from the expected location, participants are faster at shifting attention to position 1 than position 3. Why might this be?

same distance in both scenarios. They suggest instead that the pattern reflects the programming of eye movements (but not their execution as overt movements were not allowed). Specifically, a leftwards eye movement can be made to go further leftwards with minimal additional processing effort, but changing a leftwards movement to a rightwards movement requires a different motor program to be set up and the original one discarded.

The term "premotor" refers to the claim that attention is a preparatory motor act and is not referring to the premotor cortical region of the brain (discussed in Chapter 10). The theory does, however, make strong neuroanatomical predictions: namely, that the neural substrates of attention should be the same as the neural substrates for motor preparation (particularly eye movements). As discussed previously, there is evidence to support this view from single-cell recordings (Bisley & Goldberg, 2010) and human fMRI (Nobre et al., 2000). There is also intriguing evidence from brain stimulation studies. Electrical stimulation of neurons in the FEF of monkeys can elicit reliable eye movements to particular locations in space. Moore and Fallah (2001) identified such neurons and then stimulated them at a lower intensity such that no eye movements occurred (the animal continued to fixate centrally). However, the animals did show enhanced perceptual discrimination of a stimulus presented in the location where an eye movement would have occurred (Figure 9.18). This suggests that attention was deployed there and is consistent with the idea that covert orienting of attention is a non-executed movement plan.

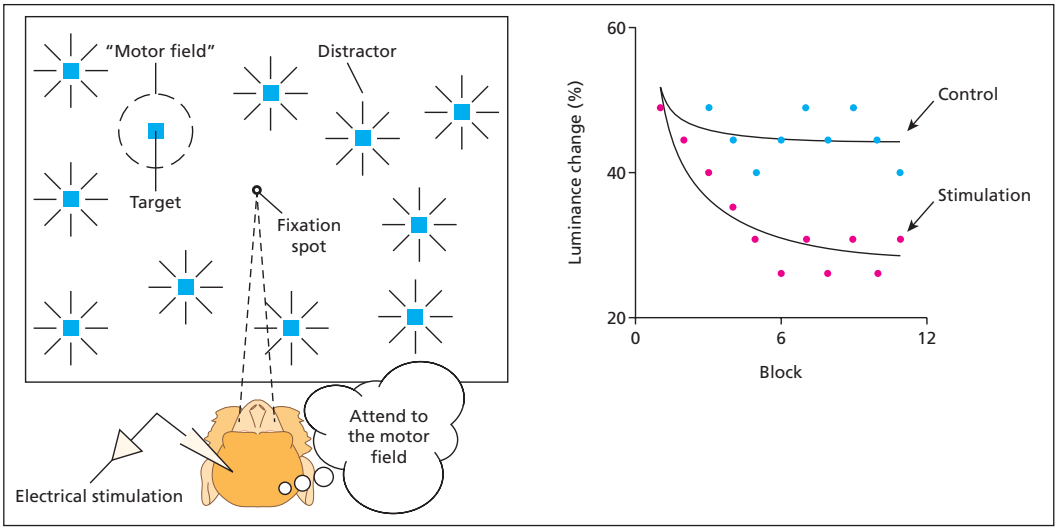

FIGURE 9.18: In Moore and Fallah (2001) the task of the animal was to press a lever when one of the stimuli "blinked" (a small change in luminance). They were better at doing the task (i.e., able to detect weaker luminance changes) when a part of the brain involved in generating eye movements was stimulated than in a no-stimulation control condition (even though no eye movements occurred), provided the light stimulus fell in the appropriate receptive field. This is consistent with the idea that attending to a region of space is like a virtual movement of the eyes.

Left image from www.nature.com/neuro/journal/v5/n9/fig_tab/nn0902–819_F1.html. Right image from Moore and Fallah (2001).

The premotor theory of attention has not been without criticism. Smith and Schenk (2012) argue that it fails as a general theory of attention and may only be valid in certain situations (e.g., exogenous orienting of attention to, say, flashes of light). For instance, patients with chronic lesions of the FEF have a saccadic deficit but no deficit of endogenous attention in covert orienting tasks involving arrow cues (Smith et al., 2004).

SEEING ONE OBJECT AT A TIME: SIMULTANAGNOSIA AND BALINT'S SYNDROME

The idea that one could perceive an object but not its location is highly counterintuitive, because it falls outside of the realm of our own experiences. However, there is no reason why the functioning of the brain should conform to our intuitions. Patients with **Balint's syndrome** (Balint, 1909, translated 1995) typically have damage to both the left and the right parietal lobes (Figure 9.19) and have severe spatial disturbances. Patients with Balint's syndrome may notice only one object at a time: this is termed **simultanagnosia**. For example, the patient may notice a window, then, all of a sudden, the window disappears, and a necklace is seen, although it is unclear who is wearing it. In terms of the two visual streams idea, it is as if there is no "there" there (Robertson, 2004). Within the biased competition theory, it could be regarded as an extreme form of perceptual competition due to a limited spatial selection capacity. Within feature integration theory, it can be construed as an inability to bind features to locations and, hence, to each other. Recall that if a blue "H" and a red "E" are presented very quickly to normal participants, then illusory conjunction errors may be reported (e.g., red "H"). Balint's patients show these errors even when they are free to view objects for as long as they like (Friedman-Hill et al., 1995). In addition to simultanagnosia, patients typically have problems in using vision to guide hand actions (optic ataxia; considered in Chapter 10) and fail to make appropriate eye movements (optic apraxia).

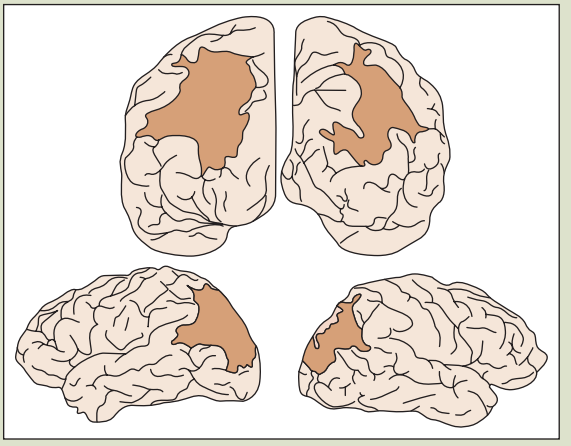

FIGURE 9.19: Patient RM has extensive damage to both the left and right parietal lobes and severe difficulties in perceiving spatial relationships (top diagrams are viewed from the back of the brain; bottom diagrams are viewed from the side). RM was unable to locate objects verbally, or by reaching or pointing (Robertson et al., 1997). In contrast, his basic visual abilities were normal (normal 20/15 visual acuity, normal color vision, contrast sensitivity, etc.). He was impaired at locating sounds, too.

KEY TERMS

Balint's syndrome
A severe difficulty in spatial processing normally following bilateral lesions of the parietal lobe; symptoms include simultanagnosia, optic ataxia, and optic apraxia.

Simultanagnosia
Inability to perceive more than one object at a time.

Line bisection
A task involving judging the central point of a line.

Cancellation task
A variant of the visual search paradigm in which the patient must search for targets in an array, normally striking them through as they are found.

Evaluation

Although there are many theories of attention, three prominent ones have been considered here. Feature integration theory and the premotor theory are necessarily limited in scope in that they are specifically theories of *spatial* attention, whereas biased competition theory has the advantage of offering a more general account. Feature integration theory has been successful in explaining much human behavioral data in visual search. Biased competition theory offers a more neuroscientific account of these data in which competition arises at multiple levels (e.g., perceptual crowding, and response competition), and attention is synonymous with the selection function of this overall system. Premotor theory offers an interesting explanation as to how attention can be considered as a combination of both "where" (spatial) and "how" (motor) functions of the dorsal stream.

NEGLECT AS A DISORDER OF SPATIAL ATTENTION AND AWARENESS

Patients with neglect (also called hemispatial neglect, visuo-spatial neglect, or visual neglect) fail to attend to stimuli on the opposite side of space to their lesion – normally a right-sided lesion resulting in inattention to the left side of space.

Characteristics of neglect

There are a number of common ways of testing for neglect (Figure 9.20). Patients may omit features from the left side when drawing or copying. In tests of **line bisection**, patients tend to misplace the center of the line toward the right (because they underestimate the extent of the left side). The bias in bisection is proportional to the length of the line (Marshall & Halligan, 1990). **Cancellation tasks** are a variant of the visual search paradigms already discussed, in which the patients must search for targets in an array (normally striking them through as they are found). They will typically not find ones on the left. In extreme cases, neglect patients may shave only half of their face or eat half of the food on their plate.

Mort et al. (2003) examined the brain regions critical for producing neglect in 35 patients and concluded that the critical region was the right angular gyrus of the inferior parietal lobe, including the right temporoparietal junction (TPJ), as shown in Figure 9.21. Functional imaging studies of healthy participants performing line bisection also point to an involvement of this area in that particular task (Fink et al., 2000), as do the results from a TMS study (Fierro et al., 2000). While there is good consensus over the role of this region in neglect, it is not the only region that is implicated. For instance, Corbetta and Shulman (2011) argue that the right posterior parietal cortex, containing salience maps, may tend to be functionally deactivated (because of its connectivity with the damaged right TPJ) despite not being structurally damaged.

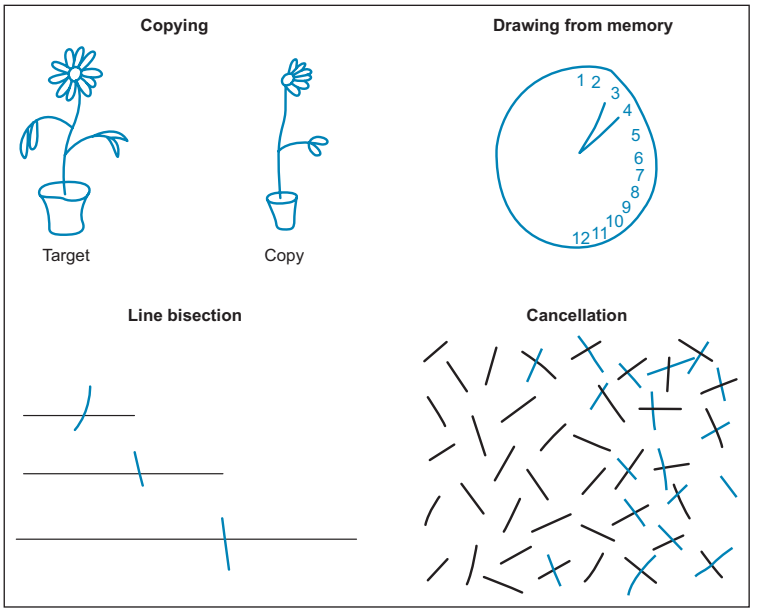

FIGURE 9.20: Different ways of assessing neglect include copying, drawing from memory, finding the center of a line (line bisection), and crossing out targets in an array (cancellation).

Others have argued that neglect itself can be fractionated into different kinds of spatial processes with differing neural substrates, as considered later.

ONLINE RESOURCES

To discover more about neglect, visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience).

Neglect and the relationship between attention, perception, and awareness

It is important to stress that neglect is not a disorder of low-level visual perception. A number of lines of evidence support this conclusion. Functional imaging reveals that objects in the neglected visual field still activate visual regions in the occipital cortex (Rees et al., 2000). Stimuli presented in the neglected field can often be detected if attention is first cued to that side of space (Riddoch & Humphreys, 1983). This also argues against a low-level perceptual deficit. The situations in which neglect patients often fare worse are those requiring voluntary orienting to the neglected side and those situations in which there are several stimuli competing for attention. Although the primary deficit in neglect is related to attention, not perception, it does lead to deficits in *awareness* of the perceptual world.

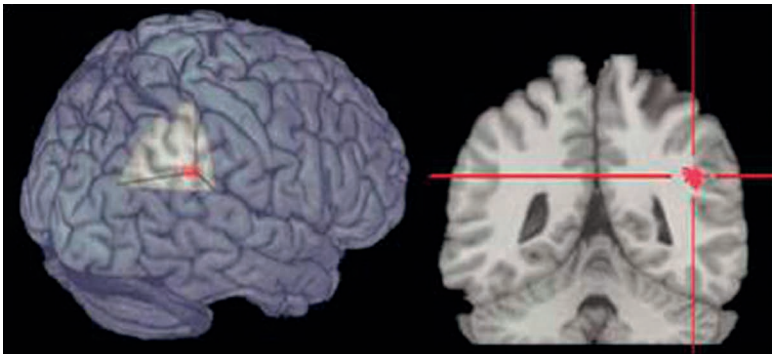

FIGURE 9.21: Neglect is associated with lesions to the right inferior parietal lobe.

This photo shows the region of highest overlap of the lesions of 14 patients.

Neglect is not just restricted to vision but can apply to other senses as well. This is consistent with the evidence presented earlier that the parietal lobes have multisensory characteristics. Pavani et al. (2002) have shown that neglect patients show a right-skewed bias in identifying the location of a sound (but note that they are not "deaf" to sounds on the left). Extinction can also cross sensory modalities. A tactile (or visual) sensation on the right will not be reported if accompanied by a visual (or tactile) stimulus on the left but will be reported when presented in isolation (Mattingley et al., 1997).

Patients with neglect can be shown to process information in the neglected field to at least the level of object recognition. The ventral "what" route seems able to process information "silently" without entering awareness, whereas the dorsal "where" route to the parietal lobe is important for creating conscious experiences of the world around us. Vuilleumier et al. (2002b) presented brief pictures of objects in the left, right, or both fields. When two pictures were presented simultaneously, the patients extinguished the one on the left and only reported the one on the right, and when later shown the neglected stimuli, they claimed not to remember seeing them (a test of explicit memory). However, when later asked to identify a degraded picture of the object, their performance was facilitated, which suggests that the extinguished object was processed unconsciously. Other lines of evidence support this view. Marshall and Halligan (1988) presented a neglect patient with two depictions of a house that were identical on the non-neglected (right) side but differed on the left side such that one of the two houses had flames coming from a left window. Although the patients claimed not to be able to perceive the difference between them, they did, when forced to choose, state that they would rather live in the house without the flames! This, again, points to the fact that the neglected information is implicitly coded to a level that supports meaningful judgments being made.

HOW IS A "LACK OF AWARENESS" IN NEGLECT DIFFERENT FROM LACK OF AWARENESS IN BLINDSIGHT?

Neglect	Blindsight
• Lack of awareness is not restricted to vision and may be found for other sensory modalities	• Lack of awareness is restricted to the visual modality
• Whole objects may be processed implicitly	• Implicit knowledge is restricted to basic visual discriminations (direction of motion; but see Marcel, 1998)
• Lack of awareness can often be overcome by directing attention to the neglected region	• Lack of awareness is not overcome by directing attention to the "blind" region
• Neglected patients often fail to voluntarily move their eyes into the neglected region	• Blindsight patients do move their eyes into the "blind" region
• Neglected region is egocentric	• Blind region is retinocentric

Different types of neglect and different types of space

Space, as far as the brain goes, is not a single continuous entity. A more helpful analogy is to think of the brain creating (and perhaps storing) different kinds of "maps." Cognitive neuroscientists refer to different spatial reference frames to capture this notion. Each reference frame ("map") may have its own center point (origin) and set of coordinates. Similarly, there may be ways of linking one map to another – so-called remapping. How neurons may remap the spatial position of sounds from a head-centered reference frame to an eye-centered reference frame (so-called retinocentric space) has already been described. Remapping is necessary for sounds to trigger eye movements. The same can happen for other combinations: for instance, visual-receptive fields may be remapped so that they are centered on the position of the hands rather than the position of the eyes (facilitating hand-eye coordination during manual actions). The parietal lobes can perform remapping because they receive postural information about the body as well as sensory information relating to sound, vision, and touch (Pouget & Driver, 2000).

The main clinical features of neglect tend to relate to **egocentric space** (reference frames centered on the body midline), and it is these kinds of spatial attentional disorders that are linked to brain damage to the right temporoparietal region (Hillis et al., 2005). However, neglect is also linked to other kinds of spatial reference frames, as outlined next. Although this could be conceptualized as losing particular kinds of spatial representations, another way of thinking about it is in terms of attention deficits that are created by disrupting competition at different levels of processing.

KEY TERM

Egocentric space
A map of space coded relative to the position of the body.

Perceptual versus representational neglect

Bisiach and Luzzatti (1978) established that neglect can occur for spatial mental images and not just for spatial representations derived directly from perception. Patients were asked to imagine standing in and facing a particular location in a town square that was familiar to them (the Piazza del Duomo, in Milan; Figure 9.22). They were then asked to describe the buildings that they saw in their "mind's eye." The patients often failed to mention buildings in the square to the left of the Duomo. Was this because of loss of spatial knowledge of the square or a failure to attend to it? To establish this, the patients were then asked to imagine themselves at the opposite end of the square, facing in, and describe the buildings. In this condition, the buildings that were on the left (and neglected) are now on the right and are reported, whereas the buildings that were on the right (and reported previously) are now on the left and get neglected. Thus, spatial knowledge of the square is not lost but is unavailable for report. Subsequent research has established that this so-called representational neglect forms a double dissociation with neglect of perceptual space (Bartolomeo, 2002; Denis et al., 2002). The brain

FIGURE 9.22: The Piazza del Duomo in Milan featured in a classic neuropsychological study. When asked to imagine the square from one viewpoint, patients with neglect failed to report buildings on the left. When asked to imagine the square from the opposing viewpoint, they still failed to report buildings on the left, even though these had been correctly reported on the previous occasion. It suggests a deficit in spatial attention rather than memory.

Image from http://en.wikipedia.org.

KEY TERM

Allocentric space
A map of space coding the locations of objects and places relative to each other.

appears to contain different spatial reference frames for mental imagery and for egocentric perceptual space. The hippocampus is often considered to store an **allocentric** map of space (the spatial relationship of different landmarks to each other, rather than relative to the observer), but the parietal lobes may be required for imagining it from a given viewpoint (Burgess, 2002).

Near versus far space

Double dissociations exist between neglect of near space (Halligan & Marshall, 1991) versus neglect of far space (Vuilleumier et al., 1998). This can be assessed by line bisection using a laser pen and stimuli in either near or far space, even equating for visual angles. Near space is defined as "within reach," but it can get stretched! Berti and Frassinetti (2000) report a patient with a neglect deficit in near space but not far space. When a long stick was used instead of a laser pointer, the "near" deficit was extended. This suggests that tools quite literally become fused with the body in terms of the way that the brain represents the space around us. This is consistent with single-cell recordings from animals suggesting that visual-receptive fields for the arm get spatially stretched when the animal has been trained to use a rake tool (Iriki et al., 1996).

Personal and peripersonal space

Patients might show neglect of their bodily space. This might manifest itself as a failure to groom the left of the body or failure to notice the position of the left limbs (Cocchini et al., 2001). This can be contrasted with patients who show neglect of the space outside their body, as shown in visual search type tasks, but not the body itself (Guariglia & Antonucci, 1992).

Within objects versus between objects (or object-based versus space-based)

Look at Figure 9.23. Note how the patient has attempted to draw all of the objects in the room (including those on the left) but has distorted or omitted the left parts of the objects. Similarly, the patient has failed to find the As on the left side of the two columns of letters even though the right side of the left column is further leftwards than the left side of the right column. This patient would probably be classed as having object-based neglect.

The object in question may be more dynamically defined according to the current spatial reference frame being attended. Driver and Halligan (1991) devised a task that pitted object-based coordinates with environmentally based ones. The task was to judge whether two meaningless objects were the same or not (Figure 9.24). On some occasions, the critical difference was on the left side of the object but on the right side of space, and the patient did indeed fail to spot such differences.

Written words are an interesting class of object because they have an inherent left to right order of letters. Patients with left object-based neglect may make letter substitution errors in reading words and nonwords (e.g., reading "home" as "come"), whereas patients with space-based (or between object) neglect may read individual words correctly but fail to read whole words on the left of a page. In one unusual case, NG, the patient made neglect errors in reading words that were printed normally but also made identical errors when the words were printed vertically, printed in mirror image (so that the neglected part of the word was on the opposite side of space) and even when the letters were dictated aloud, one

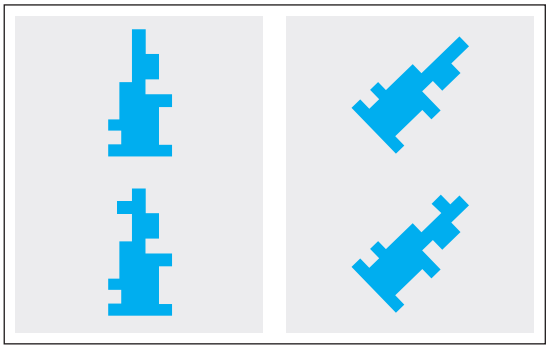

FIGURE 9.24: Are these objects the same or different? The critical difference lies on the left side of the object but, in the slanted condition, on the right side of space.

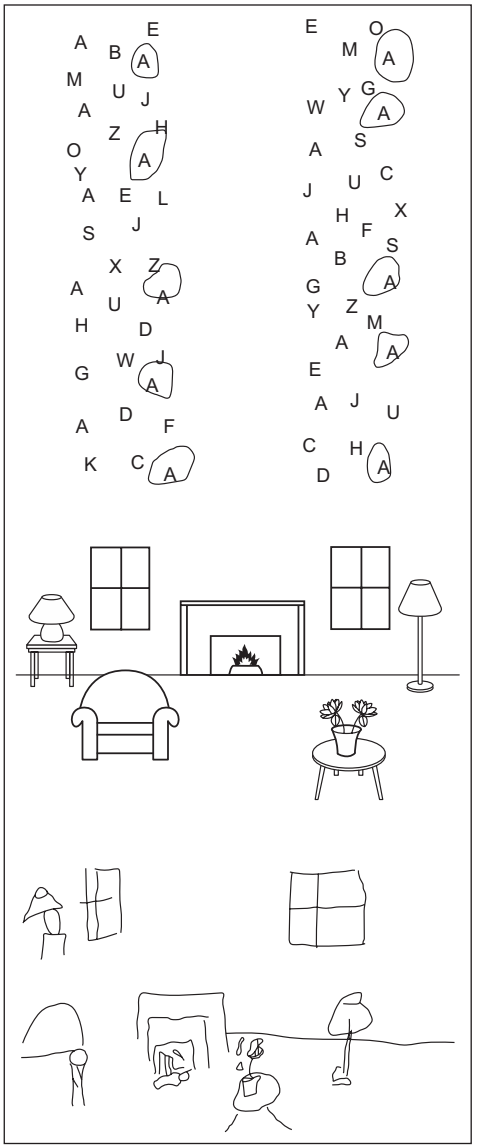

FIGURE 9.23: The patient makes omission errors on the left side of objects irrespective of the object's position in space.

From Robertson (2004). Reproduced by permission of Taylor & Francis Group.

by one (Caramazza & Hillis, 1990a). This strongly suggests that it is the internal object frame that is neglected.

Neglect within objects is linked to brain damage in different regions than that associated with neglect of egocentric space; in particular, it seems to be linked to ventral stream lesions including to the white matter (Chechlacz et al., 2012). This raises the interesting possibility that this form of neglect represents a disconnection between object-based perceptual representations and more general mechanisms of attention.

Evaluation

Although the cardinal symptom of neglect is a lack of awareness of perceptual stimuli, neglect is best characterized as a disorder of attention rather than perception. This is because it tends to be multisensory in nature, the deficit is more pronounced when demands on attention are high (e.g., voluntary orienting, presence of competing stimuli), and there is evidence that neglected stimuli are perceived (albeit unconsciously and perhaps less detailed). However, neglect is a heterogeneous disorder, and this may reflect the different ways in which space is represented in the brain. Basic attention processes (involving competition and selection) may operate across different spatial reference frames, giving rise to the different characteristics of neglect.

SUMMARY AND KEY POINTS OF THE CHAPTER

- Attention is the process by which certain information is selected for further processing and optimizes efficiency by preventing sensory overload.
- This is a dynamic system in which there is an interaction between top-down (task-relevant) and bottom-up (sensory-driven) influences and in which selection can operate at multiple levels (perceptual, semantic, response-based).
- The parietal lobes may transform sensory-based maps of space (e.g., retinocentric coordinates) into various egocentric (viewer-centered) maps of space. These maps contain a sparse code of the perceptual environment in which salient features predominate (either due to bottom-up or top-down constraints).
- The orienting of attention (at least from bottom-up, exogenous cues) taps mechanisms involved in preparing eye movements.

- Attended relative to unattended stimuli are associated with greater activity in the neural system involved in perceiving that stimulus (e.g., visual ventral stream) and with activity in a frontoparietal network. The latter is normally linked to conscious awareness of perceptual stimuli.
- There is evidence for different attention-related mechanisms in the parietal lobes (e.g., contrasting posterior parietal versus temporoparietal; or left and right hemispheres), although it is less clear how these different mechanisms normally operate together.
- Studies of neglect have been important for establishing that space is represented at several different levels within the brain.

EXAMPLE ESSAY QUESTIONS

- How has evidence from neuroscience changed the way that cognitive science thinks about attention?
- Can any theory account for spatial and nonspatial aspects of attention?
- What is the relationship between orienting attention and moving the eyes?
- What have studies of human brain damage contributed to our understanding of attention and its neural basis?

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Visit the Instructor & Student Resources website at routledgelearning.com/wardcognitiveneuroscience for:

- Videos including interviews with key psychologists Geoff Boynton and Marlene Behrmann, examples and accounts of change blindness, and hemispatial neglect
- Bitesize video and online lecture by author Jamie Ward on the attending brain
- Multiple-choice questions and interactive flashcards to test your knowledge

CHAPTER 10

The acting brain

CONTENTS

Action is our way of interfacing with the world and our means of putting all our goals and desires into practice. Action has traditionally been viewed as the endpoint of cognition. Having perceived an object and made a cognitive decision about what to do with it, we may then, depending on our goals, act toward it. Findings from cognitive neuroscience have radically shaken up this viewpoint. For example, in some situations it is possible to accurately act toward objects that have not been consciously seen. In addition, it has been claimed that not only is our action system equipped to produce our own actions, it may also be used to understand the actions of others – an important part of social cognition. Moreover, the processes that generate and control actions also appear to generate and control thought and cognition more generally. These ideas will also be explored in this chapter, together with an overview of more traditional areas of research on the "acting brain," such as Parkinson's disease, the role of the basal ganglia, and tool use.

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A BASIC COGNITIVE FRAMEWORK FOR MOVEMENT AND ACTION

A simple model of movement and action is presented in Figure 10.1 and is unpacked in more detail throughout the chapter. Note that the model is hierarchically organized. At the highest level, there is action planning based on the goals and intentions of the individual. At the lowest level, there are the perceptual and motor systems that interface with the external world. Action can be considered to be an outcome of all these processes that work together in a concerted fashion, combining the needs of the person with the current environmental reality. As such, the term "action" needs to be contrasted with the physical *movement* of the body that ensues. Movements can sometimes occur in the absence of cognition. A reflex movement generated, say, when a hand goes near a flame occurs in the absence of a centrally generated command.

There are a number of computational problems faced when performing an action. Imagine a task of turning off a light switch. There are potentially an infinite number of motor solutions for completing the task in terms of the angles of the joints and their trajectories through space. This has been termed the **degrees of freedom problem** (see Haggard, 2001). There are likely to be physical constraints on the solution (e.g., to minimize the torque on joints), but there could also be cognitive constraints too (e.g., to minimize the amount of planning). It is probably not the case that actions are calculated from scratch each time one needs to be performed. Most theories of action postulate the existence of generalized **motor programs** (Schmidt,

KEY TERMS

Degrees of freedom problem
There are potentially an infinite number of motor solutions for acting on an object.

Motor programs
Stored routines that specify certain motor parameters of an action (e.g., the relative timing of strokes).

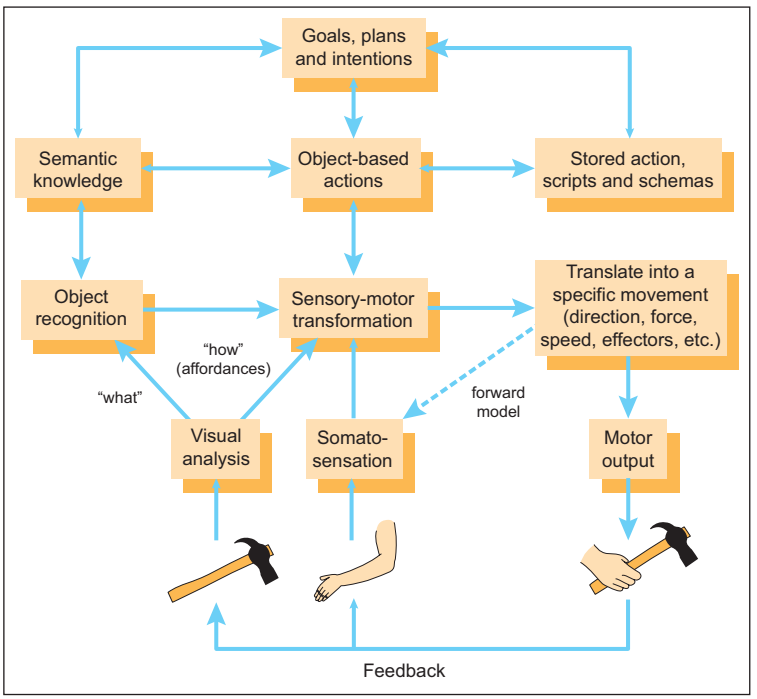


FIGURE 10.1: A very basic cognitive framework for understanding movement and action.

1975). This may simplify the computations (and computational speed) underlying movement. For example, in producing a tennis serve, the different movement components may be linked together. Motor programs may code general aspects of the movement (e.g., the timing of different components) rather than the actual means of performing the movement (e.g., the joints and muscles). One commonly cited example is the fact that handwriting does not change when different effectors are used (e.g., writing with feet) or when the amplitude is changed (e.g., writing on a blackboard versus a notebook).

Most actions are directed toward externally perceived objects, particularly via vision. Different objects in the environment may also be linked to different motor programs that reflect their cultural usage: for instance, the way that chopsticks are manipulated or scissors are used. Object–action associations typically have to be learned, but they can also be lost as a result of brain damage. After early visual analysis, two routes diverge into different streams specialized for object recognition (the "what" or ventral stream) and object location (the "how," "where," or dorsal stream). This was introduced in Chapter 9.

One aspect that is particularly relevant to the present topic is how this visual information is integrated with somatosensory information. **Somatosensation** refers to a cluster of perceptual processes that relate to the skin and body and includes touch, pain, thermal sensation, and limb position. The position of the limbs in space is computed by receptors in the muscles and joints, and this is termed **proprioception**. Information concerning the location of objects coded on the surface of sensory receptors (e.g., on the retina) is insufficient to permit interaction with that object unless the position of the sensory receptors themselves is taken into account (e.g., gaze direction and head position). As such, there is a need to co-register these two different types of information into a common spatial reference frame. In the context of action, this process will be referred to as **sensorimotor transformation**, although more generally it is referred to as remapping.

The way in which the goals, plans, and intentions of an individual are represented in the brain is the least understood aspect of the action system. The difficulty lies in explaining the intentions of an individual without recourse to what psychologists have termed a **homunculus**. We all have a sense in which "I" make a decision to go somewhere or "I" intend to make tea. The homunculus problem is that there is no "I" in the brain that makes all these decisions (the word homunculus literally means "little man"); the "I" is simply a product of the firing of neurons. A sense of ownership over our actions may emerge by being accurately able to predict the sensory consequences of our actions, which is referred to as a **forward model** in this figure. Chapter 4 already introduced an example of this in that tickling oneself feels less ticklish than being tickled by another person, because we can use our own motor commands to predict what the sensation will feel like (Blakemore et al., 1998).

Note that, in this simple framework, there are bidirectional arrows to and from the "goals, plans and intentions." This implies

KEY TERMS

Somatosensation
A cluster of perceptual processes that relate to the skin and body, and include touch, pain, thermal sensation, and limb position.

Proprioception
Knowledge of the position of the limbs in space.

Sensorimotor transformation
Linking together perceptual knowledge of objects in space and knowledge of the position of one's body to enable objects to be acted on.

Homunculus problem
The problem of explaining volitional acts without assuming a cognitive process that is itself volitional ("a man within a man").

Forward model
A representation of the motor command (a so-called efference copy) is used to predict the sensory consequences of an action.

that the system may also be used to observe and understand the actions and intentions of other people, as well as to generate one's own actions. This may be vital for learning skills by observation and may form an important component of comprehending actions.

THE ROLE OF THE FRONTAL LOBES IN MOVEMENT AND ACTION

The frontal lobes take up around a third of the cortical area and comprise a number of functionally and anatomically separate regions. Moving from the posterior to the anterior of the frontal lobes, their function becomes less specific to movement and action (Figure 10.2). The more anterior portions are involved in the control of behavior irrespective of whether it results in an overt action (i.e., in aspects of thought such as planning, reasoning, and working memory). Given this hierarchical organization, it is useful to consider the roles of the different frontal regions separately.

Primary motor cortex

KEY TERM

Primary motor cortex
Responsible for execution of voluntary movements of the body.

The **primary motor cortex** (in the precentral gyrus, Brodmann's area 4, BA4) is responsible for the execution of all voluntary movements of the body. Most other frontal regions are related to action planning, irrespective of whether actions are actually executed. Different regions of the primary motor cortex represent different regions of the body – that is, it is *somatotopically organized* (Figure 10.3). The left hemisphere is specialized for movements of

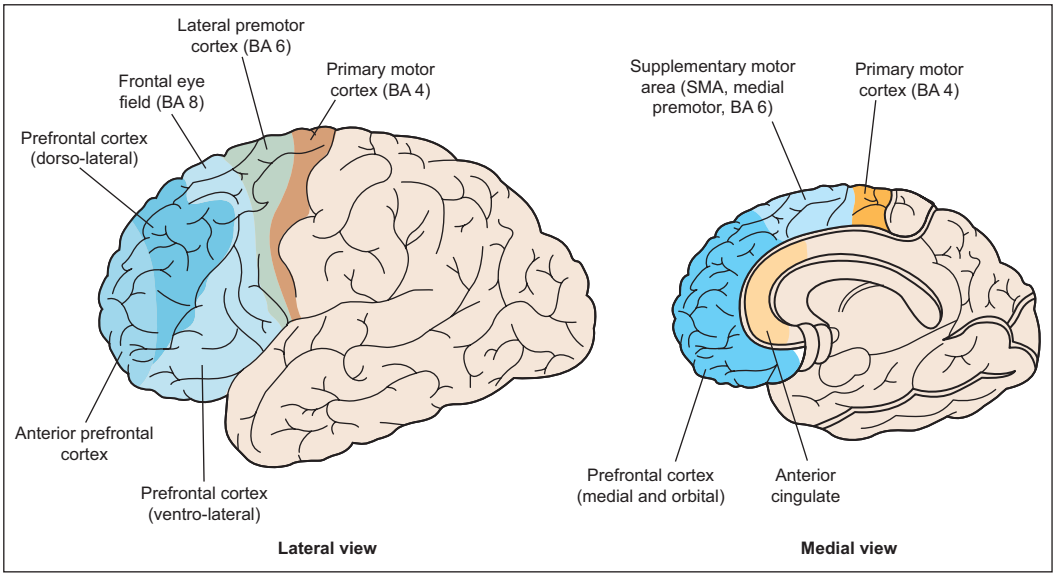


FIGURE 10.2: Anatomical and functional divisions of the frontal lobes. Broadly speaking, the primary motor cortex initiates voluntary movements, the premotor regions are involved in online coordination of movements, and the prefrontal regions plan and select actions according to goals.

the right side of the body and the right hemisphere is specialized for movements of the left side of the body (although the division is not as strict as once believed; Tanji et al., 1998). Thus, damage to one hemisphere as a result of, say, a stroke could result in a failure to move the other side of the body – **hemiplegia**. Note that some parts of the body, such as the hands, have a particularly large representation because of the need for fine levels of movement control.

The relationship between the activity of individual neurons and resultant limb movement is understood in some detail (Figure 10.4). Studies of the firing of single cells in the primary motor cortex show that activity for each neuron is highest for a particular direction of movement (the preferred direction), and it decreases gradually with directions further and further away (for reviews, see Georgopoulos, 1997; Georgopoulos et al., 1986). Different neurons "prefer" different directions, and the firing is indeed related to the direction of movement rather than the spatial location of the endpoint. Thus, a neuron would fire equivalently with different starting and ending positions assuming the direction is the same (Georgopoulos et al., 1985).

One computational issue raised by these findings is this: how do the neurons decide on a single movement to execute given that lots of different neurons with lots of different preferred movements will be active at a given point in time? One possible solution could be that the most active neuron(s) at that point in time is the one that

KEY TERM

Hemiplegia
Damage to one side of the primary motor cortex results in a failure to voluntarily move the other side of the body.

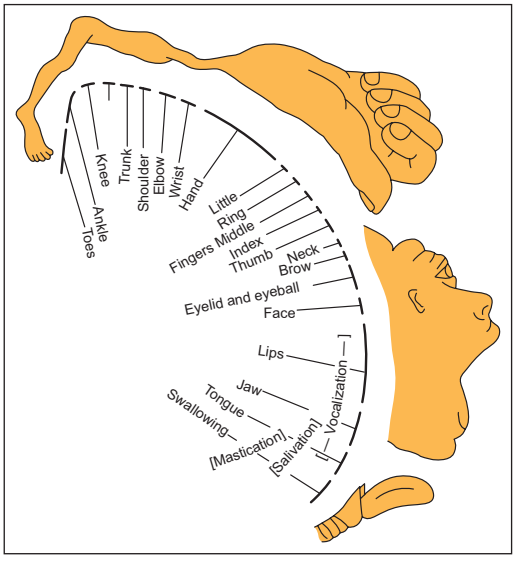


FIGURE 10.3: The primary motor cortex controls movement in different parts of the body. Areas governing different parts of the body are arranged spatially (somatotopic organization) but do not strictly reflect the spatial arrangement of the body.

From Penfield and Rasmussen (1950).

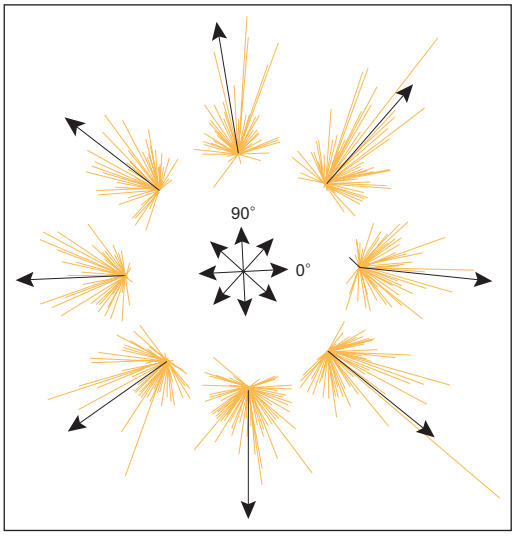


FIGURE 10.4: Each line represents the preferred direction of many neurons in the primary motor cortex, and their length represents the amount of firing. The population vector, calculated for eight different directions, is the gray line and this predicts the direction of movement.

From Georgopoulos et al. (1983). Reproduced with permission from Springer Nature.

dictates the actual movement (i.e., a winner-takes-all solution). This idea is not satisfactory because movements tend to be very precise, whereas the coding of preferred direction is broad (e.g., a neuron with a preferred direction of 70 degrees would still respond strongly at 60 and 80 degrees). This idea also turns out to be empirically incorrect. The direction of the resultant movement appears to be computed by summing together the vectors (i.e., degree of activity multiplied by preferred direction) of a whole population of neurons (the so-called **population vector**). This principle has been used to create brain–computer interfaces that control robotic arms in patients who have lost the use of their limbs (see Box).

KEY TERM

Population vector
The sum of the preferred tunings of neurons multiplied by their firing rates.

Frontal eye fields

Voluntary movement of the eyes is not determined by the primary motor cortex but by a separate region of the frontal lobes known as the frontal eye fields (FEFs, Brodmann's area 8). Stimulation of this region in monkeys with microelectrodes results in movement of the eyes (Bruce et al., 1985). The separation of body and eyes may reflect the different nature of the input signals that guide movement: eye movement is primarily guided by external senses (vision and hearing), whereas skeletal-based movements rely more heavily on proprioceptive information concerning the position of the limbs (the somatosensory cortex). Studies in monkeys show that the FEF is activated rapidly (within 100 ms) following a visual stimulus (Lamme & Roelfsema, 2000). Moreover, electrical stimulation of the FEF can enhance activity within the primary visual cortex in the presence of a visual stimulus, and it can increase activity in higher (extrastriate) visual regions even in the absence of a visual stimulus (Ekstrom et al., 2008). This is another example of the action system influencing cognition (in this case, visual attention) rather than being a mere endpoint of cognition.

ONLINE RESOURCES

To discover more about brain–machine interfaces in paralyzed patients, visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience).

COULD NEURAL ACTIVITY IN THE PRIMARY MOTOR CORTEX BE USED TO GUIDE A PROSTHETIC LIMB?

The direction of resulting limb movement can be computed from measurements in fewer than 100 neurons (Salinas & Abbott, 1994). This holds out the promise of being able to use this information to guide an artificial limb in patients with amputated or paralyzed limbs. This principle has been demonstrated in a small number of human patients. One study demonstrated that two tetraplegic patients could exert some control over the speed and direction of movement of a computer cursor based on recording of motor cortical activity from 96 neurons in the dominant hand area (Kim et al., 2008). The patients in this study had an inability to move all four limbs arising from brainstem stroke and motor neuron disease. Subsequent studies have shown that tetraplegic patients are able

to move a robotic arm for reaching and grasping, including, in one case, to drink from a bottle (Hochberg et al., 2012), as shown in Figure 10.5. More recent studies have used machine learning (in which the algorithm learns without being explicitly taught) to try to decode complex movements from neural data, resulting in finer movements of individual fingers (Bouton et al., 2016).

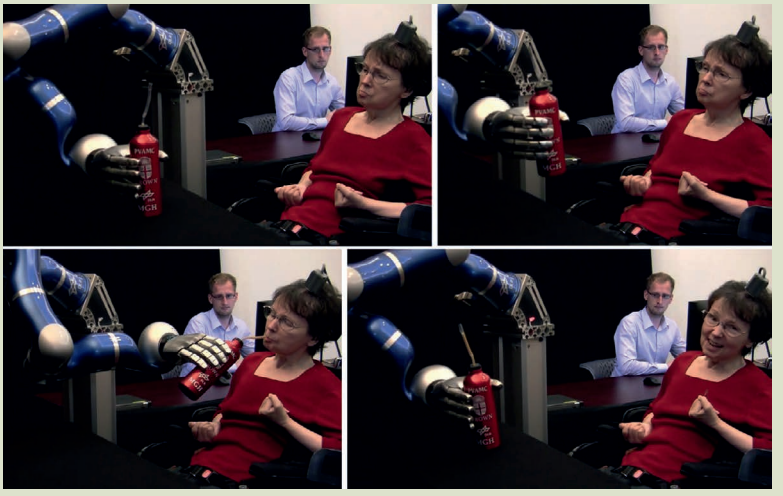


FIGURE 10.5: A tetraplegic patient drinks from a bottle using a robotic arm controlled by electrical recordings from her primary motor cortex.

From Hochberg et al. (2012). Reproduced with permission from Springer Nature.

Lateral and medial premotor cortex

The area immediately in front of the primary motor cortex is termed the **premotor cortex**. In contrast to the primary motor cortex, electrical stimulation of the premotor cortex does not result in movement per se, but rather it modulates the activity of the primary motor cortex (Shimazu et al., 2004). Many studies have drawn attention to the different roles played by the lateral premotor cortex and the medial premotor cortex (also known as the **supplementary motor area, SMA**) (Goldberg, 1985; Passingham, 1988). Whereas the lateral premotor cortex has been associated with acting on objects in the environment (e.g., reaching for a coffee cup), the SMA has conversely been associated with dealing with spontaneous, well-learned actions, particularly action sequences that do not place strong demands on monitoring the environment (e.g., playing a familiar tune on a musical instrument). This functional difference reflects the different anatomical connections of these regions. The lateral premotor cortex receives visual signals via the parietal cortex (the dorsal route in vision), whereas the medial premotor cortex (SMA) receives strong proprioceptive signals concerning the current position of the limbs.

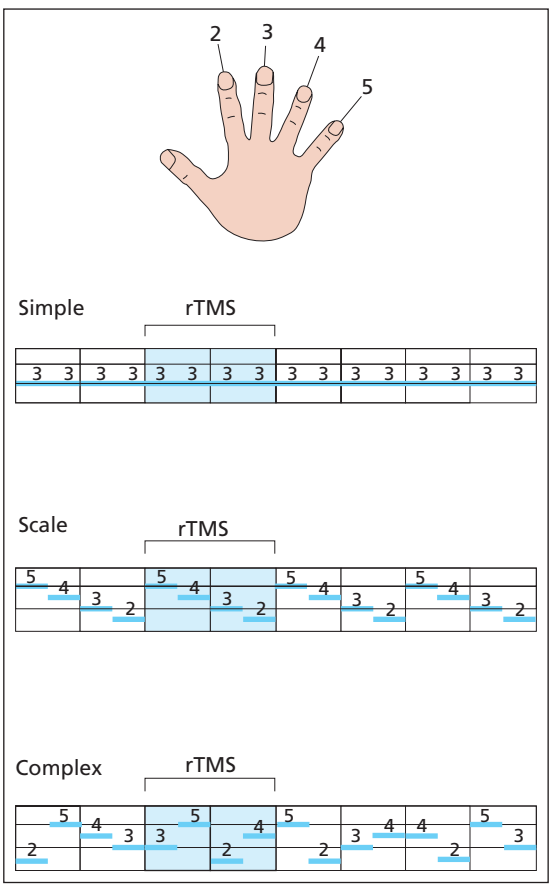
KEY TERMS

Premotor cortex
The lateral area is important for linking action with visual objects in the environment; the medial area is known as the supplementary motor area and deals with self-generated actions.

Supplementary motor area (SMA)
Deals with well-learned actions, particularly action sequences that do not place strong demands on monitoring the environment.

In one experiment, TMS was delivered to three frontal regions in three conditions: "simple" button presses (pressing the same key over and again), "scale" button presses (pressing consecutive buttons as in a musical scale), and "complex" button presses (as in playing a pre-learned musical piece) – see Figure 10.6. TMS over the SMA disrupted the sequence in the "complex" condition only, whereas TMS over the primary motor cortex affected both "complex" and "scale" action sequences; TMS over the lateral prefrontal cortex had no effects (Gerloff et al., 1997). Gerloff et al. (1997) suggested that the SMA has a critical role in organizing forthcoming movements in complex motor sequences that are rehearsed from memory and fit into a precise timing plan.

If the SMA is important for implementing internally generated actions, the lateral premotor region is more important for producing movements based on external contingencies (e.g., "pull a handle if the light is blue, rotate it if it is red"). In the monkey, lesions in this area prevent these kinds of associations being formed but without loss of basic sensory or motor abilities (Passingham, 1988). Single-cell recordings in the monkey also show that neurons in the lateral premotor region respond when movement is required to an external cue, but not to spontaneous movements from memory, whereas the opposite is true for the SMA (Halsband et al., 1994). Lateral premotor regions are also considered to contain a "vocabulary" of actions (e.g., tearing, grasping) that have both a sensory and motor component (Rizzolatti et al., 1996). These will be discussed later in terms of mirror neurons and sensorimotor transformation.



Prefrontal contributions to action

Prefrontal regions lie anteriorly to the premotor regions and are principally involved in planning and higher aspects of

FIGURE 10.6: Gerloff et al. (1997) contrasted three different types of action sequence: repetitive movements of the same finger (top), a regular pattern of finger movements as in a scale (middle), and an irregular memorized pattern of finger movements (bottom). Only the latter condition was disrupted by TMS applied over the supplementary motor area. This suggests that this region is critical for coordinating complex learned movement patterns.

From Gerloff et al. (1997). Reprinted by permission of Oxford University Press.

the control of action. Unlike premotor and motor regions, prefrontal regions are involved extensively in higher cognition more generally rather than action specifically. Premotor regions have a primary role in preparing actions (to internally or externally triggered events), while the prefrontal region mediates their selection and maintains the goal of the action. For example, recordings of single neurons in the monkey prefrontal cortex show that they may respond to the rule that is being followed (e.g., "match the triangles" or "match the circles") rather than the mechanics of the movement being performed (White & Wise, 1999). Similarly, when monkeys are trained to move a cursor through a maze using joystick movements, prefrontal neurons respond to the predicted sensory consequences (i.e., the direction in which the cursor will move after the action) rather than the limb movements per se (Mushiake et al., 2006). In the same study, the primary motor cortex showed the opposite pattern.

The imaging study of Frith et al. (1991) provides a good illustration of prefrontal function in humans (Figure 10.7). Participants were required to generate finger movements that were either predetermined (i.e., move the finger that is touched) or in which the participant could freely choose which finger to move. Note that the actual motor response is identical in both tasks. Nevertheless, the dorsolateral prefrontal cortex showed greater activation in the free choice task, suggesting that it is involved in "willed" or intentional aspects of action (for a review, see Jahanshahi & Frith, 1998). Its role may extend to the open-ended selection of responses more generally. Similar activation was found when participants were asked to generate any word from a specified letter ("S" or "F") in contrast to producing a predetermined word (Frith et al., 1991).

Damage to prefrontal regions does not impair the movement or execution of actions per se. Instead the actions themselves become poorly organized and do not necessarily reflect the goals and intentions of the individual. In many ways, the errors of these patients reflect those associated with "lapses of attention" in us all. Reason (1984) documented many everyday action slips, including putting a match in the mouth and striking the cigarette instead of vice versa. A patient with damage to the prefrontal cortex may repeat an action that has already been performed and is

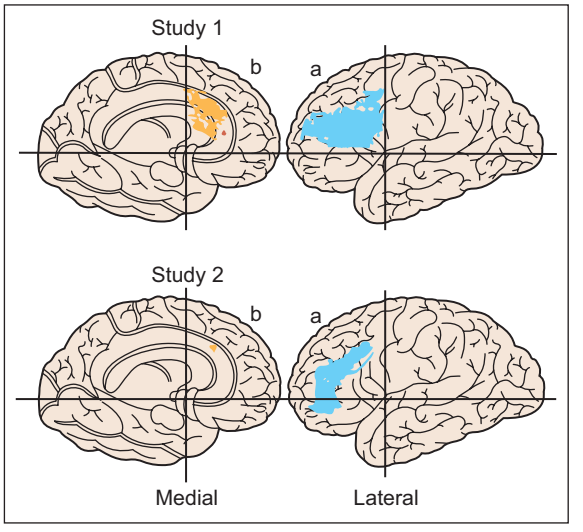


FIGURE 10.7: Activation in the (a) left dorsolateral prefrontal cortex and (b) anterior cingulate, when participants generate words beginning with S or F relative to being given the words (top), and when participants choose which finger to move relative to being instructed which to move (bottom). These regions may be important for response selection and willed action.

Redrawn from Frith et al. (1991). Royal Society of London. Used with permission of The Royal Society. Permission conveyed through Copyright Clearance Center, Inc.

KEY TERMS

Perseveration
Repeating an action that has already been performed and is no longer relevant.

Utilization behavior
Impulsively acting on irrelevant objects in the environment.

Schema
An organized set of stored information (e.g., of familiar action routines).

no longer relevant (called **perseveration**), or might act impulsively on irrelevant objects in the environment (called **utilization behavior**). An example of this, in the acute phase of a stroke, was described by Shallice et al. (1989, p. 1588):

> The patient was found early in the morning wearing someone else's shoes, not apparently talking or responding to simple commands, but putting coins into his mouth and grabbing imaginary objects. He went around the house, moving furniture, opening cupboards and turning light switches on and off.

Norman and Shallice (1986; see also Cooper & Shallice, 2000) proposed a model to explain goal-driven action. The model is called the SAS or "Supervisory Attentional System" and has subsequently been applied to explain the control of cognition more generally. One of the key distinctions that they make is between actions that are performed automatically (with minimal awareness) versus actions that require attention and some form of online control. For example, when driving it may be possible to change gears, stop at traffic lights, turn corners, and so on in a kind of "autopilot" mode. In fact, drivers often have no recollection of having gone through traffic lights, even though they know that they must have done so. These actions may be using well-learned **schemas** and are assumed not to require SAS control. By contrast, imagine that you are required to reverse into a narrow space, or that you are diverted down an unfamiliar route. Situations such as these may require an interruption of automatic behavior or setting up a novel action sequence, and these are assumed to require intervention of the SAS.

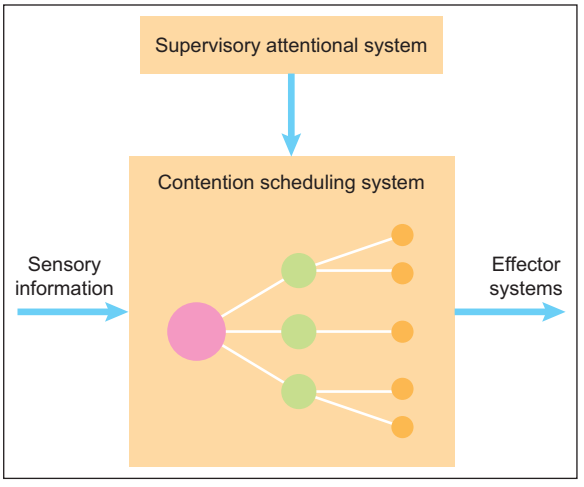


FIGURE 10.8: In the supervisory attentional system (SAS) model, contention scheduling selects the most active schema. The activation of schemas depends partly on the environment (derived from sensory input) and partly on the biasing influence of current and future goals (derived from the SAS component).

The SAS model contains a number of different components (Figure 10.8). Familiar actions and action routines may be stored as schemas. For example, specific objects (e.g., chopsticks, hammer) may have their own action schema (in this case, a motor program). Specific tasks (e.g., making tea) may be stored as a hierarchical collection of schemas (sometimes called scripts). In many respects, this organization of actions into abstract scripts and object-based schemas is akin to the distinction between

syntax and word-based knowledge in language and, as with language, there is a debate about the extent to which action-based semantics and syntax are separable (Patriot et al., 1996; Zanini et al., 2002).

Contention scheduling is the mechanism that selects one particular schema to be enacted from a host of competing schemas, which could be considered a form of "motor attention." The idea of competition between schemas is the key part of this model. Schemas can be activated by objects in the environment (e.g., a hammer will activate its own particular schema), and may correspond to different sensorimotor processes in the parietal lobes (see later). Schemas also receive biasing top-down activation from the SAS system that represents information about the needs of the person. If these two sources of activation are combined, then the most appropriate schema (i.e., that satisfies the current needs and is consistent with the environmental reality) should have the highest activation. This schema will then be selected by the contention-scheduling mechanism and translated into a specific action. As such, there is no need for a special entity with decision-making powers (i.e., a homunculus) as the decision to act is directly determined by the activation levels of schemas.

The action errors made by patients with prefrontal lesions can be explained by this model if one assumes that there is an imbalance in the type of information that enters into the contention-scheduling process. Utilization behavior can be accounted for by assuming that schemas are activated solely by environmental cues without any SAS regulation. Repetition of the same action (perseveration) is accounted for by assuming that activated schemas are not deactivated when they are no longer relevant to the current goal, or that the goal itself is not deselected once it has been successfully accomplished.

KEY TERM

Contention scheduling
The mechanism that selects one particular schema to be enacted from a host of competing schemas.

Evaluation

The movement and action system of the frontal lobes is hierarchically organized. The *primary motor cortex* is essential for the execution of voluntary movements. The *premotor cortex* is important for the preparation of actions and may be functionally subdivided into actions that are elicited by external cues (lateral premotor) or that are internally generated (medial premotor, SMA). The *prefrontal cortex* is involved in the selection of actions and their corresponding goals. Damage to the prefrontal cortex does not prevent movement, but instead can produce actions that are disorganized, inappropriate, and/or unintentional. This set of behaviors has frequently been characterized as a dysexecutive syndrome and can be accounted for within the SAS model. This model makes an important distinction between automatic actions and those requiring attention and online control.

THE ANARCHIC (OR "ALIEN") HAND SYNDROME

FIGURE 10.9: The anarchic (or alien) hand syndrome. The eponymous protagonist of the film *Dr. Strangelove* is a type of "mad scientist," whose eccentricities include a severe case of alien hand syndrome – his right hand, clad in an ominous black leather glove, occasionally attempts to strangle him.

> [T]he pathological hand of these patients is seen to wander involuntarily, and to perform purposeless movements. Often the arm levitates spontaneously, sometimes with tentacular movements of the fingers.
> (Marchetti & Della Sala, 1998)

> [W]hen G.C. had a genital itch, the right hand scratched it vigorously, in view of other people, causing considerable embarrassment to the patient, who tried to stop the right hand with her left . . . The patient considered the left hand to be the one she could trust . . . while the right hand was the untrustworthy one that "always does what it wants to do."
> (Della Sala et al., 1991, p. 1114)

In the anarchic or "alien" hand syndrome, the hand and arm of a patient may produce an action such as grasping an object or interfering with the activities of the other hand that the patient regards as *unintentional* (Figure 10.9). Although unintentional, the patient typically acknowledges that the arm and action belong to them. Some researchers have suggested that the terms "anarchic" and "alien" should refer to situations in which the patient does and does not, respectively, acknowledge them as their own (Della Sala et al., 1991). In common use, the term "alien" is used to denote both scenarios.

Assal et al. (2007) examined the neural basis of voluntary and alien movements using fMRI in a patient with a right parietal lesion and left alien hand. Alien hand movements were associated with activity in the right primary motor cortex. Voluntary hand movements also activated this region but additionally recruited a wider network of action-related regions (right premotor, left prefrontal cortex), suggesting that joint activity in this wider network is important for the feeling of intentionality over actions.

ACTION COMPREHENSION AND IMITATION

There are broadly two ways in which to reproduce the actions of another person. The first way involves a shallow level of analysis. It is possible to reproduce an action via sensorimotor transformations that do not make any inferences about the goals and intentions of the actor; this is *mimicry*. The second way involves observing the action, computing the goals and intentions of the actor and

then reproducing the actions oneself based on the goal. This is **imitation** proper, and it implies a deeper level of processing of the observed action. Aside from imitation, another situation in which goals are shared between individuals is in *joint action*; for example, when several people are lifting a heavy object or several people are operating different parts of a machine (Sebanz et al., 2006).

KEY TERM

Imitation
The ability to reproduce the behavior of another through observation.

There is evidence to suggest that humans tend to reproduce the actions of others by representing the goal state rather than by mimicry, particularly when the action is more complex. Wohlschlager et al. (2003) found that, when asked to "copy" the actions of another, there is a tendency to reproduce the goal of the action (e.g., putting an object in a cup) rather than the means of the action (e.g., which particular arm is used). Infants appear to imitate based on goals too (Gergely et al., 2002). In this study, the infants watched an adult press a button on a table by using their forehead, as shown in Figure 10.10. In one condition, the adult's hands and arms are bound up under a blanket, and in the other condition the adult's hands are free. When the adult's hands are free, the infants copy the action directly – they use their foreheads too. But when the adult's hands are not free, the infants imitate the goal but not the action, that is, the infants use their hands rather than their head. The implication is that the infants understand that the goal of the action is to press the button, and they assume that the adult would have used his or her hands had they been free.

Despite the fact that we use the verb "to ape" to refer to imitation and mimicry, other primate species tend not to spontaneously imitate or do so only for rewards such as food. After considerable training, chimpanzees (Custance et al., 1995), but not macaque monkeys (Mitchell & Anderson, 1993), are capable of learning a "do-as-I-do" game to produce complex

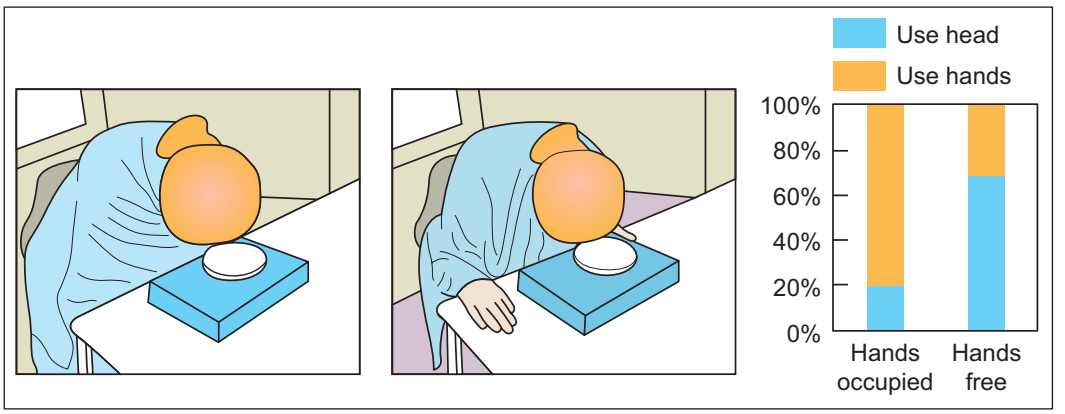


FIGURE 10.10: Infants imitate the goal of actions rather than the motor aspects of actions. If the experimenter presses a button with his or her head because their arms are occupied, the infants "copy" the action by using their hands rather than heads – that is, they appear to infer that the experimenter would have used his or her hands to achieve the goal had they been free.

From Gergely et al. (2002). Reproduced with permission from Springer Nature.

KEY TERM

Mirror neuron
A neuron that responds to goal-directed actions performed by oneself or by others.

arbitrary actions (e.g., grab thumb of other hand). Chimpanzees raised in captivity tend to imitate the goals of an action rather than simply reproducing the same movement with the same body part (Buttelmann et al., 2007) in an adaptation of the human infant study by Gergely et al. (2002).

Mirror neurons

One of the most fascinating discoveries in cognitive neuroscience over the last three decades has been of the **mirror-neuron** system. Rizzolatti and colleagues found a group of neurons in the monkey ventral premotor cortex (area F5) that respond both during the performance *and* the observation of the same action (Di Pellegrino et al., 1992; Rizzolatti et al., 1996). Thus, the response properties of mirror neurons disregard the distinction between self and other. It responds to actions performed by the experimenter or another monkey as well as to actions performed by itself. The response properties of these neurons are quite specific. They are often tuned to precise actions (e.g., tearing, twisting, grasping) that are goal-directed (Figure 10.11). They do *not* respond to mimicked action in the absence of an object, or if the object moves robotically without an external agent. This suggests that it is the purposeful nature of the action rather than the visual/motoric correlates that is critical.

Subsequent research has found mirror neurons in other parts of the macaque brain. Figure 10.12 summarizes the main regions linked to mirror neurons in macaques and humans. Mirror neurons in other regions do not necessarily have the same functional properties as those originally discovered in the premotor cortex. Mirror neurons in the parietal lobe tend to be more sensitive to the wider context in which an action is situated,

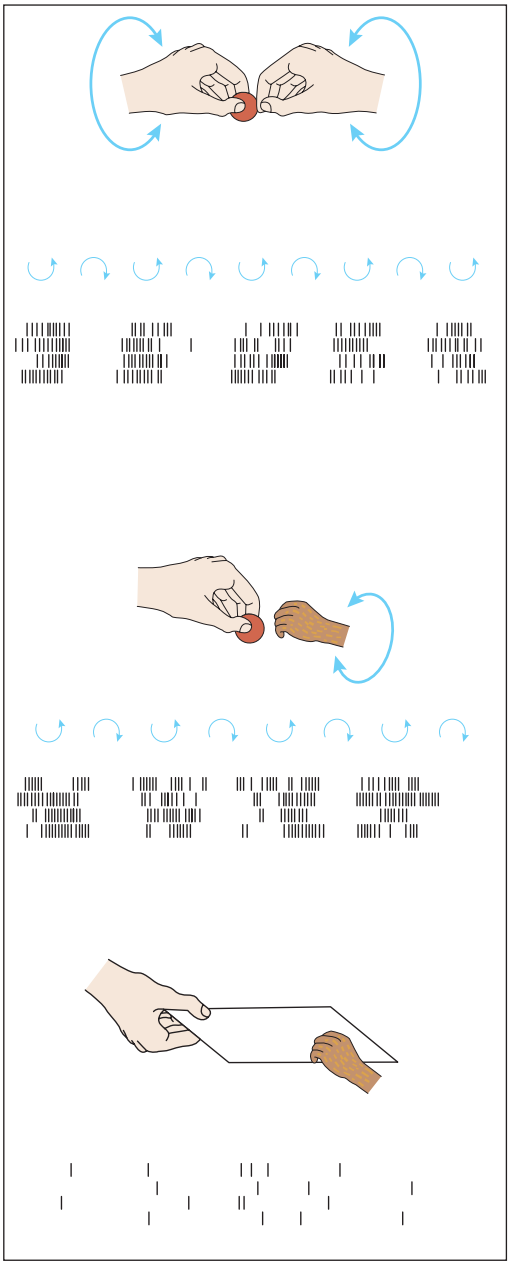


FIGURE 10.11: This "mirror neuron" responds to observing the rotating action of an object in the experimenter's hands (a) or when the monkey performs part of the rotating action (b), but not during grasping without rotation (c). Notice that the neuron is even sensitive to the direction of rotation (responding counter-clockwise, not clockwise).
Adapted from Rizzolatti et al. (1996).

for instance responding to a grasping action differently depending on whether the subsequent goal is to eat it or put it in a container (Bonini et al., 2010). The primary motor cortex itself contains neurons with motor and visual properties, but they respond to the mechanics of particular movements rather than more abstract features such as goals (Dushanova & Donoghue, 2010). By contrast, other regions such as the superior temporal sulcus also respond to specific movements of body parts but have a purely non-motoric visual component (Perrett et al., 1989) that may act as input to the mirror-neuron system.

Umiltà and colleagues (2001) compared viewing of a whole action with viewing of the same action in which a critical part (the hand–object interaction) was obscured by a screen. Mirror neurons responded both when the action was directly observed and when inferred from a hidden view (but not control conditions of an action without an inferred object). Their findings suggest that the premotor cortex contains abstract representations of action intentions that are used both for planning one's own actions and interpreting the actions of others (perhaps enabling goal-based imitation).

The aforementioned evidence is derived from nonhuman primates. What is the evidence that humans possess such a system? The human analogue of area F5 is believed to be in Broca's area (specifically, in Brodmann's area 44) extending into the premotor area (Rizzolatti et al., 2002). This region is activated by the observation of hand movements, particularly when imitation is required (Iacoboni et al., 1999), and also the observation of lip movements within the human repertoire (e.g., biting and speaking, but not barking; Buccino et al., 2004). Moreover, TMS applied over the primary motor cortex

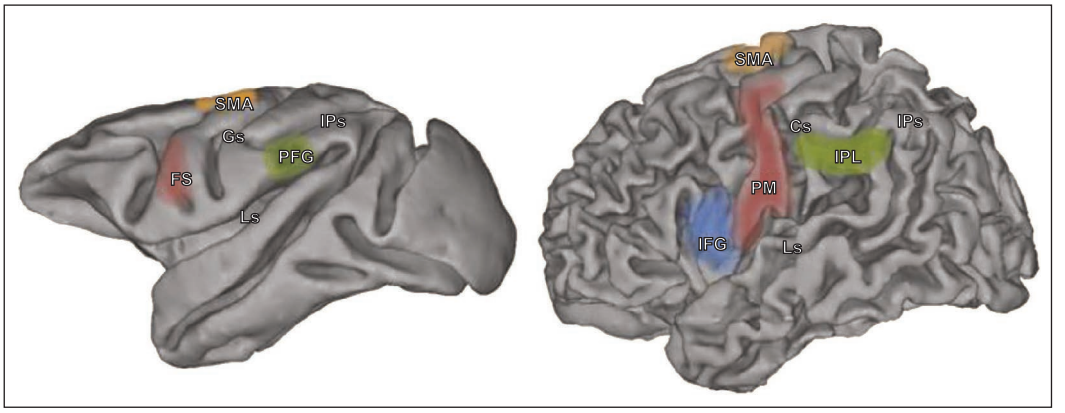


FIGURE 10.12: The main regions linked to mirror-neuron activity in the macaque and human brain (left and right, respectively). Colors show homologous regions in different species. PM = premotor; SMA = supplementary motor area; IPL = inferior parietal lobule; IFG = inferior frontal gyrus.

From Vanderwert et al. (2013).

ONLINE RESOURCES

Check out the debate between Professors Vittorio Gallese and Gregory Hickok on "Do Mirror Neurons Explain Anything?", and GoCognitive interviews with the discoverer of mirror neurons, Professor Giacomo Rizzolatti. Scan the QR code or visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience) for more information.

increases the amplitude of motor-evoked potentials elicited in the hands/arms when participants also observed a similar action (Strafella & Paus, 2000). This suggests that action observation biases activity in the primary motor area itself. Direct evidence of mirror neurons in humans, in terms of the firing response properties of individual neurons, was lacking until much later (Mukamel et al., 2010). These were patients undergoing surgery, and this limited the regions that could be explored. Although Broca's area and the premotor area were not studied, mirror neurons were found in other regions of the brain (e.g., medial temporal region).

Mirror neurons have been subjected to intense critical scrutiny in recent times, with one book referring to "The Myth of Mirror Neurons" (Hickok, 2014). The controversy surrounds their functionality (what they actually do) rather than their existence (which isn't disputed). For instance, some researchers argue that mirror neurons can arise via associative learning (Cook et al., 2014). When we move our own bodies, we see the visual consequences of our actions and learn to associate action observation with action execution. In this view, mirror neurons are not genetically preprogrammed for imitation or any other function. Similarly, one can debate whether mirror neurons give rise to action understanding, in its entirety, or whether there is a separate system involved in action understanding with mirror neurons acting as an interface. One theory argues that the function of mirror neurons is to predict what the consequences of actions are, such as how the limbs will move through space in order to achieve a goal, but that other regions (frontotemporal) represent the intended goals necessary for action understanding (Kilner, 2011).

WIDER IMPLICATIONS OF THE MIRROR-NEURON SYSTEM

- Did human language evolve from hand gestures? The human homologue of monkey area F5 is Broca's area (Rizzolatti & Arbib, 1998) – an area traditionally associated with language.
- Are mirror neurons important for being able to empathize with others, by internally simulating their behavior (Gallese, 2003)?
- Do individuals with particular difficulties in understanding others (e.g., autistic people) have impaired mirror-neuron systems? Dapretto et al. (2006) present fMRI evidence to suggest that autistic people have lower activity in the mirror system when imitating and observing expressions, but others have questioned whether this can explain the range of autistic behaviors (Southgate & Hamilton, 2008).

ACTING ON OBJECTS

This chapter has, so far, only considered in detail the role of the frontal lobes in some of the highest levels of action processing – namely, action planning and organization, the intention to act, and comprehending the actions and intentions of others. The remaining sections will deal with topics related to how specific actions are put into place and enacted. This involves, among other things, an appreciation of where things are in space and what certain objects (e.g., tools) can be used for. The parietal lobes appear to be specialized for this type of information.

ONLINE RESOURCES

Check out the author's Cognitive Neuroscience Bitesize on Vision in Action – The Dorsal Stream by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

"What" versus "how": the dorsal and ventral streams reconsidered

Ungerleider and Mishkin (1982) first described two routes of visual processing, which they labeled the "what" route (or ventral stream from occipital to temporal) and the "where" route (or dorsal stream from occipital to parietal). Goodale and Milner (1992; Goodale, 2011) have offered a somewhat different characterization of these routes in terms of "what" versus "how." In doing so, they placed an emphasis on output requirements (identification versus action) rather than input requirements (identity versus location). As they noted, we do not reach to locations in space but to objects. The idea that parietal (and frontal) regions are involved in a process of competitive selection between multiple alternatives applies equally to selecting appropriate actions as it does to selective attention of perceived stimuli.

Damage to dorsal versus ventral streams has different consequences for action. First of all, consider damage to the ventral route, running along the inferior temporal lobes. Patient DF has visual agnosia that impairs her ability to recognize objects from vision, despite intact basic visual processes. Milner and colleagues (1991) presented DF with a letter box in which the orientation of the slot could be rotated (see Figure 10.13). DF had difficulty in matching the orientation of the slot to *visually* presented alternatives. However, when asked to post a letter she was able to reach toward the slot and orient her hand appropriately. This suggests a dissociation between visual perception (based on the impaired ventral stream) and visual

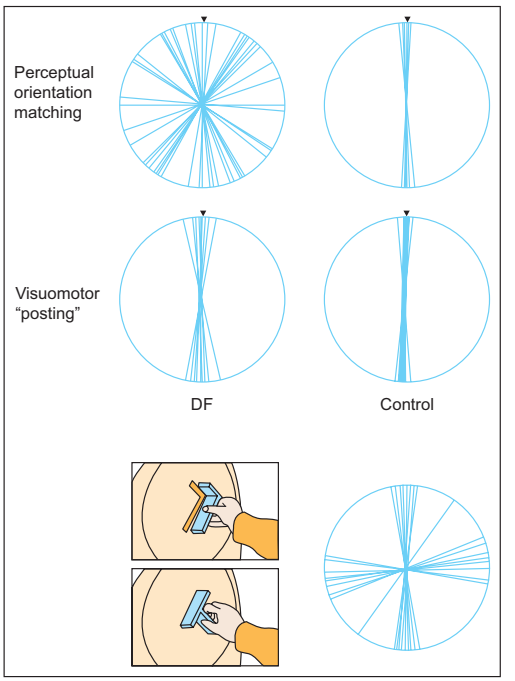


FIGURE 10.13: Can the hand "see" better than the eye? Patient DF can accurately post objects through slots even though she cannot report the orientation of the slots from vision. With more complex objects (e.g., T-shaped), she appears to use single orientations to guide action.

Adapted from Milner et al. (1991) and Goodale et al. (1994).

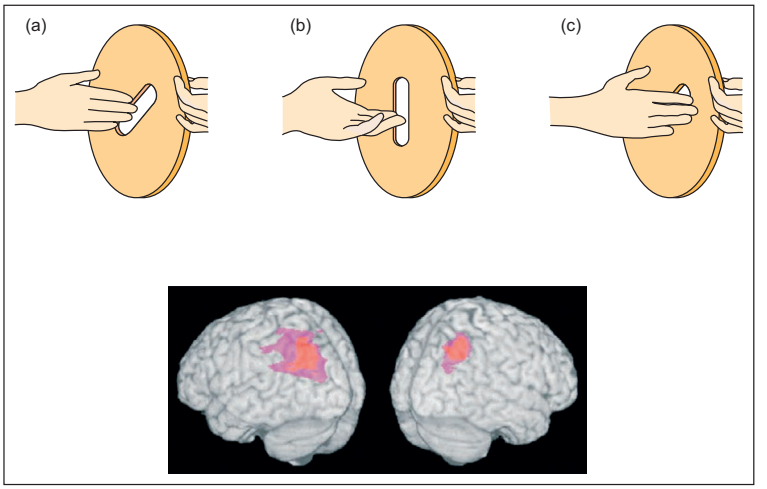


FIGURE 10.14: Optic ataxia may arise following lesions to either the left or right parietal lobe (often affecting the opposite hand), and results in both misreaching (c) and hand posture problems (b); the correct solution is shown in (a). It reflects an inability to link visual and motor information together.

Top: from Perenin and Vighetto (1988). Reproduced by permission of Oxford University Press. Bottom: from Karnath and Perenin (2005). Reprinted by permission of Oxford University Press.

KEY TERM

Optic ataxia
An inability to use vision to accurately guide action without basic deficits in visual discrimination or voluntary movement per se.

control of action (using the spared dorsal stream). When DF was given a more complex T-shaped object and slot, she was still fairly accurate, but she did make some errors, which tended to be at 90 degrees. This suggests that her action is driven by orientation of a single edge. Thus, the dorsal route cannot adequately integrate different edges into whole objects (Goodale et al., 1994).

Turning next to impairments of the dorsal stream – some patients with damage to the parietal lobe have deficits in acting toward objects in space. However, they do not (unlike DF) have problems in recognizing single objects. **Optic ataxia** is a symptom arising from damage to the occipitoparietal junction (Karnath & Perenin, 2005). These patients are unable to accurately reach toward objects under visual guidance. Perenin and Vighetto (1988) argue that this reflects a failure to transform visual perceptual information into appropriate motor commands. For example, when acting toward an oriented slot their hands may be oriented incorrectly or they may miss the slot altogether as shown in Figure 10.14 (a double dissociation with the visual agnosia patient, DF). The deficits would sometimes be restricted to a particular hand (typically the hand opposite the side of the lesion) or even a particular hand when it was in a particular half of space. The latter suggests that it is unlikely to be purely motoric (because the "bad" hand functions well in the "good" side of space) or purely visual (because the "good" hand functions well in the "bad" side of space) but due to a failure to integrate the two (when the "bad" hand is in the "bad" side of space).

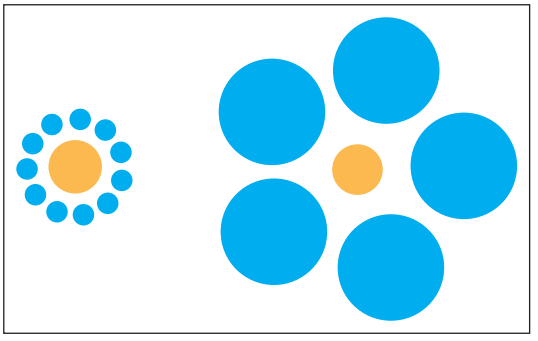


FIGURE 10.15: The Titchener circle illusion affects perception but not action. When a participant is asked to pick up the central circle, the grip aperture more closely resembles the true rather than the distorted size.

Interestingly, dissociations between vision for action and visual perception have been found in the normal population. Certain *visual illusions*, such as the Ponzo or railway track illusion and the Titchener circles illusion, result in physically identical

objects being perceived as different in size. If one is asked to pick up the size-distorted object (e.g., a poker chip in the Titchener illusion; see Figure 10.15), then the grip aperture between thumb and finger is not influenced by the illusion (Aglioti et al., 1995).

In summary, evidence from brain-damaged individuals points to specialized visual mechanisms that guide action. The next section will consider in more detail how the brain implements this.

FREE INSTRUCTOR & STUDENT RESOURCES

ONLINE RESOURCES

Visit the online test demonstration library (www.testable.org/ward) to try out the Ponzo and Titchener illusions.

Neural mechanisms of sensorimotor transformation

The previous section introduced the notion of a dorsal stream that transforms visually based information (e.g., location, shape) into motor-based actions: this process is known broadly as sensorimotor transformation. Evidence from primate single-cell recordings and human fMRI suggests that there are different kinds of neurons, clustered in different frontoparietal regions, that underpin this process. These are summarized in Figure 10.16. It should be noted that although much of the evidence comes from vision, these regions are multisensory in that they also respond to sound and, in some cases (regions AIP and VIP), to touch (Sereno & Huang, 2014).

In the dorsal stream, one of the first distinctions is whether the resulting action toward an object will be a hand movement (reaching) or an eye movement (a saccade). Area LIP (lateral intraparietal) was introduced in Chapter 9. Neurons in this region

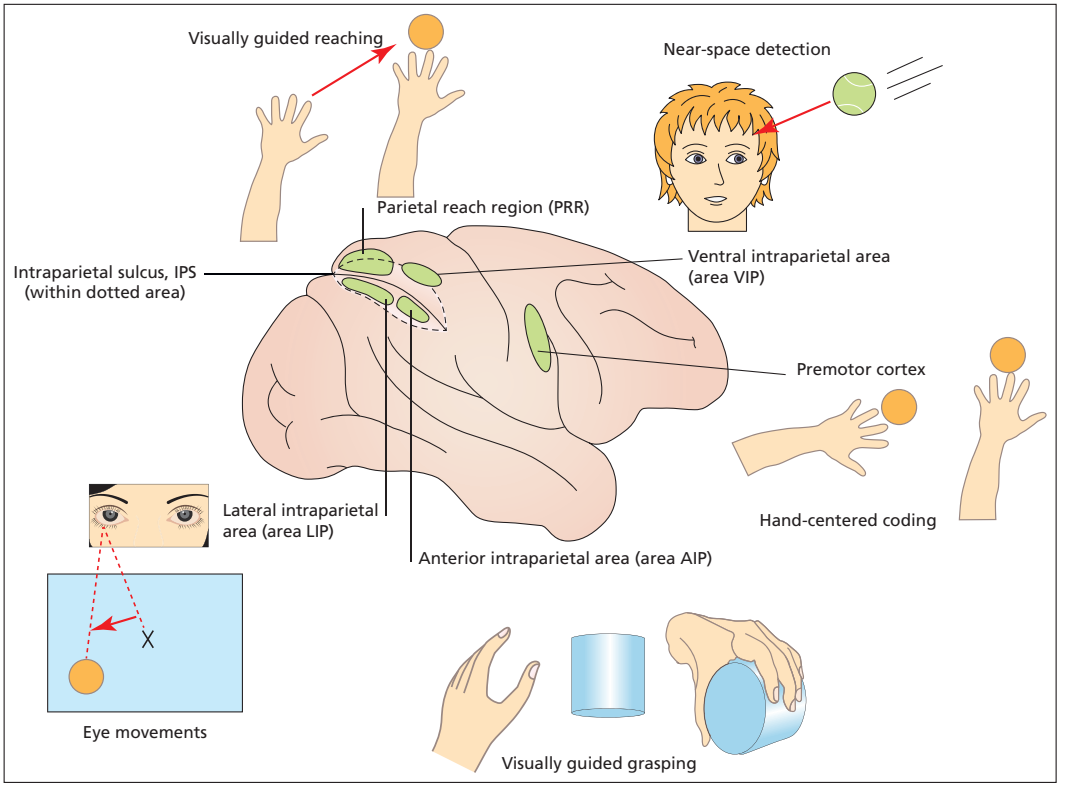


FIGURE 10.16: Approximate locations and representative functions of different parietal and premotor regions involved in sensorimotor transformation, here shown on the macaque brain.

KEY TERMS

Parietal reach region (PRR)
A part of the occipitoparietal cortex that responds, in particular, to reaching movements.

Anterior intraparietal area (AIP)
A part of the intraparietal sulcus that responds, in particular, to manipulable shapes or 3D objects (from vision or touch).

effectively code the distance and direction needed to move the eyes from the current location to a visual stimulus in its receptive field (Bisley & Goldberg, 2010). By contrast, neurons in a region called the **parietal reach region (PRR)** effectively code the distance and direction needed to move a hand from its current (visually perceived) location to another endpoint (e.g., signaled by a flash in another location) (Buneo et al., 2002). It has been suggested that, in humans, damage to the PRR might give rise to the visually guided reaching difficulties in optic ataxia (Hwang et al., 2012). As with neurons in the primary motor cortex, neurons in areas such as LIP and PRR have preferred directions but, in these regions, the preferred direction is strongly dependent on the location of sensory information (vision, sound), whereas the primary motor cortex represents movement direction alone.

Cui and Andersen (2007) explored the relationship between these two regions by allowing a monkey to voluntarily choose to either move its eyes or its hand to a visual target in order to obtain a reward. An eye movement activated neurons in LIP whereas a hand movement activated neurons in PRR (but note that it would have been the primary motor cortex or frontal eye field that actually executed the chosen action). Given that the sensory stimulus was physically the same in both cases, it suggests that these parietal regions are indeed action-related (consistent with the dorsal "how" framework) as well as being a marker of the animal's intentions (i.e., the choice of which body part to move). On tasks that require two consecutive reaches (Baldauf et al., 2008) or two consecutive saccades (Duhamel et al., 1992), the neural activity switches to the second action even before the first one is executed. This suggests that these regions are involved in planning actions (e.g., selection amongst competing actions).

As well as a distinction between eyes and hands, there is also an important distinction between reaching and grasping. Grasping may require greater processing of object-based properties than reaching or pointing (Jeannerod, 1997). fMRI studies of human participants reveal that different regions within the dorsal stream might support reaching versus grasping. Reaching depends more on the PRR (occipitoparietal region), whereas grasping depends more on the **anterior intraparietal area (AIP)** and premotor cortex (Cavina-Pratesi et al., 2010). The AIP area contains neurons that respond selectively to certain shapes (e.g., cylinder, sphere, cube), sizes, and orientations (Murata et al., 2000). Some neurons respond to visual information, some to motor information (grasping), and others to both (Sakata et al., 1995). An fMRI study in humans found that AIP responded to volumetric shapes but not flat line drawings of objects (Culham, 2004). Area AIP has anatomical connections to motor regions of the frontal lobes (including the premotor area and frontal eye fields) and, importantly, to the inferotemporal cortex of the visual ventral stream, which is involved in object recognition (Borra et al., 2008). This suggests that it is well placed to act as a key hub in tool use. Using a tool to grasp an object, instead of using the hand itself to grasp an object, also activates area AIP and the premotor cortex in humans (Jacobs et al., 2010). This suggests that these neural regions code relatively abstract properties of an action

(rather than the actual movement mechanics) which may enable transfer of skill from hands to tools.

One of the first basic problems in sensorimotor transformation is that visual information is coded retino-centrically (relative to the position of eye gaze), but actions need to be body-centered. We don't reach and grasp toward our retina, but to the objects that are "out there" in front of us. Progression along the dorsal stream is associated with this shift from gaze-centered to body-centered. The regions LIP and PRR are gaze-centered. By contrast, the region known as the **ventral intraparietal area (VIP)** contains many head-centered neurons (Colby et al., 1993) and some hand-centered neurons (Graziano et al., 2000). For instance, a neuron may respond to a variety of stimuli to the upper right of the face including an approaching object from upper right, a sound in this area or a touch to this part of the face but – importantly – it would do so irrespective of which direction the eyes were looking. Electrical stimulation of VIP neurons evokes avoidance behavior such as eye closure and contraction of facial muscles (Cooke et al., 2003). Thus, this region may be involved in detecting (and responding to) sensory stimuli near the body.

KEY TERM

Ventral intraparietal area (VIP)
A part of the intraparietal sulcus that responds to objects close to the body and in body-centered (as opposed to gaze-centered) coordinates.

The premotor cortex receives strong inputs from regions such as VIP and AIP, and its neurons tend to code visual information in body-centered coordinates. Graziano (1999) identified neurons in the macaque premotor regions that respond to both the felt position of the arm (irrespective of whether the arm was covered or in view) and the visual position of the arm (irrespective of whether it was the monkey's own arm or a stuffed arm in that position). If the arm was moved, then the visual receptive field would move too. This suggests that vision was coded relative to the body. This facilitates interaction with the external world irrespective of changes in eye fixation, including tool use and imitation.

The premotor cortex also has other properties important for tool use including responding to specific motor actions both when executed and when observed. Rizzolatti and Luppino (2001) describe them in terms of an action vocabulary, including grasping, holding, and tearing. For example, a neuron that responds to performed finger movements for grasping may not discharge for scratching. Other neurons may be specialized for different types of hand shaping (e.g., precision grip, whole-hand prehension). The advantage of having a stored repertoire is that the brain does not have to compute certain aspects of the action each time and may also enable certain types of action to become associated with familiar objects (schemas and scripts, as noted earlier).

The studies noted in the previous section provide the building blocks for a theory of how sensory and motor systems may be interfaced. But of course, the *meaning* of objects is going to be as critical for determining how and when they are used. This is likely to be especially important for humans. Whereas other species may use objects found in their natural environments as tools, humans have created for themselves a wide range of manipulable objects to perform specific functions, each with specific associated actions. The next section considers how these may be represented in the brain.

HOW TO MOVE A PHANTOM LIMB

Almost everyone who has a limb amputated will experience a **phantom limb** – a vivid sensation that the limb is still present and, in some cases, painful (for a fascinating review, see Ramachandran & Hirstein, 1998). Phantom limbs can be explained by plasticity in the brain. The neurons in the brain that previously used to respond to stimulation of the limb may instead be stimulated by activation in nearby regions of cortex (perhaps representing other parts of the body). This gives rise to an illusory sensation that the limb has returned.

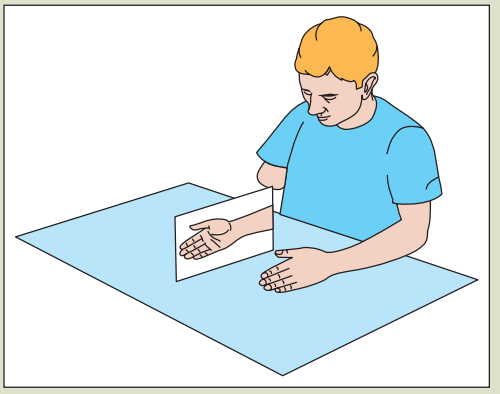


FIGURE 10.17: This patient has one real arm and a phantom limb that is immobile (i.e., the amputated arm feels as if it still exists and feels paralyzed). When the patient looks in the mirror, it creates the illusion that the amputated arm has returned and can move again.

The nature of the phantom differs significantly from one patient to another. Some report being able to move the phantom (e.g., it may appear to be gesturing). The motor cortex presumably doesn't "know" that the limb is missing and continues to send commands. For other patients, the limb may be immobile and potentially painful (this may relate to whether the limb was paralyzed prior to amputation). Ramachandran and Rogers-Ramachandran (1996) report a clever experiment, based on visual feedback, which enables such patients to reexperience movement in the phantom and, in some cases, alleviate pain. The patient puts the intact arm into a box with a mirrored side so that a second hand can be seen reflected in the position where the phantom is felt (Figure 10.17). When asked to move both hands they can experience movement in the phantom based on the visual feedback. This study illustrates the point that sensory (touch and vision) and motor information is highly integrated in the brain.

KEY TERM

Phantom limb
The feeling that an amputated limb is still present.

Tool use

A number of evolutionary developments appear to have facilitated the skilled use of tools found in modern humans. First, there is the freeing of the hands by walking upright rather than on all fours that occurred around 6 million years ago. Second, there is the development of the hands themselves, in which the thumb has become much longer in humans relative to chimps (Figure 10.18). This facilitates a precision grip, such as that used in picking up a peanut. Finally, there is the corresponding development of the brain in terms of the disproportionate amount of space dedicated to representing the hands. It is hard not to underestimate the impact that tool use has had in terms of human beings' mastery of the

environment, from the deserts to the poles. Note that the term **tool** is used broadly, not only to encompass hammers and chisels, but also cups, pencils, and so on. What distinguishes tools from other classes of object (e.g., cats, clouds, carpets) is the fact that they have specific gestures and functions associated with them.

Tools, like other classes of object, are represented in the brain at several levels:

- A stored visual representation of the shape of the object that is computed by the visual ventral stream (or inferotemporal cortex, IT, in monkeys).
- A semantic representation of the object linked to medial and anterior temporal lobes.
- A volumetric representation of the tool that has both visual and motoric components related to grasping. This may correspond to area AIP in the parietal lobes (discussed previously).
- A motor-based component that stores the conventional gestures associated with the tool, and typically linked to the left inferior parietal lobe.

Figure 10.19 shows a simplified model of tool use showing ventral and dorsal stream components. As already noted, there are pathways linking visual representations (of objects and body parts) to motor actions, via various parietal regions, that enable imitation (e.g., of hand gestures) and simple object manipulation (e.g., grasping). These routes link sensory and motor properties of objects that are independent of their conventional (i.e., learned) usage, but they are not necessarily arbitrary either. For example, semi-spherical shapes may imply a container, a handle may imply grasping, and a sharp edge may imply cutting. Gibson (1979) has referred to these as **affordances**. Over and above this, humans learn a large number of object–action associations that may require a different, specialized neural pathway: picking up a pair of scissors versus using a pair of scissors are two very different actions. According to the fMRI meta-analysis of Sakreida et al. (2016), affordances unrelated to learned object–action association (e.g., how best to grasp a long object) rely on a more dorsal branch of the dorsal stream, whereas stable, learned object-based actions (e.g., how to use a pair of scissors) rely more on the inferior parietal cortex and temporal cortex.

A number of lines of evidence suggest that the store of object-based actions is located in the left inferior parietal lobe. Chao and Martin (2000) compared activity (fMRI) when viewing tools relative to other classes of objects and found activity in both the left inferior parietal lobe and Broca's area. Rumiati and colleagues (2004) examined object-based action more directly by asking participants to generate actions while being scanned. They used the factorial design depicted in Figure 10.20, in which participants were presented with either static objects or actions (without the object)

KEY TERMS

Tool
An object that affords certain actions for specific goals.

Affordances
Structural properties of objects imply certain usages.

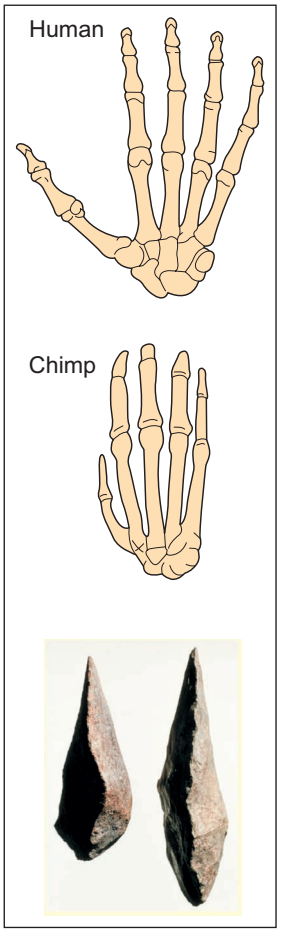


FIGURE 10.18: The thumb of humans has evolved to be considerably longer than that of the chimp's, enabling precision grip. The figure also shows Acheulean tools dating from 1.5 million years ago found in central East Africa.

Stone tools: John Reader/ Science Photo Library.

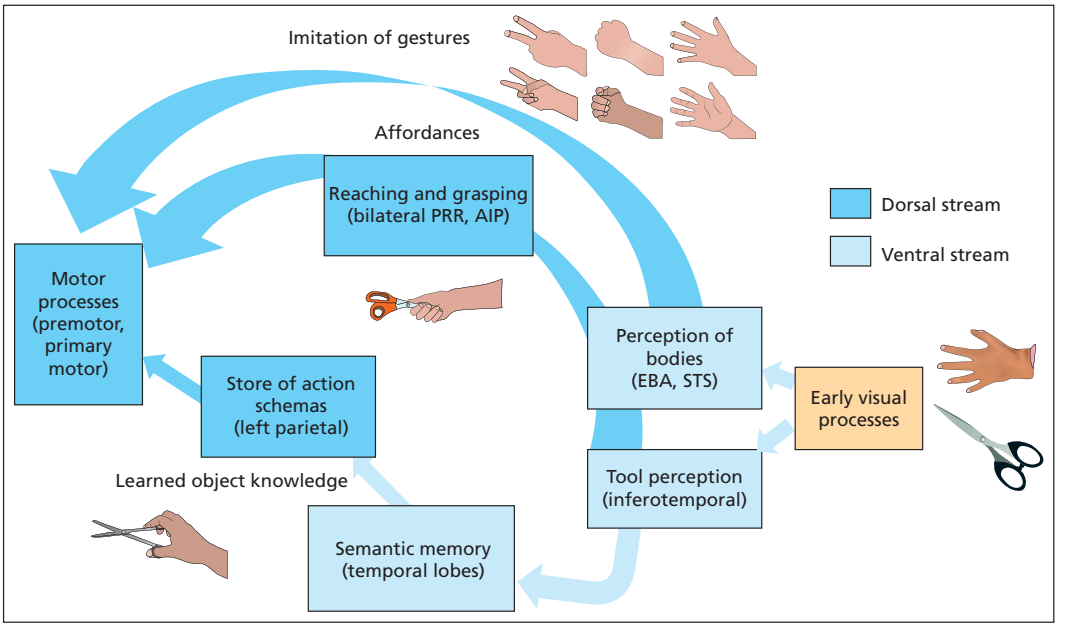
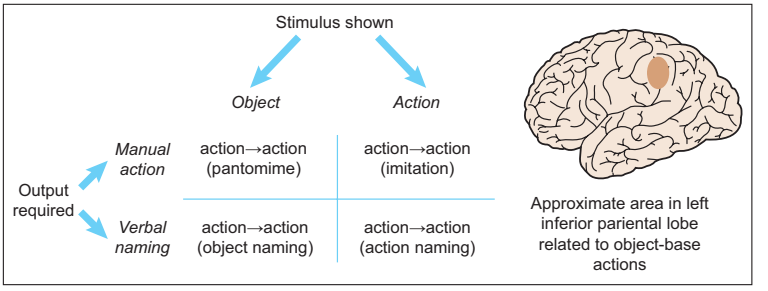


FIGURE 10.19: A simple model of tool use showing ventral stream and dorsal stream components. Different mechanisms are implicated in grasping an object (sensorimotor transformations using regions such as PRR and AIP) versus using a tool based on learned object knowledge (inferior parietal lobes, via temporal regions). For completeness, regions involved in perceiving body parts and gestures (EBA = extrastriate body area, STS = superior temporal sulcus) are shown as providing an input into premotor mirror systems.

FIGURE 10.20: Rumiati et al. (2004) compared the brain activity when participants were asked to generate actions or name actions from either an object or action. They found a region in the left inferior parietal lobe that appears specific to object-based action in their "pantomime" condition.



and were required to either gesture the appropriate action or produce the name of it. Producing an action from a static picture of an object (called *pantomiming*) was found to be particularly associated with the left inferior parietal lobe and a left lateral premotor region, after controlling for other factors (e.g., object recognition). Consistent with the imaging data, some patients with damage to the left parietal lobe may be unable to produce appropriate actions on command given either an object (e.g., an iron), a word (e.g., "iron"), or a command (e.g., intransitive gestures such as "waving goodbye"). These patients are traditionally classified as having **ideomotor apraxia** (Gonzalez Rothi et al., 1991). These patients would typically be able to imitate meaningless gestures

KEY TERM

Ideomotor apraxia
An inability to produce appropriate gestures given an object, word, or command.

(e.g., holding the left palm upwards) or produce these gestures on command, provided their lesion doesn't extend to other aspects of sensorimotor transformation (Buxbaum & Kalenine, 2010).

An important debate in the literature concerns the extent to which semantic representations of objects are critical for the production of object-related gestures. There is some evidence that objects can activate their corresponding action schemas without (fully) accessing semantic memory. Disrupting regions involved in core aspects of semantic memory (anterior temporal lobes) using TMS does not interfere with decisions about how tools are manipulated (how held, how moved) but does interfere with judgments about their functions (e.g., for eating, cutting). Conversely, TMS over the left inferior parietal lobes produces the opposite pattern (Ishibashi et al., 2011). More severe impairments in semantic memory in patients with semantic dementia are linked to impairments in tool use (Hodges et al., 2000). For example, one patient correctly held the scissors by the handle rather than the blade but did so bimanually (plausibly correct) rather than unimanually (conventionally correct). The semantic dementia patients could copy actions performed by the experimenter and use novel tools. In the previous framework, damage to the ventral stream prevents the retrieval of learned object actions but still permits sensorimotor-based affordances and imitation.

Finally, one long-standing question is why object-based actions should reside predominantly in the left hemisphere of humans (no such bias has been found in other primates). One possibility dating back to the work of Liepmann (1905) is that it reflects the fact that the majority of people are right-handed for tool use. Functional imaging studies of left-handers have shed light on this. Regions of the *left* hemisphere involved in tool use (area AIP and the ventral premotor cortex) are activated to the same degree in left-handers and right-handers, irrespective of which hand is used and irrespective of whether the action involves tool use or hand-based grasping (Martin et al., 2011). However, left-handers do show more bilateral activity in the equivalent right hemispheric regions. This suggests that handedness is a factor, but it is not simply the case that left-handed and right-handed people are mirror images of each other in terms of brain activity when they use tools.

An alternative possibility is that the apparent bilateral pattern in left-handers is due to differences in language dominance rather than handedness itself. Left-handers tend to show more variability in which hemisphere is dominant for language production (either right, left, or mixed dominance), whereas right-handers are almost always left-hemispheric dominant (Rasmussen & Milner, 1977). When left-handers are assessed for language dominance (assessed by silently generating words during fMRI), parietal regions relating to praxis (assessed by generating gestures to words, e.g., "cutting") tend to be lateralized to the language dominant hemisphere (Kroliczak et al., 2011). Thus, language laterality rather than handedness per se seems to be the main determinant of

hemispheric asymmetry for tool use. It is less clear which aspects of language (speech production, conceptual knowledge, etc.) are most relevant to the association.

Evaluation

In order to act on objects, different neurons in the frontal and parietal lobe become activated depending on the nature of the action (reaching, grasping) and the sensory properties of the object (its size, shape, location). This sensorimotor transformation thus links perception with action. The human brain contains a store of object-dependent actions that may reside in the left inferior parietal lobe and are impaired in ideomotor apraxia. These actions may normally be accessed from semantic representations of objects, but actions can often be inferred from the non-arbitrary relationship between the structures of tools and the functions they serve (affordances).

FRONTO-STRIATAL AND CEREBELLAR NETWORKS IN ACTION

Role of subcortical structures in movement and action

The chapter so far has concentrated on cortical influences on action and movement. However, subcortical structures have an important role to play, particularly with regards to the preparation and execution of actions. These structures may be important for setting the particular parameters of the movement, such as the force and duration of movement and for controlling the movement in progress. One imaging study that highlights the different roles of cortical and subcortical structures was conducted by Krams and colleagues (1998). In one condition, participants were shown a hand position, given 3 seconds to *prepare*, and were then asked to *execute* it (PE condition). In another condition, they were required to *execute* it as soon as it was shown (E condition), and in the final experimental condition, they were asked to *prepare* but not to execute (P condition). (The baseline condition was viewing the hand movement without preparation or execution.) The cerebellum and basal ganglia were found to be more active when both preparation and execution were required (PE relative to P; also PE relative to E). In contrast, the prefrontal cortex including Broca's area was more active when merely preparing to produce observed movements (P relative to PE; also P relative to E).

Figure 10.21 summarizes the two main types of cortical-subcortical loop involved in the generation of movement. One set of loops pass through the basal ganglia, and the other set of loops through the cerebellum. These loops have somewhat different functions. The *cerebellar loop* is involved in the coordination of movements. Given this role, it is perhaps not surprising that the cerebellum connects strongly with lateral premotor and parietal

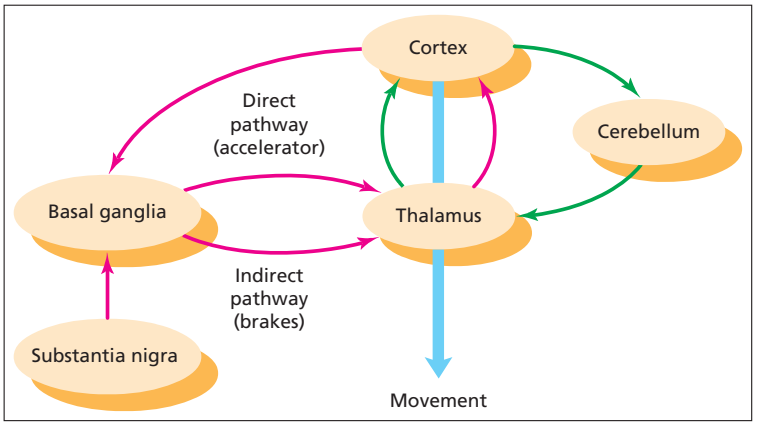


FIGURE 10.21: Two main types of subcortical loop are involved in movement generation. The cerebellar loop (green) coordinates the timing and trajectory of movement using sensory and motor information. The basal ganglia motor circuit (purple) regulates the excitability of frontal motor structures (SMA) and biases the likelihood of movement and the nature of the movement (e.g., the force).

regions involved in sensorimotor transformation (Bostan et al., 2013). It may utilize a copy of the cortical motor commands to ensure that the desired movement occurs accurately and occurs at the desired time (Ohyama et al., 2003). For example, it is physiologically active during coordination tasks that require one movement to be synchronized with another (Ramnani et al., 2001). Moreover, patients with cerebellum lesions produce tremulous movements that suggest that they are unable to use information about the progress of the movement to update the initiated motor program (Haggard et al., 1995).

The basal ganglia "loop" actually consists of around five different loops. Each loop has essentially the same architecture (a set of interconnected excitatory and inhibitory pathways) but projects to different structures in the basal ganglia and in the cortex (Alexander & Crutcher, 1990). Of primary relevance here is the so-called motor circuit that passes through dorsal regions of the basal ganglia and projects to premotor areas and particularly strongly to the SMA. Other loops target different regions of the frontal lobes and pass through different structures in the basal ganglia and the thalamus: for instance, an oculomotor circuit projects strongly to the frontal eye fields; a limbic circuit passes through more ventral regions of the basal ganglia and projects to the orbitofrontal cortex, amygdala, and anterior cingulate; and other loops project to the lateral prefrontal cortex. These different circuits modulate different aspects of behavior. The prefrontal loop relates to the control of cognition, the oculomotor circuit relates to the control of eye movements, and the limbic circuit is linked to reward-based learning. The motor circuit itself appears to be particularly important for the initiation and execution of internally generated movements (more so than cued movements), sequencing of actions, and procedural learning. It is to be noted that the basal ganglia do not generate the signals to execute a movement (this is achieved from connections from the primary motor cortex down the brainstem to the spinal cord). They function, instead, to modify activity in frontal motor structures and influence the nature of the movement such as its amplitude (Turner & Desmurget, 2010).

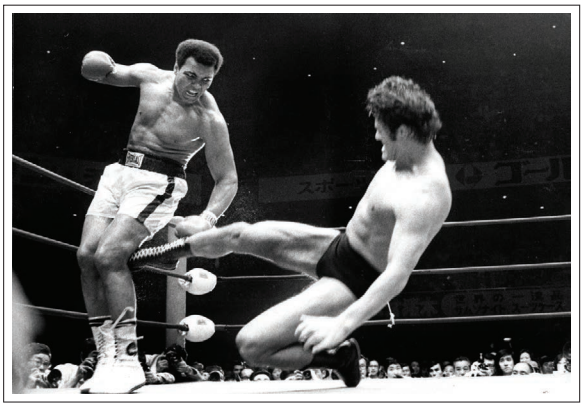


FIGURE 10.22: The former champion boxer Muhammad Ali was diagnosed with Parkinson's in 1984 at the age of 42 and is one of the most high-profile people to have had the condition.
KEYSTONE Pictures USA/Alamy Stock Photo

The spinal cord makes connections between the brain and the muscles and controls simple reflexive movements (e.g., to avoid sudden injury). Unlike the other actions considered so far, reflexes can't be construed as cognitively based. As well as these descending fiber tracts, the spinal cord also contains ascending fibers that provide sensory feedback about the state of the body and the fate of the executed movement. For example, patient GO lost these pathways from a severe peripheral sensory disease (Rothwell et al., 1982). Although he could make accurate quick movements with appropriate force, his lack of sensory feedback meant that he was unable to sustain motoric tasks. For example, when carrying a suitcase, he would quickly drop it unless he continually looked down to see it was there.

KEY TERM

Parkinson's disease
A disease associated with the basal ganglia and characterized by a lack of self-initiated movement.

Hypokinetic disorders of the basal ganglia: Parkinson's disease

Parkinson's disease affects about 0.15 percent of the total population and has a mean age of onset at around 60 years (Figure 10.22). It was first described by James Parkinson in 1817 in his "Essay on the shaking palsy." No single cause has yet been found, although in some cases a genetic link has been suggested. However, the neuropathologic signs of the disease are well understood. Dopaminergic brain cells are lost in the pathways linking the substantia nigra and basal ganglia (Brooks et al., 1990). Dopamine agonists therefore tend to be used in the treatment of Parkinson's disease, but direct electrical stimulation of the basal ganglia circuit (termed deep brain stimulation) through an implanted device is becoming increasingly common (Obeso et al., 2001).

To understand the symptoms of Parkinson's disease, it is necessary to understand the nature of the basal ganglia motor circuit in more detail. The loops connecting the basal ganglia and thalamus consist of a mix of inhibitory and excitatory connections that combine together to form two complementary routes: a direct route that promotes action (increases activity in the cortex) and an indirect route that inhibits action (decreases activity in the cortex) (DeLong, 1990). These direct and indirect routes act like an accelerator and brake in the initiation of action. Lesions of the connections between the substantia nigra and the basal ganglia in Parkinson's disease have a net effect of increasing the output of the indirect pathway (the brakes) and decreasing the output

ONLINE RESOURCES
Visit the Instructor & Student Resources website (routledge learning.com/ward cognitiveneuro science) to discover more about deep brain stimulation for neurodegeneration, and scan the QR code to see the TED talk by Professor Andres Lozano on "Parkinson's, depression and the switch that might turn them off."

on the direct pathway (the accelerator). The result is a poverty of self-initiated movement.

Not all types of movement and action are affected equally in Parkinson's disease. For example, an ordinarily immobile patient may walk or run normally in situations of risk such as fire, and the shuffling gait can be improved by provision of lines on the floor over which the patients must step (Martin, 1967). This suggests that there is not a simple movement failure, but that there is a failure in self-initiating the action that can to some extent be overcome by external cues. The motor programs themselves also appear to be preserved. For example, signatures and handwriting style are preserved even though the kinematics are impaired such that writing is very slow and shrunken in size (a symptom called *micrographia*; McLennan et al., 1972). One common finding is that patients with Parkinson's disease are relatively spared at initiating actions in which the response is determined by some property of the stimulus (e.g., left finger if stimulus is green, right finger if stimulus is red), but significantly impaired on simple reaction time tasks (e.g., press a single button, or any button, when the stimulus appears) (Evarts et al., 1981). How are we to account for the relatively spared actions? Recall that there is an additional subcortical route that bypasses the basal ganglia altogether and goes via the cerebellum (note: this is not to be confused with the direct and indirect pathways, both of which go through the basal ganglia). This route may be more involved in actions specified by environmental cues, whereas the routes through the basal ganglia are more involved with self-initiated actions associated with the SMA. Functional imaging studies have shown that patients with Parkinson's disease have reduced fronto-striatal activation during self-initiated action but can show normal activation in externally triggered actions (Jahanshahi et al., 1995), and cortico-cerebellar functional connectivity is enhanced whilst connectivity between the basal ganglia and cortex is reduced (Wu et al., 2011).

MOTOR SYMPTOMS OF PARKINSON'S DISEASE

Symptoms include the following (Beradelli et al., 2001):

- akinesia (lack of spontaneous movement)
- bradykinesia (slowness of movement)
- decay of movement sequences (walking degenerates to a shuffle)
- failure to scale muscle activity to movement amplitude
- failure to weld several movement components into a single action plan
- rigidity
- tremor (when stationary)

The pattern of spared and impaired action in patients with Parkinson's disease is also found in cognitive tasks with minimal motor requirements. This is perhaps not surprising since the lesioned pathway (from the substantia nigra to the basal ganglia) contributes to loops other than the motor circuit. Patients with Parkinson's disease perform poorly on tasks of executive function that involve the self-initiation of cognitive strategies (Taylor et al., 1986). Brown and Marsden (1988) used a variant of the Stroop Test in which the subject must either name the INK color (e.g., say "red" when the written word *green* is printed in red ink) or the WORD color (e.g., say "green" when the written word *green* is printed in red ink). Participants would either have to spontaneously switch between naming the ink and naming the color or they would receive a written cue (INK or WORD) before each trial. The patients with Parkinson's disease were impaired on the uncued self-initiated trials but not the cued trials.

Hyperkinetic disorders of the basal ganglia: Huntington's disease and Tourette's syndrome

If Parkinson's disease is characterized as a poverty of spontaneous movement **(hypokinetic)**, then a number of disorders exist that can be characterized as an excess of spontaneous movement **(hyperkinetic)**. **Huntington's disease** is a genetic disorder with a well-characterized neuropathology (MacDonald et al., 2003). The symptoms consist of dance-like, flailing limbs (chorea) and contorted postures. The symptoms arise in mid-adulthood and degenerate over time. Many of those condemned in the Salem witch trials of 1692 are now believed to have suffered from the illness. Huntington's disease arises because of depletion of inhibitory neurons in the early part of the indirect pathway linking the basal ganglia with the thalamus (Wichmann & DeLong, 1996). The net effect of this lesion is that the output of the indirect pathway (the brakes) is reduced, whereas the output of the direct pathway (the accelerator) remains normal. This shift in the balance of power promotes movement in general.

Tourette's syndrome is characterized by excessive and repetitive actions such as motor tics or vocalizations. Functional imaging (fMRI) of children with Tourette's revealed a correlation between tic severity and activation of the substantia nigra and cortical, striatal, and thalamic regions in the direct (accelerator) pathway during a cognitive task (Baym et al., 2008). The prefrontal cortex also tends to be activated more in people with Tourette's syndrome relative to controls in complex motor and cognitive tasks (Jackson et al., 2011). This could be interpreted as a compensatory mechanism to try to control the tics.

KEY TERMS

Hypokinetic
A reduction in movement.

Hyperkinetic
An increase in movement.

Huntington's disease
A genetic disorder affecting the basal ganglia and associated with excessive movement.

Tourette's syndrome
A neuropsychiatric disorder with an onset in childhood characterized by the presence of motor and/or vocal tics.

SYMPTOMS OF TOURETTE'S SYNDROME

Symptoms include:

- motor tics (e.g., eye blinks, neck movements)
- echolalia (repeating someone else's words)
- palilalia (repeating one's own words)
- coprolalia (production of obscenities)

Evaluation

A number of circuits involving the cortex (notably frontal) and subcortical structures are critical for the initiation and execution of movement. One circuit, involving the cerebellum, is involved in coordinating the movement once initiated. Another circuit, involving the basal ganglia, is involved in establishing self-initiated movements. The basal ganglia loop contains two parallel pathways known as the direct and indirect pathway that promote or reduce cortical excitability. Disruptions in the direct and indirect pathways are implicated in a number of movement-related disorders including Parkinson's disease, Huntington's disease, and Tourette's syndrome.

SUMMARY AND KEY POINTS OF THE CHAPTER

- Action can be considered an outcome of a number of processes working together in a concerted fashion. These processes include selection and maintenance of goals; the identification of objects in the environment and translation of their visuo-spatial properties into motor commands; preparing movements; and executing and online control of movements.
- The prefrontal cortex is involved in the highest stages of action planning and cognitive control in general. The SAS model provides a good account of action selection and its breakdown following frontal lobe damage.
- The lateral premotor cortex may be involved both in the preparation of action (particularly toward external objects) and in observing the actions of others (using "mirror neurons"). The medial premotor cortex (SMA) prepares actions without external cues (e.g., from memory, or self-initiated).
- Visual processing of objects contains both a ventral stream (involved in explicit object recognition) and a dorsal stream. The dorsal stream codes action-relevant properties of objects (e.g., their absolute size, position in egocentric space).

- The dorsal stream terminates in the parietal lobes, and parieto-frontal networks are responsible for developing action plans based on the current external reality and the goals of the individual.
- Humans use a vast range of tools. Tool use may be achieved by retrieving stored knowledge of objects and their actions via semantic memory, or may be partially achieved using "affordances" based on sensorimotor properties of objects. A difficulty in using objects is referred to as apraxia.
- The preparation and execution of action is influenced by two main subcortical circuits involving: (1) the cerebellum and (2) the basal ganglia. The cerebellar loop is involved in the online coordination of movement by comparing intended motor acts with sensory outcomes.
- The basal ganglia regulate action via a balance of action-promoting and action-inhibiting pathways and are particularly involved in self-generated actions (prepared in the supplementary motor area). Parkinson's and Huntington's diseases can be explained as a disruption of this balance, leading to a poverty or excess of movement.

EXAMPLE ESSAY QUESTIONS

- What is the role(s) of the frontal lobes in action?
- What are mirror neurons and how has their discovery changed the way that people think about action?
- How are object-related actions stored and retrieved?
- How are vision and action integrated in the brain?
- Compare and contrast the role of the cerebellum and the basal ganglia in action.

ONLINE RESOURCES

Visit the Instructor & Student Resources website at routledgelearning.com/wardcognitiveneuroscience for:

- Video interviews on key topics with leading psychologists Giacomo Rizzolatti and Ann Graybiel
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CHAPTER 11

The remembering brain

CONTENTS

The ability to learn and remember has several evolutionary advantages. It enables one to predict future outcomes on the basis of experience and adapt to new situations. One can learn to avoid situations previously associated with threat, or to return to locations where food has previously been found. Given that all neurons in the brain are capable of plasticity, even later in life, one could regard learning and memory as a feature of the brain as a whole rather than a specialized module or faculty. Indeed, there are no instances in which memory is completely lost or abolished. Even amnesic patients can learn and remember certain things. Although the whole brain may make contributions to learning and memory, it is crucial to recognize that different regions contribute in different ways. Some regions may be specialized for learning and remembering words, other regions specialized for learning and remembering visual objects, and other

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regions may be especially important for recollecting episodes from one's life. The latter is the traditional sense in which the word "memory" is used, but there is far more to memory than that.

The general approach of this chapter is to consider different types of memory, how they are implemented in the brain, and how they interact. The chapter begins by considering the distinction between long-term and short-term or working memory. The chapter then considers different types of long-term memory and discusses amnesia in terms of this theoretical framework. It then goes on to discuss whether the hippocampus has a time-limited role, whether there are separate neural substrates for familiarity and recollection and the cognitive/neural mechanisms of forgetting. Finally, the chapter discusses frontal lobe contributions to memory.

SHORT-TERM AND WORKING MEMORY

The labels "short-term" and "long-term" appear to suggest that there could be different types of memory evoked for different periods of time with, perhaps, separate stores for things that happened a few days ago relative to several years ago. This is a popular misconception. It is not how psychologists distinguish between short- and long-term memory. **Short-term memory (STM)** is defined as memory for information currently held "in mind" and has limited capacity. **Long-term memory (LTM)** refers to information that is stored; it need not be presently accessed or even consciously accessible. The long-term store is considered to have essentially unlimited capacity within the inherent limitations of the brain. According to this definition, memory for things that happened several hours, days, or years ago is all stored within long-term memory.

KEY TERMS

Short-term memory
Memory for information currently held "in mind"; it has limited capacity.

Long-term memory
Memory for information that is stored but need not be consciously accessible; it has an essentially unlimited capacity.

Models of STM and working memory

The influential model of Atkinson and Shiffrin (1968) regarded short-term memory as a single entity that was essential for all long-term learning. Both of these assumptions turned out not to be correct. For instance, if both STM for verbal material (e.g., words) and STM for visuo-spatial material (e.g., routes) use the same limited-capacity system, then it should not be possible to hold both kinds of information in mind at the same time without substantial interference. However, this is not the case (e.g., Logie et al., 1990), suggesting that there are different kinds of short-term memory depending on the nature of the information being held in mind (e.g., verbal, visual), each with their own limited capacity. Subsequent evidence from brain imaging also supports the view that there are separable systems with different neural foundations (for a review see D'Esposito & Postle, 2015). Finally, evidence from neuropsychology suggested that it was possible to have some kinds of long-term learning (e.g., pairing words together) despite impaired STM (Warrington & Shallice, 1969), suggesting that LTM can be accessed separately from STM.

Beyond Atkinson and Shiffrin (1968), the next significant approach was the model of Baddeley and Hitch (1974). This original model consists of three components. There are two storage components: one for verbal material (the phonological loop) and one for visual material (which they termed the visuo-spatial sketchpad). The third component was termed the central executive. The central executive coordinates the storage components and cognition in general, specifying task goals, initiating and terminating cognitive routines, and so on. The other significant aspect of the model is that it was regarded as a model of working memory and not just short-term memory. The concept of **working memory** is essentially an extension of the one already described for short-term memory. The key difference is that working memory emphasizes a wider role in cognition (reasoning, comprehension, etc.), whereas short-term memory is often taken to imply a more passive retention of material. In the Baddeley and Hitch (1974) model it is the interaction between the flexible executive system and the more specific processing routines that is the essential characteristic of working memory. Subsequently, an additional STM system – the episodic buffer – was added to the model for maintaining and manipulating information from episodic long-term memory (Baddeley, 2000), as shown in Figure 11.1.

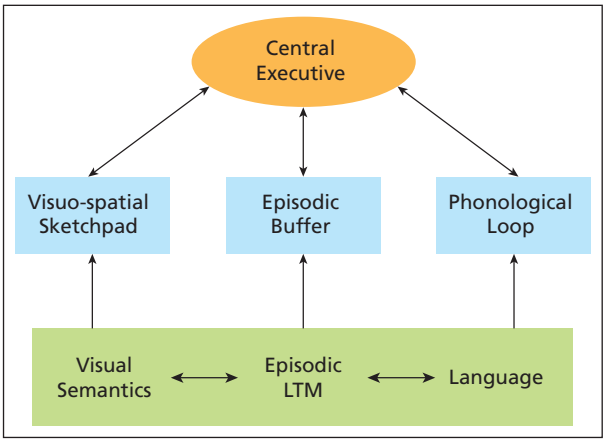


FIGURE 11.1: Baddeley's (2000) model of working memory was revised to incorporate three kinds of short-term systems (blue) that interface with long-term memory (shown in green).

KEY TERM

Working memory
A system for the temporary storage and manipulation of information.

Working memory models such as those of Baddeley and colleagues propose that information (e.g., words) gets transferred or copied into a separate dedicated system (e.g., a phonological short-term memory store), which may then be acted on by an executive system. The alternative approach is to "cut out the middle man" and suggest that there are no short-term stores, but that working memory is, instead, just the temporary activation of long-term memories (including perceptual representations of words and objects) by a prefrontal/executive system (Cowan, 2001; D'Esposito & Postle, 2015). There are some advantages to this approach: it is a simpler explanation, and it can be used to account for working memory for all kinds of information (e.g., touch, smell) and not just those for which separate STM systems are assumed to exist. An example of such a model is shown in Figure 11.2. This approach is currently the most common within cognitive neuroscience, although it is not without its critics (e.g., Norris, 2017). Norris (2017) argued that a separate short-term system is needed for repeating made-up words (that are, by definition, not stored in long-term memory) and for recalling sequences with repeated items (e.g., the number 5 in "8235915" needs to be represented as occurring twice rather than as being

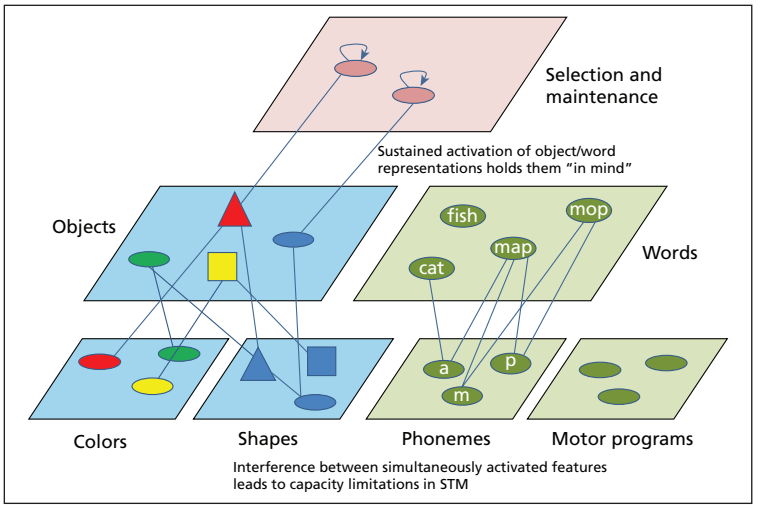


FIGURE 11.2: Many contemporary models assume that there are no specialized STM stores. Instead, short-term memory is simply the top-down activation (from frontoparietal attention and executive mechanisms) to stored object and word representations (e.g., in the visual ventral stream, or speech system) and their perceptual-motor features. This can occur in the absence of any current sensory signal (i.e., sustaining activity of a previously seen visual array or a previously heard string of words).

doubly activated in LTM). Whether these effects can be modeled from a system in which STM is just the temporary activation of words (and the sensorimotor features of words) remains to be seen.

The remaining sections consider the evidence for different kinds of limited-capacity short-term memory stores, and their neural basis. The extent to which the evidence favors the existence of STM stores versus STM being the temporary activation of long-term memory (and perceptual) representations is also considered in more detail.

Phonological short-term memory

Phonological short-term memory and verbal working memory are synonymous with each other. The capacity limitation of phonological short-term memory is typically investigated with span tasks, in which participants are read a sequence of, say, digits, and must repeat them back immediately or after brief retention. Miller (1956) argued that humans have a span of seven items plus or minus two (i.e., between five and nine items). He argued that the seven items are meaningful "chunks" of information rather than words or syllables. For example, familiar dates such as "1812" may be one chunk, but "5297" may be four single-digit chunks. However, others have argued that chunking is relying on long-term memory to recode information and that the true capacity limitation is lower, around four (Cowan, 2001). Evidence against Miller's proposal comes from research showing that the capacity limitation is related to phonological characteristics of the stimuli and not merely their meaningfulness. Span length is lower when lists of words are polysyllabic (e.g., "skeleton, binocular"; Baddeley et al., 1975) or when they are phonologically similar (e.g., "map, can, cap, mat"; Baddeley, 1966).

Another factor that may influence span is the opportunity to rehearse the material. Span is reduced if participants are asked to silently mouth irrelevant speech (e.g., saying "the, the, the" or "1, 2, 3") while encoding a list (Baddeley et al., 1984); see Figure 11.3. This is termed **articulatory suppression**. Baddeley argues that span tasks

KEY TERM

Articulatory suppression Silently mouthing words while performing some other task (typically a memory task).

involve at least two components: a phonological store and a rehearsal mechanism based on subvocal articulation (i.e., saying the words "in the head") that refreshes the store. Articulatory suppression impairs the latter. Collectively, he terms the store and rehearsal mechanism the "phonological loop" or the "articulatory loop" (Baddeley et al., 1984).

In terms of its neural basis, current research considers the loop in terms of reciprocal activation between speech perception processes and mechanisms of speech production (Buchsbaum & D'Esposito, 2008; Jones et al., 2004). This was considered in more detail in Chapter 8, "The hearing brain." In these neural models there isn't a dedicated short-term store; instead, the sensory and motor aspects of speech co-activate each other in a neural loop.

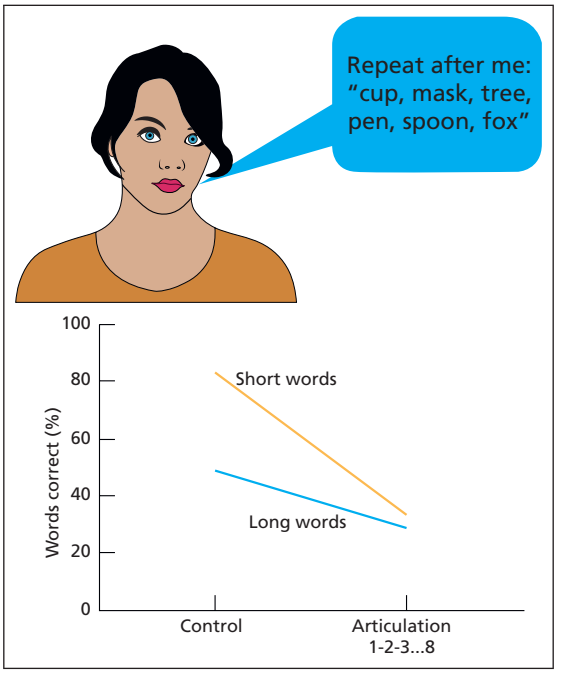


FIGURE 11.3: Recall of word lists from short-term memory is reduced for longer words and affected by articulatory suppression (counting under one's breath whilst listening to the word sequence).
Data from Baddeley et al. (1975).

Visuo-spatial short-term memory

It has been proposed that there is a limited-capacity short-term memory system for visuo-spatial information that is analogous to the one involving phonological information described previously (Logie, 1995). One approach to studying this is to display an array of objects and then retain them over a brief delay period (several seconds). Memory can then be probed via recognition (was this object present?), change detection (is the array the same?), or cued recall (what object was at this location?) – see examples in Figure 11.4. Luck and Vogel (1997) displayed arrays of different colored squares or arrays of different line orientations. In both cases, memory deteriorates when holding in mind more than four items. The interesting comparison was when conjunctions of features had to be remembered (i.e., an oriented *and* colored line). Even though the conjunction involves holding twice as many features in mind, it was found that memory performance was not halved but remained constant; that is, around four feature conjunctions could be remembered. They even extended this finding to a quadruple feature condition: 16 features distributed across four objects can be retained as accurately as four features distributed across four objects. The explanation is that the capacity limitation relates to visual objects/locations rather than visual features.

What is the neural basis of visuo-spatial STM? There is evidence that holding in mind an object, over a delay period, involves sustaining activity in regions of the brain involved in object perception. Ranganath et al. (2004) examined visual short-term memory for images of faces or places using fMRI. The

ONLINE RESOURCES

Watch Charan Ranganath speak on "How Memory Works and Can You Make It Better" by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

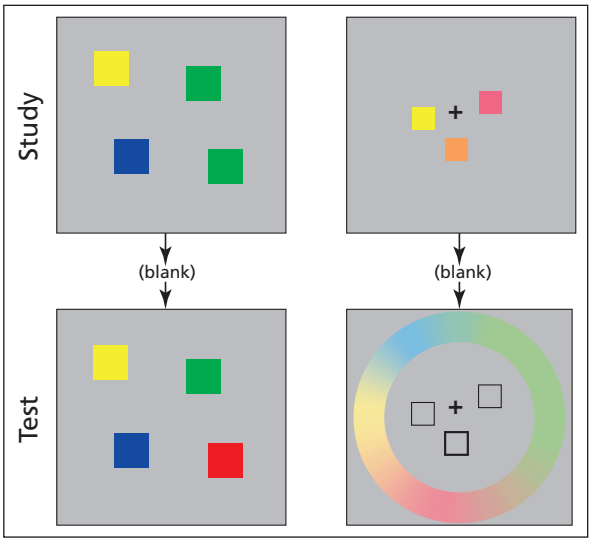


FIGURE 11.4: Different approaches for exploring the capacity limits of visual STM: the number and type of stimuli would typically be varied. In the left example, the participant must detect whether any change occurred. In the right example, the participant must recall which color was in the cued square.

findings are shown in Figure 11.5. In delayed matching to sample, participants were shown a face/place (for 1 sec) and asked to keep it in mind (for 7 sec) followed by a test stimulus (is it the same or different item?). Holding in mind a face or place sustains activity in parts of the ventral stream specialized for perceiving faces and places respectively. In delayed paired associates, a similar procedure was used except that participants had previously learned to pair particular place and face images together (e.g., face A paired with place A). In this condition, BOLD activity relating to the delay period reflected the type of

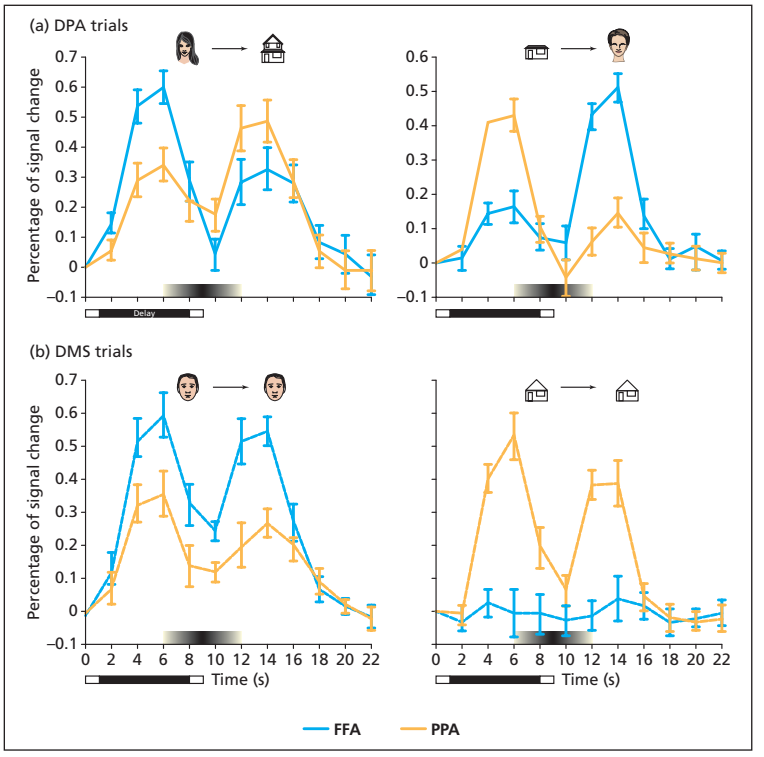


FIGURE 11.5: In this study a visual stimulus (face or house, presented for 1 sec) must either be held in STM to be recognized after a delay (DMS, delayed matching to sample) or an associated item from the other category must be held in STM (DPA, delayed paired associates). These stimuli activate the fusiform face area (FFA, blue lines) and parahippocampal place area (PPA, orange lines). The critical part of the study is the blank delay period between stimuli where visual STM is engaged. Holding in mind a stimulus during the delay (DMS) sustains activity in that region, whereas retrieving a different kind of associate (DPA) flips the activity to be consistent with the new stimulus even before it is physically presented.

From Ranganath et al. (2004). Copyright 2007 Society for Neuroscience.

stimulus being recalled rather than the one just presented (i.e., it reflects memory rather than perception). This kind of study is taken as evidence in support of the view that STM involves the temporary activation of LTM extending to perceptual features. As noted by Baddeley (2012), studies of this kind do not disprove additional short-term stores, but they do support the idea that working memory and long-term memory are not completely distinct.

One challenge for those models that regard working memory as temporary activation of long-term memory is to explain where capacity limitation comes from in the first place. (Note: this is not a problem for traditional models, because capacity limitation is an intrinsic property of short-term stores; for instance, by having four or seven "slots.") One explanation is that the more items that are simultaneously activated in a long-term memory store, the more interference there is between them and the less precision there is (e.g., "mop" may become confusable with "map" when holding multiple other words in mind, but not when holding one word in mind). In visual STM, for instance, knowing the exact location of an object in a just-seen array becomes increasingly less precise as the array size increases, but doesn't immediately become error-prone when the array size reaches a "magic-number" of four objects (Bays & Husain, 2008).

The contents of visual STM may reside in visual areas of the brain, but other regions are responsible for selecting and maintaining information in STM, and for this reason there are close parallels with visual attention and visual STM. Visual regions are functionally connected to frontal and parietal regions during the STM delay period (Gazzaley et al., 2004). Moreover, distracting stimuli presented in the delay period (e.g., irrelevant faces when trying to hold in mind a face) disrupts connectivity in that network as well as disrupting visual STM performance (Yoon et al., 2006). fMRI activity in regions in the posterior parietal cortex (intraparietal sulcus), together with regions involved in visual perception, are related to individual differences in visual STM capacity (Todd & Marois, 2004, 2005).

Evaluation

Short-term memory systems have two essential features: a capacity limited storage system and a mechanism for refreshing and maintaining activity in that system. The nature of the store itself is more controversial and could either be a separate memory system (with capacity limitation deriving primarily from the size of that system) or temporary activation of long-term stores (e.g., for words) or perceptual resources (e.g., for visual patterns), with capacity limitation arising solely from interference between active items. Evidence from cognitive neuroscience suggests some role for the latter.

ONLINE RESOURCES

Test your visual and verbal short-term memory via our demo test library (www.testable.org/ward).

DIFFERENT TYPES OF LONG-TERM MEMORY

Just as short-term memory may have several components (e.g., visuo-spatial, phonological), long-term memory may be further subdivided

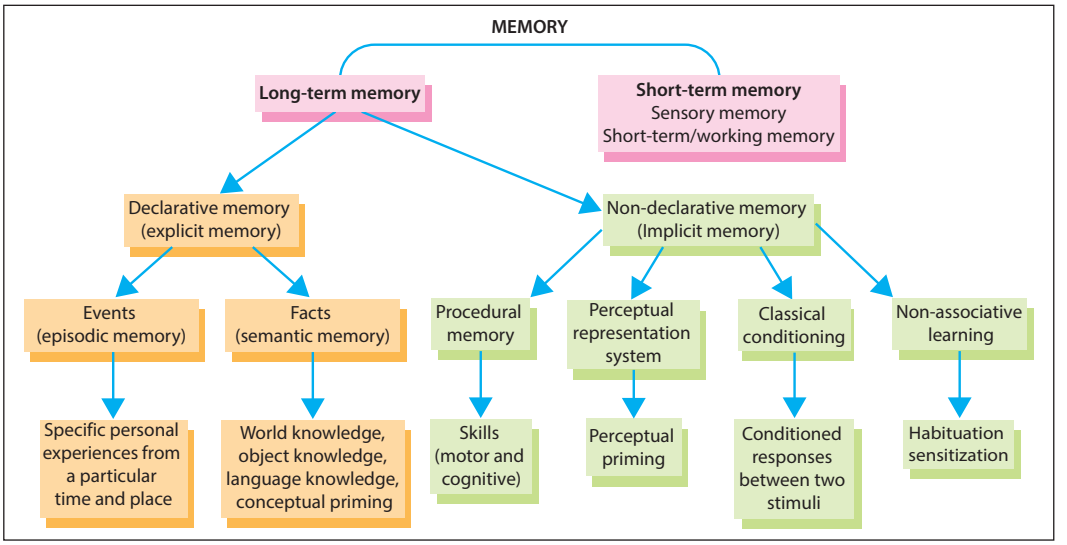


FIGURE 11.6: Long-term memory can be thought of as a number of different systems. But are the systems fully independent, or do they depend on each other to some extent?

KEY TERMS

Declarative memory
Memories that can be consciously accessed and, hence, can typically be declared.

Non-declarative memory
Memories that cannot be consciously accessed (e.g., procedural memory).

Explicit memory
See declarative memory.

Implicit memory
See non-declarative memory.

Procedural memory
Memory for skills such as riding a bike.

into different components. This has been termed the multiple memory systems approach (Nyberg & Tulving, 1996) and is summarized in Figure 11.6. One distinction that can be made is whether the memories are consciously accessible or not; termed **declarative memory** and **non-declarative memory**, respectively (Squire et al., 1993) or, alternatively, **explicit memory** and **implicit memory**, respectively.

Non-declarative memory can be thought of as consisting of several subdomains. **Procedural memory** refers to memory for skills such as riding a bike. It is not consciously accessible in the sense that the contents of the memory are not amenable to verbal report. Evidence suggests that the basal ganglia are important for the learning of procedural skills and habits (Packard & Knowlton, 2002). Perceptual representation systems are those used for perceiving sounds, words, objects, and so on (Schacter, 1987). They are memory systems in the sense that they store knowledge of the perceptual world and are capable of learning. Evidence for perceptual learning comes from priming studies. Priming refers to the fact that information is easier to access if it has recently been encountered. For example, people are more likely to complete a word fragment such as H__SE as HORSE if that word has recently been encountered. This is assumed to reflect the fact that the perceptual representation of the word is more accessible the second time around (Tulving & Schacter, 1990). The neural signature of priming appears to be reduced activity on the second presentation relative to the first (Schacter & Badgaiyan, 2001). The fact that enhanced performance on a second occasion is linked to less neural activity, rather than more, may seem counterintuitive. This efficiency may reflect a more precise (less noisy) neural response on the second occasion, or greater neural synchrony despite a reduction in overall response (Gotts et al., 2012). Imaging studies (Schacter & Badgaiyan, 2001) and a report of a patient with occipital lobe lesion (Gabrieli et al., 1995) are consistent with the notion that priming involves brain regions involved in perception.

Within declarative or explicit memory, Tulving (1972) has proposed the influential distinction between episodic and semantic memory. **Semantic memory** is conceptually based knowledge about the world, including knowledge of people, places, the meaning of objects and words. It is culturally shared knowledge. By contrast, **episodic memory** refers to memory of specific events in one's own life. The memories are specific in time and place. For example, knowing that Paris is the capital of France is semantic memory, but remembering a visit to Paris or remembering being taught this fact is episodic memory. Episodic memory has a first-person characteristic to it, that is, the memories involve oneself as an observer/participant. For this reason, it is also known as autobiographical memory. Facts about oneself (e.g., addresses, the name of your spouse) are normally regarded as semantic memory and are usually called personal semantic memory (although their first-person nature resembles episodic memory; Renoult et al., 2012). There is good evidence for multiple memory systems, but there is nevertheless likely to be some overlap between them. This will be outlined in subsequent sections.

KEY TERMS

Semantic memory Conceptually based knowledge about the world, including knowledge of people, places, the meaning of objects and words.

Episodic memory Memory of specific events in one's own life.

Anterograde memory Memory for events that have occurred after brain damage.

Retrograde memory Memory for events that occurred before brain damage.

AMNESIA

One of the most famous patients in the neuropsychological literature is HM (Corkin, 2002). HM began to experience epileptic seizures at the age of 10, and by the time of leaving high school, his quality of life had deteriorated to a point where surgeons and family decided to intervene surgically. The procedure involved removing the medial temporal lobes, including the hippocampus, bilaterally (Scoville & Milner, 1957). What the surgeons did not foresee was that HM would develop one of the most profound amnesias on record. Several decades after the operation, it was observed that HM

> does not know where he lives, who cares for him, or where he ate his last meal. His guesses as to the current year may be off by as much as 43 years . . . In 1982 he did not recognize a picture of himself that had been taken on his fortieth birthday in 1966.
> *(Corkin, 1984, p. 255)*

On his death, HM was identified as Henry Molaison (1926–2008), and his brain has been preserved in histological sections.

Global amnesics have memory problems both in terms of learning new information (**anterograde memory** impairment) and remembering information prior to their brain damage (**retrograde memory** impairment). This is shown in Figure 11.9. HM's retrograde deficit extended back to age 16 (11 years before his surgery), and his anterograde deficit was extremely severe (Sagar et al., 1985). It is to be noted that amnesia is a heterogeneous disorder, with patients differing both in terms of severity and also in some qualitative respects (Spiers et al., 2001b). This may reflect different sites of damage in and around the medial temporal lobe (see Figure 11.7). It is also to be noted that HM's lesion affected

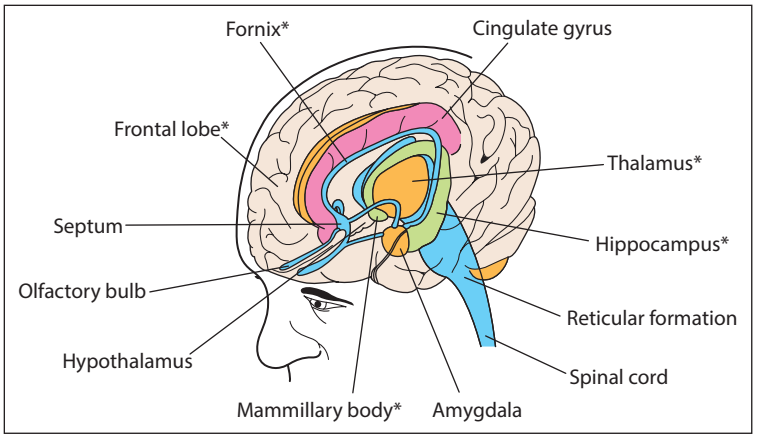


FIGURE 11.7: Damage to a number of regions in the medial temporal lobes and surrounding structures (marked with an asterisk) can produce an amnesic syndrome.

From Parkin (2001). Reproduced by permission of Taylor & Francis Group.

several regions, not just the hippocampus. HM's amnesia was a result of neurosurgery. However, in most people amnesia arises as a result of stroke, head injury, or viral infection (notably herpes simplex encephalitis). Amnesia is also the cardinal feature of Alzheimer's dementia, although this tends to be studied separately from the other causes of amnesia.

Preserved and impaired memory in amnesia

Within the framework of different types of memory outlined previously, which type of memory appears to be disturbed in amnesia? Is it indeed possible to impair one particular aspect of long-term memory without there being consequences to the other systems? This section considers four different types of memory in turn.

Episodic memory

Amnesic patients are impaired on tests of episodic memory both for events related to their own lives (autobiographical memory) and other types of episode (e.g., learning lists of words). Learning of new material is normally assessed on test batteries such as the Wechsler Memory Scale (Wechsler, 1984). This contains tests of recall and recognition for verbal and visual material. Amnesia is clinically defined as poor performance on memory tests relative to that expected based on their IQ scores. Knowledge of events and facts pertaining to their life prior to the onset of amnesia (i.e., in the retrograde period) can be assessed with tests such as the Autobiographical Memory Interview (Kopelman et al., 1990). The degree of retrograde memory loss can vary significantly between patients (Kapur, 1999). It is debatable whether retrograde memory loss can exist without any anterograde impairment in cases of organic amnesia (Kopelman, 2000), although this pattern is reported in amnesia arising from psychiatric illness and "mental breakdown" (Kritchevsky et al., 2004).

AMNESIA AT THE MOVIES

Amnesia has been a favorite topic in Hollywood since the earliest days of cinema (no fewer than ten silent movies on the topic were made) and continues to inspire filmmakers today (for a thorough review, see Baxendale, 2004). Rich socialites may become caring mothers after falling from a yacht (*Overboard*, 1987), trained assassins may forget their vocation and become stalked themselves (*The Bourne Identity*, 2002; *The Long Kiss Goodnight*, 1996), and others just require a second bump on the head to be restored to their former selves (*Tarzan the Tiger*, 1922).

Clinical amnesia tends to affect both memory for events that happened prior to injury (retrograde memory) and learning of new information (anterograde memory), although relatively selective impairments can be found. In movie amnesia, the extent of retrograde or anterograde amnesia is often very pure. For example, Leonard from the film *Memento* (2000) has total anterograde memory loss but no loss of retrograde memory (he can even remember sustaining the injury). The film vividly captures the fact that he is stuck in the present, relying purely on his retrograde memory and memory aids (notes, photos, tattoos). In one scene, he is trying to hold in mind a clue (in working memory) and searching for a pen to write it down. But as soon as he is distracted and stops rehearsing, the clue disappears from his mind as if it was never there. Whereas the portrayal is generally accurate, his description of it as a "short-term memory problem" is not.

Selective difficulties in retrograde amnesia have been noted in the academic literature, but there is controversy as to whether these have organic or psychogenic origin related to extreme stress (Kopelman, 2000). Fortunately for Hollywood scriptwriters, psychogenic amnesia can arise after committing a violent crime (Schacter, 1986). *The Bourne Identity* (2002) (Figure 11.8) offers one example of focal retrograde amnesia in the movies. It is not clear whether the character's amnesia is organic or psychogenic. According to one reviewer:

> Its protagonist, who's found floating off the coast of Marseilles with two bullets in his back and the number of a Zurich safe-deposit box in some sort of laser body-implant, has no idea who he is. But he has somehow retained lightning martial-arts reflexes, fluency in a handful of languages, and the wired instincts of a superspy.

FIGURE 11.8: There have been five films to date in which Matt Damon stars as the amnesic CIA assassin Jason Bourne. Some aspects of amnesia are portrayed accurately (e.g., his retention of previous languages and skills), whereas others are less so (e.g., confused identity, sudden recovery of lost memories).

AF archive/Alamy Stock Photo

These skills would indeed be expected to be preserved in amnesics.

Many films portraying amnesia show a loss of identity or a change in personality. This is not what is found in amnesia of neurological origin, in which one's sense of identity is preserved (although perhaps frozen in time). For instance, amnesic patients are able to accurately reflect on their own personality traits as corroborated by the ratings of family members (Klein et al., 2002). Personality changes can indeed arise from brain damage but are normally associated with a different pathology from amnesia (namely, orbitofrontal regions) or with psychiatric illness.

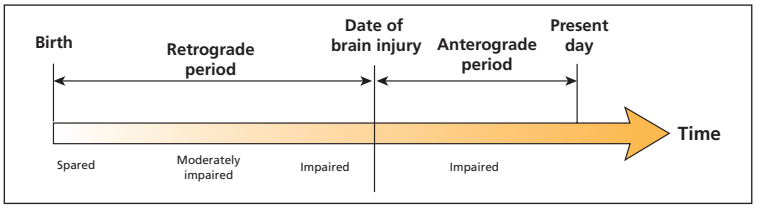


FIGURE 11.9: Amnesia normally consists of a severe impairment in anterograde memory, with a more variable impairment in retrograde memory (shading represents the degree of impairment).

Short-term memory

One of the most consistent findings in the literature is that short-term memory in tasks such as digit span is spared (Baddeley & Warrington, 1970). Milner (1971) noted an occasion in which HM held on to a number for 15 minutes by continuously rehearsing it and using mnemonic strategies. A minute or so after stopping, he had no recollection of being asked to remember a number.

More recently it has been claimed that short-term memory problems are found in amnesia when holding in mind (or even perceiving) one particular kind of information: specifically the 3D layout of large-scale scenes (Hartley et al., 2007). This may point to a particularly important role of the hippocampus in processing spatial environments that may, to some degree, be separable from other memory functions. Others have questioned this assumption by arguing that these kinds of tasks/scenes may rely on support of long-term memory (even when there is no delay) because the information exceeds the capacity of visual STM (Jeneson & Squire, 2012).

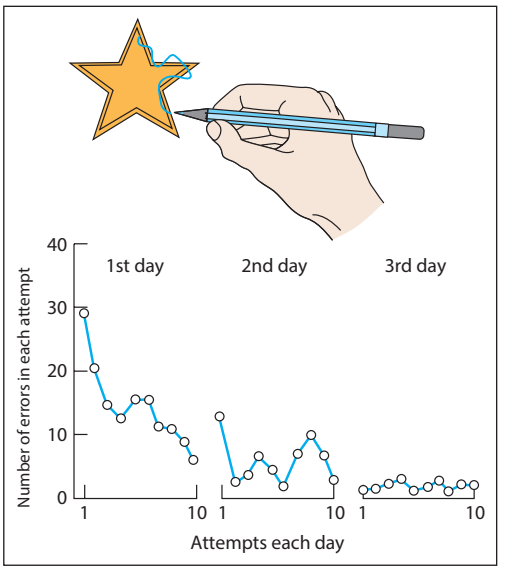


FIGURE 11.10: Patient HM was able to learn mirror drawing over a three-day period, despite no apparent memory for having performed the task before.

From Blakemore (1977). Reproduced with permission of the Licensor through PLSclear.

Procedural and perceptual (implicit) memory

When given new tasks requiring visuo-motor coordination, such as drawing around a shape when the hand is viewed in a mirror, performance is initially poor but improves with practice (Figure 11.10). The same is true

of amnesic patients (Milner, 1966). Thus, procedural knowledge appears to be spared. The same is true of other implicit memory tasks that do not have a strong motor component. Knowlton et al. (1994) devised a weather prediction game in which geometric shapes predict weather patterns with a partial degree of certainty (60–85 percent predictive), as shown in Figure 11.11. Participants often feel that they are guessing although they exhibit learning over 50–100 trials. That is, there is evidence of implicit learning. Amnesic patients also show normal learning despite poor declarative memory for the stimuli, whereas patients with Parkinson's disease show the reverse dissociation consistent with a role of the basal ganglia in the learning of habitual responses (Knowlton et al., 1996).

Graf et al. (1984) tested implicit memory for words. The amnesics were given lists of words to read (e.g., DEFEND) and, at test, were presented with fragments (e.g., DEF___). They were asked either to recall the word previously shown or to generate the first word that came to mind. The latter was considered an implicit test of memory insofar as the participants were not directly asked a memory question. They found that amnesics performed normally under the implicit testing procedure (i.e., they showed priming) but not when given explicit memory instructions. Rather than relying on the hippocampus or medial temporal lobes, these tasks involve brain regions spared in amnesia such as those involved in language (Broca's area) and word recognition in the visual ventral stream (Buckner et al., 2000). Within the framework in Figure 11.7, this would be accounted for within the perceptual representation system for words.

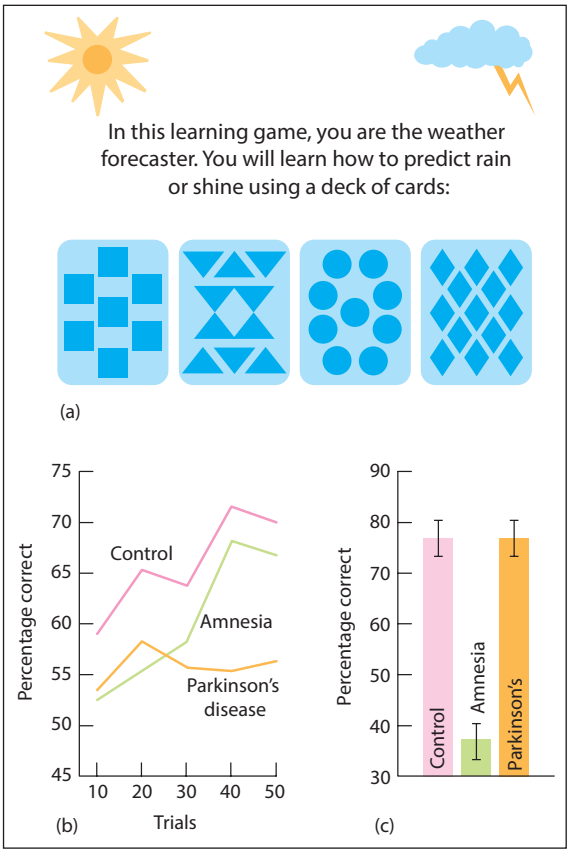


FIGURE 11.11: Four cue cards are presented in varying combinations and the participant must predict rain or shine (a). After repeated exposure, both controls and amnesics learn to predict, but patients with Parkinson's disease do not (b). When given a test of explicit memory about the test, the amnesic patients perform badly, but the Parkinson's patients perform well (c).

Adapted from Knowlton et al. (1996).

Semantic memory

At first sight, amnesic patients appear to retain their knowledge of vocabulary and the world. This was initially taken as evidence that semantic memory is intact in amnesic patients (Parkin, 1982). However, a more complex picture has emerged over the years. One critical issue is the age at which the information was acquired. Most semantic knowledge is acquired within the first few years of life, whereas episodic memory develops later and is acquired throughout the lifespan. Given that amnesia tends to preserve relatively older memories (Ribot, 1882), could the apparent sparing of semantic

knowledge reflect its early acquisition? To address this question, a number of studies have investigated knowledge of vocabulary (Verfaellie et al., 1995) and famous people (Parkin et al., 1990) that came into the public domain in the years prior to the onset of amnesia. These studies show amnesics to be impaired.

The previous discussion pertains to the retention of previously learned semantic facts by amnesics. Can amnesics acquire new vocabulary after they become amnesic (i.e., in the anterograde period)? For patient HM (Gabrieli et al., 1988) and many other amnesics (Manns et al., 2003b), the answer appears to be "no." But this is by no means common to all amnesics. One amnesic is even reported to have learned a second language, Italian, following the onset of her anterograde amnesia (Hirst et al., 1988). Others have acquired information about famous people, public events, and new vocabulary after becoming amnesic (Kitchener et al., 1998). However, there is one important caveat to bear in mind when considering these studies. Namely, it could be the case that both semantic and episodic memory are impaired but that semantic memory is less vulnerable, because it can be learned through repetition and multiple events. There is evidence that new semantic memories may be acquired but perhaps at a slower rate (Holdstock et al., 2002). If tissue surrounding the hippocampus, such as the entorhinal cortex, is spared, then semantic learning may be possible although not necessarily normal (Vargha-Khadem et al., 1997b; Verfaellie et al., 2000).

Accounting for the memory deficits in amnesia

To summarize the preceding sections: amnesic patients have impaired episodic memory, typically in both retrograde and anterograde periods. In contrast, they have generally spared short-term memory, procedural memory and perceptual priming (a type of implicit memory). Tulving and colleagues (1988) regarded amnesia specifically as a difficulty with episodic memory. However, semantic memory is impaired in amnesia including after focal hippocampal lesions, even though it is often less vulnerable to damage than episodic memory (Holdstock et al., 2002; Manns et al., 2003b). New semantic memories may be formed by repetition learning that is not dependent on the hippocampus. As such, Squire and colleagues suggest that amnesia is a deficit in declarative memory (Manns et al., 2003b; Squire, 1992). This explanation offers the most satisfactory description of the pattern of preservation and impairment.

KEY TERM

Consolidation
The process by which moment-to-moment changes in brain activity are translated into permanent structural changes in the brain.

Accounts of amnesia purely in terms of damage to a memory system (whether it be declarative or episodic) are clearly insufficient, in that they offer no account of the function of that system or the underlying mechanisms. One common mechanistic explanation of amnesia is in terms of a deficit of **consolidation** (Squire, 1992). Consolidation is the process by which moment-to-moment changes in brain activity are translated into permanent structural changes in the brain (e.g., by forming new neural connections). One challenge

for explaining amnesia in terms of consolidation is in accounting for the fact that amnesia doesn't just affect new learning, but also retrograde loss of memories. A solution to this is to assume that consolidation takes place gradually such that unconsolidated memories are lost after a lesion to the hippocampus. A related account is that the hippocampus (and medial temporal lobes) is involved in the permanent storage of certain kinds of memory in addition to supporting consolidation. Finally, an alternative suggestion is that the hippocampus (and medial temporal lobes) are specialized for processing particular kinds of information that are of crucial importance to declarative memory. One kind of information might be contextual cues (Mayes, 1988). Memory for context closely relates to Tulving's (1972) definition of episodic memory as being specifiable in time ("when did the event occur?") and place ("where did the event occur?"), although context can incorporate other types of situational information too. A more specific idea along these lines is that the hippocampus is particularly important for spatial processing both for providing spatial context to past events, but also for using past experiences for orienting within one's current environment (Burgess et al., 2002). These ideas are unpacked in detail in the next section, drawing not only on evidence from amnesic patients, but also from other methodologies.

Evaluation

Accounting for the learning and memory that amnesics *can* do is as important as understanding what they can't remember. The results broadly support a multiple memory systems view of the brain in which declarative memory is particularly affected in amnesics. Episodic memories may be special by virtue of the fact that they contain rich contextual detail. These contextual details may be linked together by structures in the medial temporal lobe, including the hippocampus, and may gradually be consolidated over time. Newly learned semantic facts may initially be context dependent but become less so over time. This view of amnesia has been refined over the years as a result of more being learned about the function of different structures in the medial temporal lobe and their interaction with other brain regions. These are considered in subsequent sections.

ONLINE RESOURCES

Watch the Royal Institution lecture on the Neuroscience of Memory by Eleanor Maguire by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

FUNCTIONS OF THE HIPPOCAMPUS AND MEDIAL TEMPORAL LOBES IN MEMORY

This section considers in more detail the role that the hippocampus (and surrounding regions) plays in consolidation, in the permanent storage of memories, and in large-scale spatial memory. The extent to which different theories can account for the empirical data will be discussed. In particular, three theories are contrasted: consolidation theory, multiple-trace theory, and cognitive map theory. The key differences between the accounts are summarized here.

	Consolidation theory	Multiple-trace theory/ Trace transformation theory	Cognitive map theory
Examples	Squire (1992); McClelland et al. (1995)	Nadel and Moscovitch (1997); Winocur et al. (2010)	O'Keefe and Nadel (1978); Moser et al. (2015)
Type of information stored in hippocampus	Episodic and semantic memories (i.e., declarative)	Contextualized memories	Spatial memories
Duration of memory storage	Temporary (years in humans)	Permanent	Permanent
Relationship to cortically based memories	Memories transferred from hippocampus to cortex	Memories in cortex are more schematic (lack context) and more semantic-like	Hippocampus stores scene information whereas cortex stores other kinds of information
Explanation of temporal gradient in amnesia	Old memories are not stored in hippocampus so spared by damage	Old memories have less rich context (more like stories), and so spared by damage	Old memories get recalled more often which creates new traces (Barry & Maguire, 2019)

Consolidation

The initial formation of memories involves an increase in the probability that a postsynaptic neuron will fire in response to neurotransmitters released from presynaptic neurons. In the laboratory, this has been studied by applying brief, high-frequency stimulation to presynaptic neurons. The induced change in responsiveness of the postsynaptic neuron is termed **long-term potentiation** (or LTP) and was first reported by Lømo (1966). In awake rats, the effects are sustained over weeks. This process is accompanied by rapid modification of existing synaptic proteins, followed by synthesis of new proteins that leads to a modified synapse (Pittenger & Kandel, 2003). The time course of this process can be assessed by injecting chemicals that inhibit protein synthesis at various stages after learning and is found to occur within an hour (Agranoff et al., 1966). This **synaptic consolidation**, although originally studied in the hippocampus, turns out to be a universal property of the nervous system.

Dudai (2004) distinguishes between two types of consolidation: a fast synaptic consolidation that may occur anywhere in the nervous system (and based on LTP), and a slower **system consolidation** that may be related particularly to the hippocampus and declarative memory. In rats, this can be studied by lesioning the hippocampus at various stages after learning (Kim & Fanselow, 1992). These studies suggest that, in rats, it takes around one month for system consolidation to be complete. In humans, evidence from retrograde amnesia suggests that the process may take years.

One of the most consistently reported findings in the amnesia literature is that recall of events in the retrograde period shows a temporal gradient such that memories from earlier in life are easier to recall than those later in life. This has been termed **Ribot's law**, after its discoverer (Ribot, 1882). For example, Butters and Cer-

KEY TERMS

Long-term potentiation (LTP)
An increase in the long-term responsiveness of a postsynaptic neuron in response to stimulation of a presynaptic neuron.

Synaptic consolidation
Restructuring of local synapses as a result of changes in pre-synaptic neural activity; generally found throughout the brain and fast acting.

System consolidation
Reorganization of connectivity patterns across disparate regions (e.g., hippocampus and neocortex); slower acting.

Ribot's law
The observation that memories from early in life tend to be preserved in amnesia.

mak (1986) reported the case of a college professor, PZ, who became amnesic a couple of years after writing his autobiography. When tested for his ability to recollect events from his life, a clear temporal gradient was found, with more remote memories spared (Figure 11.12). The most common explanation for this phenomenon is in terms of consolidation theory – namely, that the older the event, the more consolidated it is and the less dependent on the hippocampus it is (Squire, 1992; Squire & Bayey, 2007). In effect, the memory is slowly transferred from the hippocampus to the cortex. However, other explanations for the temporal gradient exist.

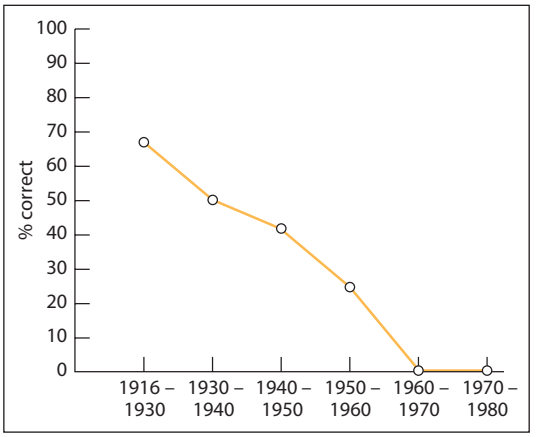


FIGURE 11.12: PZ was an eminent scientist (born 1914) who developed amnesia two years after writing his autobiography. His ability to recall events from his past life showed a clear temporal gradient.

From Butters and Cermak (1986). © Cambridge University Press. Reproduced with permission of the Licensor through PLSclear.

The mechanism by which this transfer of information occurs is not well understood but is assumed to involve the hippocampal formation sending synaptic messages to neocortical neurons that promote consolidation mechanisms in the neocortex itself, as shown in Figure 11.13. It has been suggested that "replaying" memories during sleep (and possibly during relaxed wakefulness) is involved in this process. Neural recordings in rats suggest that patterns of activity in the hippocampus and visual cortex that occurred during a previous waking event are reactivated, in the same temporal order, during certain phases of sleep (Ji & Wilson, 2007).

A number of connectionist models have been developed to mimic long-term consolidation of declarative memory. The model of McClelland et al. (1995) provides a computational motivation for having a slow transfer mechanism. They argue that adding a new memory to the neocortex straightaway would significantly distort old memories by a process called catastrophic interference. In their model, the hippocampus learns rapidly and then integrates this information gradually to enable efficient learning without disrupting existing memory structures. For instance, in order for the model to acquire new conceptual knowledge such as "a penguin is a flightless bird," this

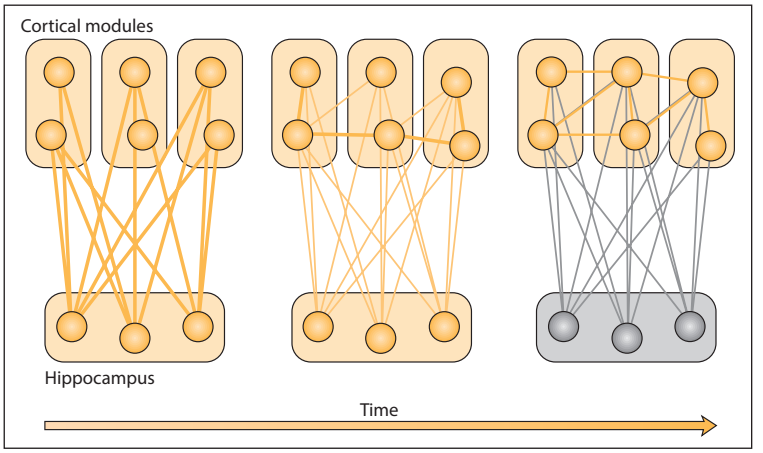


FIGURE 11.13: In models that assume a time-limited role for the hippocampus in memory consolidation, the hippocampus initially acts to bind together different aspects of memory (e.g., perceptual, affective, linguistic components) represented in disparate regions of the brain. Over time, these different aspects of the memory trace may be linked as part of a corticocortical network that is largely independent of the hippocampus. Active units/connections are shown in red.

From Frankland and Bontempi (2005). Reproduced with permission from Springer Nature.

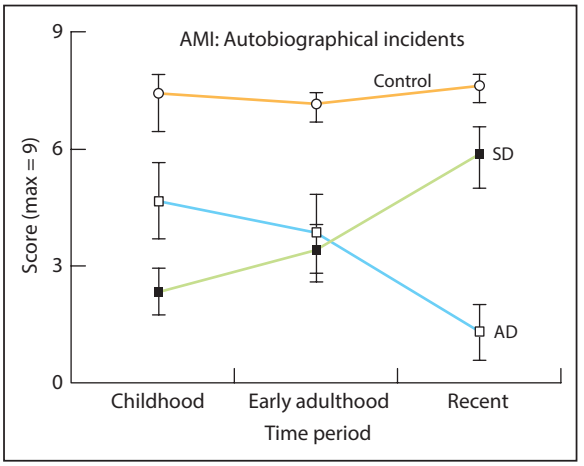


FIGURE 11.14: Semantic dementia patients (SD) show a reverse temporal gradient from that found in amnesics with Alzheimer's disease (AD). This has been used as evidence to support a time-limited role of the hippocampus in memory consolidation.

Reprinted from Nestor et al. (2002). © 2002, with permission from Elsevier.

information would need to be represented separately (as an "episode") in order to prevent it disrupting existing knowledge structures ("birds can fly"). By developing the network gradually, both the general rule and the exceptions to it are able to coexist in long-term memory.

Other evidence in support of the standard consolidation model comes from patients with semantic dementia who have lesions to the anterior temporal lobes but typically spare the hippocampus (Mummery et al., 2000). This is assumed to be part of the storage site after memories have been consolidated. However, these patients do not have intact episodic memory across all time spans and show a reversed temporal gradient to that found in amnesia: namely, better recent than remote memory (Nestor et al., 2002), as shown in Figure 11.14. Although these patients have impoverished language as well as memory, they can be tested using the same cue words for different time periods (e.g., "think of a memory related to a restaurant in 2020–2025, or 1970–1980") or using famous faces (Hodges & Graham, 1998). The explanation for the reversed gradient is that in these patients, memories for recent events have not yet been fully transferred from the hippocampus to the neocortex and so are relatively intact. In contrast, in patients with hippocampal damage (including Alzheimer's dementia) it is recent memories that are lost or otherwise not consolidated.

It is to be noted that the standard consolidation model doesn't make a distinction between the consolidation of episodic and semantic memories: both are grouped under the umbrella of declarative memory and are assumed to depend initially on the hippocampus and subsequently on the neocortex. However, other structures within the medial temporal lobe may have different roles to play. It has been suggested that the entorhinal cortex supports the acquisition of semantic memory, as is demonstrated in amnesic patients with damage to the hippocampus but relative sparing of this region (Vargha-Khadem et al., 1994; Verfaellie et al., 2000). The entorhinal cortex is the major input and output portal between the hippocampus and the neocortex (see Figure 11.15). Healthy older participants shown faces acquired from different time periods during fMRI suggest that the entorhinal cortex may consolidate over decades, whereas the hippocampus consolidates over years (Haist et al., 2001). Other research has suggested that the extent of retrograde amnesia is linked to the size of the entorhinal and parahippocampal lesion, but not of the hippocampus itself (Yoneda et al., 1994). Findings such as these suggest that the standard consolidation theory needs to be further refined. However, others have gone further than a simple refinement and suggested that entirely different theories of hippocampal/MTL function are needed.

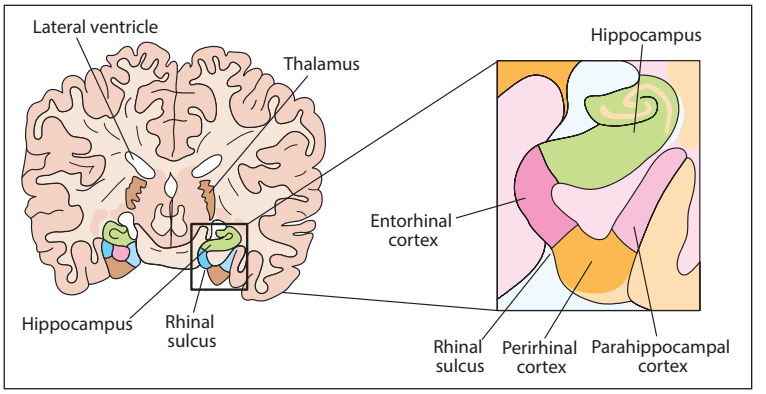


FIGURE 11.15: The different regions of the medial temporal lobe.

Multiple-trace theory/trace transformation theory

In contrast to the standard model of consolidation, others have argued that the hippocampus is involved in some permanent aspects of memory storage (Nadel & Moscovitch, 1997). The term "permanent" doesn't mean that nothing is ever forgotten. What it means, instead, is that if an event is remembered with contextually rich detail, then it is always relying on the hippocampus. In the earlier version of the multiple-trace theory, Nadel and Moscovitch (1997) argued that the temporal gradients found within amnesia were due to multiple memory traces of the event being created whenever an event is retrieved (and laid down in different parts of the medial temporal lobes), so older events are protected from brain damage because of these multiple traces. They cite as evidence in support of their theory the fact that not all amnesic patients show temporal gradients and are impaired, instead, for all remote memories (Cipolotti et al., 2001). They suggest that this is more consistent with the hippocampus playing a permanent role in memory storage, as they regard it as improbable that the brain would evolve a mechanism that takes a lifetime to consolidate memories. Other initial evidence in support of their theory came from fMRI studies showing no difference in medial temporal lobe activity comparing recall of autobiographical events from the recent past relative to the remote past as would be expected if it had a time-limited role (Gilboa et al., 2004). Research using fMRI has been able to differentiate sub-fields within the hippocampus and suggests that some regions respond to both recent (2 weeks) and remote (10 years) recall of autobiographical memories, and other regions respond to remote but not recent memories, but regions responding more to recent than remote were not found (Bonnici et al., 2013). The latter would have been predicted by standard consolidation theory.

The multiple-trace theory has been revised and refined considerably since it was originally described (see Winocur et al., 2010) and perhaps could be more accurately described as trace transformation theory (Dudai et al., 2015). In particular, the proponents of the model have articulated a clearer description of what kinds of memories are

dependent on the hippocampus: namely, contextualized memories but not schematic memories. These relate, approximately, to the concepts of episodic memory (= contextualized) and semantic memory (= schematic), although not exactly. For instance, some recently acquired semantic knowledge may be linked to the context in which it was learned (e.g., memory of the classroom setting) and hence depend on the hippocampus. By contrast, some episodic events may have been retold so many times as to be schematic in nature and largely disconnected from their original context (and hence not depend on the hippocampus). The model assumes that schematic memories depend on regions such as the neocortex (supporting most semantic memories) but could also include procedural learning (dependent on the basal ganglia) and so on. Different medial temporal lobe regions may also make differential contributions to these processes. One fMRI study concluded that the entorhinal cortex computes the similarities between events (schematic, semantic-like), whereas certain regions in the hippocampus compute the discriminating features of events (contextual, episodic-like) (Bakker et al., 2008).

In this theory, the process of system consolidation should be construed as *transforming* memories over time (from contextualized to schematic; although the initial contextual memories need not be lost) and not *transferring* them, unchanged, from one brain region to another. Insofar as the hippocampus has any bias toward the recent past, this is assumed to reflect the fact that recent memories contain more detailed contextual cues than remote ones (e.g., try to recall your last holiday and then compare it to a memory of a holiday when you were around 6 years old). In fact, the hippocampus has been shown to be involved in imagining *future* events (Addis et al., 2007; Hassabis et al., 2007). This is consistent with a more general role in binding contextual features rather than simply making past events durable (i.e., consolidation). There is some direct evidence that hippocampus-dependent memories may be transformed rather than merely transferred. In rats, conditioned fear associations to stimuli show a temporal gradient depending on the interval between learning and hippocampal lesion. However, the conditioned associations become less sensitive to context manipulations over time, suggesting that the nature of the memories are transformed rather than simply transferred (Winocur et al., 2007). A complete definition as to what kind of information constitutes "context" is presently lacking. However, one key element is generally considered to be spatial context (i.e., where the event occurred). This is based on evidence, considered next, that the hippocampus stores large-scale maps of space.

Cognitive map theory

In the 1970s, a number of lines of evidence led to the hypothesis that the hippocampus contains a spatial map of the environment (O'Keefe & Nadel, 1978). O'Keefe (1976) planted electrodes into the hippocampus of rats that subsequently explored an enclosed environment. The firing rate of the neuron was measured when the rat was located at various points in the box. It was found that a given neuron only responded

strongly when the rat was at a particular location. Neurons showing this pattern of firing are referred to as **place cells**, as illustrated in Figure 11.16. Given that each neuron responds to a given place, when a collection of neurons are considered together, they could function as a map of the environment. Subsequent research has found that place cells are more complex than originally thought. The responses of place cells are often highly context sensitive. For example, if the environment is substantially changed (e.g., the box is white instead of black), then the place that the neuron codes can also change substantially (Anderson & Jeffery, 2003). It suggests that place cells are not coding space in isolation but integrate space with other kinds of contextual cues – this is likely to be crucial for memory more generally.

KEY TERM

Place cells
Neurons that respond when an animal is in a particular location in allocentric space (normally found in the hippocampus).

It is to be noted that the kind of map (and hence the kind of spatial memory) encoded by the hippocampus is different in kind to that typically studied in tests of visuo-spatial short-term memory (e.g., arrays of colored objects on a screen). Specifically, it relates to the spatial arrangement of landmarks in an environment that can be navigated around (allocentric space). Other brain regions, notably, the parietal lobes, may code maps of space that are egocentric (i.e., coded relative to the observer) that serve largely perceptual and motor functions.

Further evidence that the hippocampus stores a spatial map of the environment comes from lesion studies of rats using the Morris water maze (Morris et al., 1982), shown in Figure 11.17. If a rat is placed in a container filled with milky water in which there is a submerged platform, then the rat will, by trial and error, eventually find the platform (rats are good swimmers!). As the water is milky, the platform is not visible, and the rat must learn the route. If the rat is placed in the environment again, it will remember the location and swim there directly without trial-and-error meandering. If, however, the hippocampus is lesioned, then the rat is unable to learn the location of the platform and relies once more on trial and error.

Most of the evidence cited previously comes from studies of rats. But what is the evidence, if any, that the human hippocampus contains a spatial map? Single-cell recordings in the primate (Rolls et al., 1997) and human (Ekstrom et al., 2003) hippocampus suggest that place cells are to be found in these species. Functional imaging and lesion studies in humans have provided converging evidence that the hippocampus stores large-scale allocentric maps of the environment. In humans,

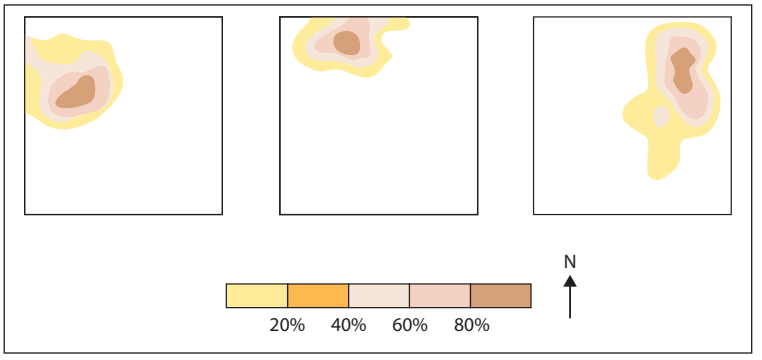


FIGURE 11.16: The firing rate of three different place cells (the darker the shade, the more likely it is to respond). The data are obtained using single-cell recordings from the rat hippocampus.

Adapted from Chakraborty et al. (2004).

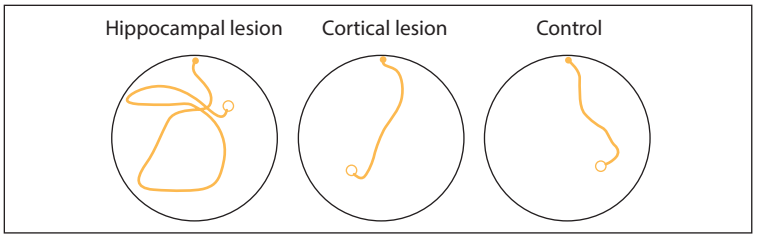


FIGURE 11.17: The route taken by a typical rat in the Morris water maze. The control rat and ones with cortical lesions can remember the location of the submerged platform and go directly there, whereas the hippocampal-lesioned rats find the platform by trial and error.

From Morris et al. (1982). Reproduced with permission from Springer Nature.

there also appears to be a greater lateralization of this function than in rodents. The right hippocampus seems to be particularly important for spatial memory, whereas the left hippocampus appears to be more specialized for remembering and storing other contextual details. Hartley et al. (2003) found that finding one's way through the virtual town activated the right hippocampus relative to a baseline task of following a visible trail. Spiers et al. (2001a) used a similar paradigm in groups of patients with either left or right hippocampal damage. The patients had to learn to navigate through the town. During their exploration they would collect different objects from different characters in different locations. Their memory was assessed by map drawing, together with forced-choice recognition of locations, characters, and objects. The patients with right hippocampal damage were impaired on navigation, map drawing, and scene recognition. In contrast, the patients with left hippocampal damage had problems in remembering who gave them the objects and the order and location in which they were received.

Is the involvement of the hippocampus in spatial memory time-limited (as predicted by the standard consolidation model) or does the hippocampus store permanent spatial maps (as predicted by the cognitive map theory and multiple-trace theory)? There is some evidence that amnesic patients can find their way around old neighborhoods despite being unable to learn to find their way in new ones (Rosenbaum et al., 2000). This supports the standard consolidation model. However, others have suggested that this preserved spatial memory appears to be schematic and lacking detail, and so there may still be a role for the hippocampus (Winocur et al., 2010). Consistent with this, a London taxi driver who suffered bilateral damage of the hippocampi retained a broad knowledge of the city (the main roads) but not detailed knowledge including the side roads (Maguire et al., 2006).

There is evidence that other regions within the medial temporal lobes also contribute to orienting within spatial environments. The entorhinal cortex (at least in rats) also contains cells that fire when the animal is in certain locations within a particular environment, but rather than responding to a single location, they respond to multiple locations within a repeating, triangular grid-like structure (Hafting et al., 2005). They are referred to as **grid cells**. Their function is not fully known, but they may

KEY TERM

Grid cells
Neurons that respond when an animal is in particular locations in an environment such that the responsive locations form a repeating grid-like pattern.

enable links between visuo-spatial and locomotive spatial signals. The parahippocampal complex, by contrast, contains visual representations of scenes and landmarks (Epstein & Kanwisher, 1998). Finally, the perirhinal cortex is linked to memory and perception of complex objects (Murray & Bussey, 1999) and is also linked to semantic memory (Davies et al., 2004). Bachevalier and Nemanic (2008) report a lesion study in the macaque showing that parahippocampal lesions impair memory for the locations of objects in an array, whereas perirhinal lesions impaired learning about object features.

Although this summary presents the briefest discussion of the wider contribution of MTL regions outside the hippocampus, there are several key points to note. The first is that while the function of all of these regions could reasonably be subsumed within the umbrella label of "declarative memory," to do so would be an oversimplification. These regions show an interesting specificity in the type of information that they process. What is less clear is whether these regions are involved in both learning and storage and how they interact with other regions of the brain.

ONLINE RESOURCES

To discover more about memory, space, and the hippocampus, see Neil Burgess' TEDx talk by scanning the QR code or visit routledgelearning.com/wardcognitive neuroscience.

DOES DRIVING A TAXI INCREASE YOUR GRAY MATTER?

London taxi drivers are required to sit an exam (called "The Knowledge") in which they are given two locations within the city and must generate a plausible route (Figure 11.18). Maguire et al. (2000) studied the gray matter volume of taxi drivers (using voxel-based morphometry) and found that the volume in the right hippocampus is greater than in IQ-matched individuals. Could it be that the taxi drivers choose their occupation because they have better spatial memories (and bigger hippocampi)? It turns out that the amount of time spent in the job correlates with the volume of the region. This suggests that this region may expand with usage and argues against a predisposition influencing the choice of occupation. This has subsequently been confirmed with a longitudinal study of the brain volume of the hippocampi of London taxi drivers as they acquire detailed knowledge of the city layout (Woollett & Maguire, 2011).

FIGURE 11.18: London taxi drivers must learn the best route to travel between any two points in the city. This is linked to an increased size of the hippocampus.

southerlycourse/iStock

Evaluation

Initial research on amnesia arising from medial temporal lobe lesions suggested a wide-ranging impairment in declarative memory. While later research has not completely over-turned this conclusion, it has suggested a far more intricate picture. This new understanding has arrived through a more detailed consideration of anatomical structures other than the hippocampus, and through carefully controlled studies of the function of the hippocampus. One function of the hippocampus that is universally accepted is its role in system consolidation. What is less clear is how this process should be conceptualized (e.g., transferring memories, transforming memories). Another key line of controversy is whether the hippocampus permanently stores certain kinds of information (e.g., that are required for detailed episodic remembering) and/or is specialized for processing certain kinds of information (e.g., spatial maps) that are crucial for some kinds of memory more than others (reliving memories as scenes from the past).

KEY TERMS

Recognition memory
A memory test in which participants must decide whether a stimulus was shown on a particular occasion.

Recall
Participants must produce previously seen stimuli without a full prompt being given (compare recognition memory).

THEORIES OF REMEMBERING, KNOWING, AND FORGETTING

Recall versus recognition and familiarity versus recollection

This chapter has, thus far, concentrated on different types of memory *systems*. But to what extent do different types of memory *tasks* use different memory systems? Within the domain of explicit tests of memory (i.e., in which participants are directly asked to remember), the main tasks used are tests of **recognition memory** and tests of **recall**. In typical tests of recall, participants may be shown a list of words and asked to recall them in any order (free recall), in the order given (serial recall) or given a prompt (cued recall, e.g., "one of the words begins with W"). In typical tests of recognition memory, participants may be shown a list of words and then, at test, asked to decide whether a given word was previously presented on that list (single probe recognition) or shown two words and asked to decide which one was previously presented in the list (forced-choice recognition). In these memory paradigms, each item in the list constitutes a mini memory "episode." Some typical results are shown in Figure 11.19.

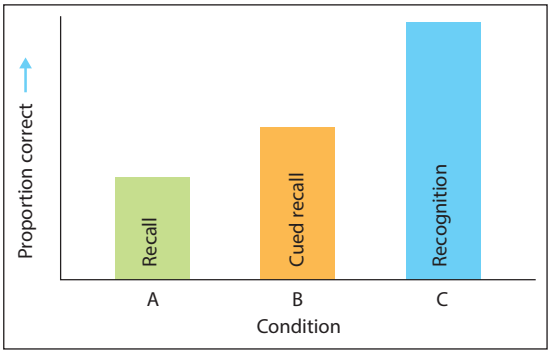


FIGURE 11.19: Typical results from different types of memory test. The relative advantage of recognition tests over recall tests may be attributable to the fact that recognition tests can be based on different sources of information (termed recollection and familiarity).

From Parkin (1999). Reproduced by permission of Taylor & Francis Group.

Mandler (1980) proposed that recognition memory consists of two distinct mechanisms and that this could account for its general advantage over tests of recall. One

mechanism, **familiarity**, is considered to be context-free, and the recognized item just feels familiar. The other mechanism, **recollection**, is context dependent and involves remembering specific information from the study episode. Tests of recall are considered almost exclusively to be dependent on recollection. Recollection and familiarity are associated with different "feelings" or conscious states. These have been called "remembering" and "knowing," respectively (Gardiner, 2000; Tulving, 1985). Recollection, in particular, has been described as "mental time travel," in which contextual detail is placed in a personal past (Wheeler et al., 1997).

KEY TERMS

Familiarity
Context-free memory in which the recognized item just feels familiar.

Recollection
Context-dependent memory that involves remembering specific information from the study episode.

In contrast to the position that familiarity and recollection are different processes, some have argued that they are just stronger and weaker forms of the same process (Wixted & Stretch, 2004) or that the processes involved in familiarity are a subset of those involved in recollection. For example, recollection may require the additional use of frontal mechanisms (Manns et al., 2003a; Squire et al., 2004). There is some problematic evidence for these accounts. Ranganath et al. (2004) conducted an fMRI study that shows hippocampal activity in recollection, whereas familiarity selectively activated an adjacent region of cortex, called the perirhinal cortex. A single-case study of a human patient with a perirhinal lesion but spared hippocampus demonstrated impaired familiarity but spared recollection (Bowles et al., 2007). This supports the idea that familiarity and recollection have partly separable neural processes.

Eichenbaum et al. (2007) offer an account of how recollection and familiarity depend on different regions within the medial temporal lobes and relate it specifically to the kinds of information that these regions are specialized for processing. Specifically, the perirhinal cortex is assumed to process item representations (important for familiarity), the parahippocampal cortex is assumed to process context (including scene perception) and the hippocampus binds items in context (important for recollection). This is shown in Figure 11.20. Certain forms of memory associations (e.g., item-to-item associations, such as word pairs) may also be supported by the perirhinal cortex and may be familiarity-based (Mayes et al., 2007).

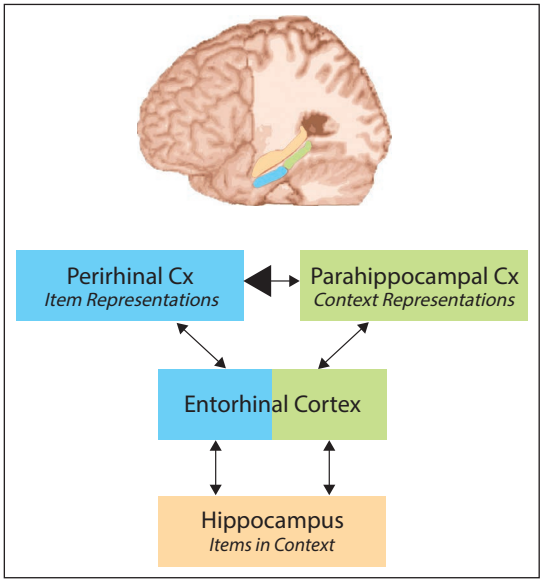


FIGURE 11.20: In Eichenbaum et al.'s (2007) model, the perirhinal cortex is assumed to process item representations (important for familiarity), the parahippocampal cortex is assumed to process context (including scene perception), and the hippocampus binds items in context (important for recollection).

Why do we forget things?

Forgetting may be important for efficient use of memory, rather than a design fault. Access to previous information needs to be prioritized so that the most relevant

information is retrieved. One needs to remember where, for example, the car is parked today, not where it was parked last week. It may be adaptive to lose information for some episodes, or to blend information from different episodes together (e.g., to be able to remember where one *tends* to park the car). Explanations of why we forget have tended to be divided into the stages of encoding, storage, or retrieval (for a more unitary account of forgetting, see Wixted, 2004). Each of these may be relevant to some degree.

If information is not processed adequately at encoding, it may be forgotten. The **levels-of-processing account** of memory states that information that is processed semantically is more likely to be remembered than information that is processed perceptually (Craik & Lockhart, 1972). For example, if participants are asked to generate an adjective for a list of words (e.g., house → big) relative to generating a rhyme (house → mouse) or counting letters (house → 5), they are much more able to later recall those words (Eysenck, 1974). Regions in the frontal lobes may be important for selecting the attributes to attend to at encoding (Kapur et al., 1994). Some studies have examined forgetting due to encoding. Wagner et al. (1998b) scanned participants when they were studying a list of words that were subsequently tested in a recognition memory test. Following the test, they then went back and looked at the brain activity during encoding to ask the question: does the brain activity at encoding predict which items are later going to be recognized and which will be forgotten? Activity in a left temporal (parahippocampal) and a left ventrolateral prefrontal site at encoding was predictive of later recognizing versus forgetting (Figure 11.21). The frontal activity may relate to selection of features to encode, whereas the medial temporal activity reflects actual memory formation. An amnesic patient has been shown to demonstrate normal frontal lobe activity at encoding despite having no subsequent memory (see Buckner et al., 1999). Electrode recordings in humans have shown that synchronous firing of neurons in hippocampal and surrounding cortical regions predicts subsequent memory versus forgetting (Fell et al., 2001).

KEY TERM

Levels-of-processing account
Information that is processed semantically is more likely to be remembered than information that is processed perceptually.

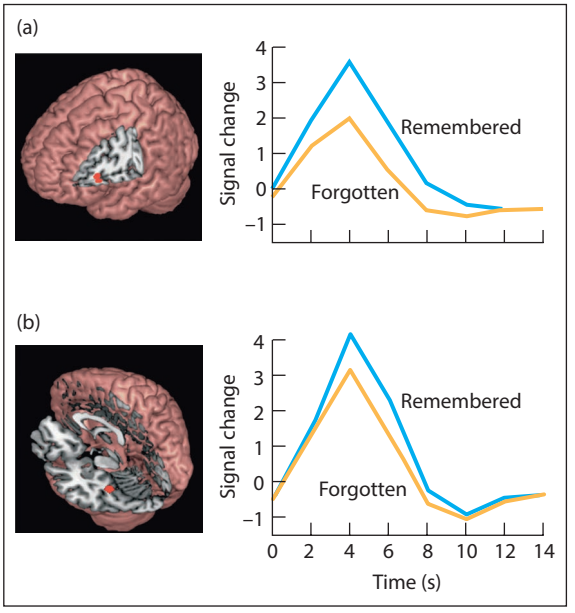


FIGURE 11.21: Activity at encoding in (a) left ventrolateral prefrontal cortex and (b) left parahippocampal region predicts whether the word is likely to be subsequently remembered or forgotten.
Data from Wagner et al. (1998b)

Distinguishing between forgetting due to loss from storage versus a failure of retrieval is very hard in practice. This is because information that appears inaccessible may subsequently be remembered (implying it was never really lost), or information may appear accessible when certain tests are

used (e.g., implicit tests) but not others. If one accepts a multiple memory systems view, then it is conceivable that memories can be lost from one store but not from other stores.

Tulving (1983) has argued that the extent to which there is contextual similarity between the retrieval attempt and the initial encoding phase predicts the likelihood of remembering versus forgetting. This has been termed the **encoding specificity hypothesis**. Godden and Baddeley (1975) taught people lists of words either on land or underwater (when diving) and tested their recall either on land or underwater. Recall was better when learning and test were in the same location (land–land, sea–sea) relative to when they differed (land–sea, sea–land), as shown in Figure 11.22. Similarly, alcoholics may hide objects when drunk, forget where they are when sober, but remember the location again on a subsequent binge (Goodwin et al., 1969). In these experiments, forgetting reflects retrieval difficulties rather than storage difficulties.

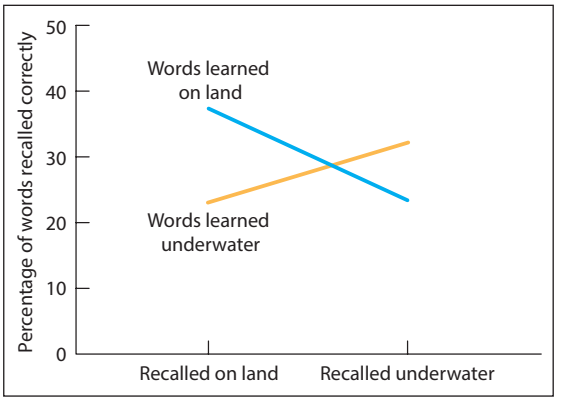


FIGURE 11.22: Words are better remembered if they are both learned and recalled in the same context.

From Baddeley (1990). Reproduced by permission of Taylor & Francis Group.

What type of mechanism gives way to forgetting things that have already been encoded? Two broad explanations exist: passive mechanisms such as trace decay (memories spontaneously weaken), or active mechanisms such as interference and inhibition (memories weaken through interactions with each other or with strategic control processes). Although trace decay is hard to rule out altogether, there is good evidence for more active forgetting mechanisms. Anderson et al. (1994) devised a memory paradigm consisting of three phases. In the first phase, participants study lists of words associated with several different category labels (e.g., fruit–orange, fruit–banana). In the second phase, they rehearse some of the associations (e.g., fruit–orange) but not others (e.g., fruit–banana). In the test phase they are given the category labels (e.g., fruit–) and asked to generate the initial studied words. Performance on unstudied exemplars (e.g., banana) was worse than for studied items in the second phase and, crucially, was worse than that expected if the second phase had been omitted altogether. Anderson et al. (1994) argue that the act of retrieval causes active inhibition of similar competing memories. This has been termed **retrieval-induced forgetting**. To return to the car analogy, remembering where one parked the car today may actively inhibit memories for where it was parked on other days.

The previous section suggested that in some situations memories can *automatically* be inhibited, leading to forgetting, but can memories be inhibited *voluntarily*? Can we choose to forget? Experiments using the **directed forgetting** paradigm suggest that it is possible. In directed forgetting experiments, participants are

KEY TERMS

Encoding specificity hypothesis
Events are easier to remember when the context at retrieval is similar to the context at encoding.

Retrieval-induced forgetting
Retrieval of a memory causes active inhibition of similar competing memories.

Directed forgetting
Forgetting arising because of a deliberate intention to forget.

read two lists of words. In the experimental condition, after the first list they are told that this was a practice block and the list can be forgotten. In the control condition, they are told that the first list needs to be remembered. After both lists have been presented they are instructed to recall from both lists even though they had previously been instructed to forget them. Recall is generally worse for the words given forget instructions (Bjork, 1998). Conway and Fthenaki (2003) found that lesions to the right frontal lobe disrupted the ability to do directed forgetting but retrieval-induced forgetting remained intact. This demonstrates a dissociation between voluntary or strategic forgetting, on the one hand, and automatic or rehearsal-based forgetting, on the other. Anderson et al. (2004) conducted an fMRI study in which pairs of words (e.g., jaw–gum, steam–train) were learned and then, at test, cue words (e.g., jaw–, steam–) were presented, and participants were instructed either to remember the associate or suppress (i.e., forget) it. Forgetting instructions relative to remembering instructions were linked to activity in the left and right dorsolateral prefrontal cortex. Remembering relative to forgetting instructions was linked to activity in the hippocampus. Given that these frontal and hippocampal regions do not connect together directly, Anderson et al. (2016) discuss possible mechanisms by which they interact. For instance, the anterior cingulate cortex (which connects strongly to the lateral prefrontal cortex) may activate inhibitory neurons in the entorhinal cortex which restricts the flow of information to and from the hippocampus.

Memory distortions and false memories

One pervasive metaphor for memory is in terms of a store of memory traces, and the act of remembering involves the retrieval of traces from the store (see Roediger, 1980). This metaphor is misleading: the past is not, by and large, represented in different brain structures from those concerned with dealing with the present. The alternative view is that the act of remembering can be construed as making inferences about the past based on what is currently known and accessible. This contrasting approach to the storehouse metaphor is termed the **constructive memory** approach (Schacter et al., 1998). Studies based on the constructive memory approach have tended to rely on evidence of memory distortions, or false memories, rather than forgetting. A **false memory** is a memory that is either partly or wholly inaccurate but is accepted as a real memory by the person doing the remembering.

Roediger and McDermott (1995) developed a paradigm that could induce high levels of false recall and false recognition in nonclinical populations. At study, participants are read lists of words (e.g., bed, night, tired) that are semantically related to a critical word that is never presented (e.g., sleep). At test, participants claim to remember many of the critical words. They do so with high confidence and will attribute recollective experience

KEY TERMS

Constructive memory
The act of remembering construed in terms of making inferences about the past, based on what is currently known and accessible.

False memory
A memory that is either partly or wholly inaccurate but is accepted as a real memory by the person doing the remembering.

to the false recognition (not just familiarity). If some of the lists are presented in male and female voices, they will state that the critical word "sleep" was heard in a particular voice, even if the instructions encourage them not to guess (Payne et al., 1996).

How can these results be explained? One explanation is that the critical word is implicitly activated at encoding through a semantic network (Underwood, 1965). However, it is not clear why this would result in a feeling of remembering as opposed to familiarity. Another explanation is that participants consciously think about the critical word ("sleep") at encoding and subsequently confuse thinking for hearing. One problem for this theory is that false recognition can be induced using abstract shapes presented at study that are based on a non-presented prototype (Koutstaal et al., 1999). It is unlikely that participants would consciously generate other abstract shapes at study. A more satisfactory explanation is that false recognition/recall occurs because the features of the non-presented item reactivate the stored features relating to true events (Schacter & Slotnick, 2004). Evidence for this comes from the observation of hippocampal activity in both true and false recognition observed by fMRI (Cabeza et al., 2001). In some situations, amnesic patients with hippocampal lesions may be less susceptible to false memories (because they are unable to store the information that gives rise to the distortion), giving them paradoxically better memory than controls (Mullally et al., 2012).

ONLINE RESOURCES

Watch the TEDx talk by Steve Ramirez and Xu Liu on implanting a false memory in the hippocampus of a mouse using laser beams by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

Try reading aloud these lists of words to a friend and then ask them to recall as many of them as possible. Do they misremember hearing the words "sleep," "foot," and "bread"? (Lists taken from Roediger & McDermott, 1995.)

bed	shoe	butter
rest	hand	food
awake	toe	eat
tired	kick	sandwich
dream	sandals	rye
wake	soccer	jam
snooze	yard	milk
blanket	walk	flour
doze	ankle	jelly
slumber	arm	dough
snore	boot	crust
nap	inch	slice
peace	sock	wine
yawn	smell	loaf
drowsy	mouth	toast

FREE INSTRUCTOR & STUDENT RESOURCES

ONLINE RESOURCES

To watch a talk by Elizabeth Loftus visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience) and discover whether you are susceptible to false memories via our demo test (www.testable.org/ward).

ONLINE RESOURCES

Watch Mark D'Esposito, MD, "A Tale About the Frontal Lobe as Told by a Neurologist" by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

There are some brain differences between true and false recognition. If words are initially presented on either the left or right side, then a contralateral ERP component is subsequently observed for true but not false memories (Fabiani et al., 2000). Moreover, in an fMRI study involving abstract shapes, activity in early visual regions was found for true but not false memories (Slotnick & Schacter, 2004). Why don't participants use this sensory signal to avoid false recognition? It is possible that the difference between true and false memories lies within implicit memory systems and makes little contribution to the conscious memory evaluation.

THE ROLE OF THE PREFRONTAL CORTEX IN LONG-TERM MEMORY

Fletcher and Henson (2001) offer a simple and effective way of characterizing the role of the prefrontal cortex in long-term memory: namely "working with memory." This is obviously a play on words with its parallel function in the short-term memory domain, that is, working memory. Working memory and working with memory should not be thought of as separate brain mechanisms: both require maintaining and manipulating information that is currently accessible but differ only in whether that information is attributed to past or present events. Fletcher and Henson (2001) make a distinction between ventral, dorsal, and anterior regions of the prefrontal cortex, as shown in Figure 11.23. The role of these regions in different aspects of memory is considered in the later sections.

Memory encoding

The ventrolateral PFC has been linked to long-term memory encoding which, in broader cognitive terms, may be a by-product of its role in selecting and maintaining information within working memory (the left ventrolateral region being synonymous with Broca's area). As already noted, activity in this region predicts subsequent remembering relative to forgetting (Wagner et al., 1998b) and is linked to levels-of-processing manipulations (Kapur et al., 1994). The left hemisphere may be important during verbal encoding, and the right hemisphere may be important when pictures or faces are presented (Wagner et al., 1998a), as illustrated in Figure 11.24.

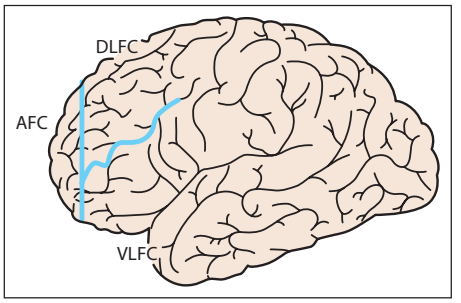


FIGURE 11.23: A number of researchers have made a distinction between the separate functions of the ventrolateral (VL), dorsolateral (DL), and anterior frontal (AF) cortex of the lateral frontal lobe.

From Fletcher and Henson (2001). Reproduced with permission of Oxford University Press.

The dorsolateral PFC is implicated in manipulating (e.g., ordering) information in working memory (Petrides, 2005). In memory encoding this region (along with the ventrolateral PFC)

is activated more when presented with structured (e.g., 2468) versus unstructured (e.g., 3972) digit strings (Bor et al., 2004). During encoding of words, dorsolateral prefrontal cortex (DLPFC) activation was predictive of subsequent semantic clustering during free recall (e.g., recalling names of fruit together; Long et al., 2010). Similarly, when participants were asked to reorder a set of words at encoding (versus passively rehearse) activity in the dorsolateral PFC predicted subsequent long-term memory for those reordered items, but ventral regions predicted long-term memory on both reordered and rehearsed trials (Blumenfeld & Ranganath, 2006).

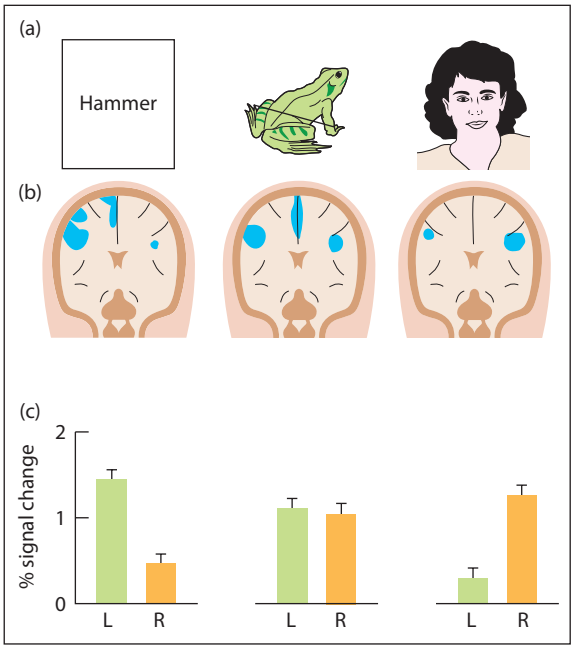


FIGURE 11.24: Attending to verbal and non-verbal stimuli at memory encoding has different consequences for left and right prefrontal activity.

Reprinted from Kelley et al. (1998). © 1998 with permission from Elsevier.

Monitoring and memory retrieval

In addition to its role in encoding, Fletcher and Henson (2001) suggest that the dorsolateral PFC (particularly in the right hemisphere) is involved in evaluating what has been retrieved from long-term memory–so-called monitoring. This also relates to the concept of source memory and recollective experience discussed in more detail later.

Retrieval demands can vary, depending on the type of retrieval cue provided (e.g., free recall, cued retrieval or recognition) and/or the amount of information that needs to be retrieved (e.g., the amount of contextual information). Activity in the dorsolateral region, particularly on the right, is greatest when the retrieval cue is minimal (e.g., free recall; Fletcher et al., 1998), is greatest when context must be recollected compared with simple recognition (Henson et al., 1999b), and is greatest when confidence in memory judgments are low irrespective of whether the stimulus was indeed old or new (Henson et al., 2000). Maril et al. (2001) found that activity was greatest in the right DLPFC when participants were in a tip-of-the-tongue state (induced by cues such as Chinatown + director, Iraq + capital), relative to when they were certain that they did not know the answer, or when the solution was accessible to them. This also suggests that activity in the region is related to uncertainty (in the tip-of-the-tongue state) rather than retrieval success or failure.

Experiential states

As noted previously, recognition memory is associated with different kinds of experiential states termed familiarity and recollection. These are frequently discussed in terms of the contributions of different

structures within the medial temporal lobes, but prefrontal regions may contribute too. For instance, the prefrontal cortex may be responsible for making decisions based on the information that resides in medial temporal structures (and linking other kinds of information such as schemas, reward outcomes, etc.). Consistent with this, fMRI activity in the hippocampus was found to predict an implicit measure of memory (amount of time looking at old/new items), whereas activity in the prefrontal cortex was linked to conscious recollection judgments (Hannula & Ranganath, 2009). In one recognition memory test using fMRI, participants were asked to judge whether they remember any context detail, or whether they know that they have seen it before but do not recollect context (Henson et al., 1999a). A left anterior frontal region was associated with "remember" responses and explained as retrieval of contextual detail, whereas a right dorsolateral frontal region was associated with "know" responses and explained as greater memory monitoring due to lack of certainty.

Source monitoring

KEY TERM

Source monitoring
The process by which retrieved memories are attributed to their original context.

Source monitoring is the process by which retrieved memories are attributed to their original context; for example, whether the event was seen or imagined, whether the story was told by Tim or Bob, whether the event happened in the morning or evening and so on. This is closely related to the process of recollection that has already been considered. However, Johnson et al. (1993) argue that placing an event in context involves an active evaluation process rather than directly retrieving information that specifies the origin of the memory. Moreover, the evaluation is based on qualitative characteristics of the information retrieved, such as the level of perceptual, temporal, spatial, semantic, and affective information. External events contain richer spatial, temporal, affective, and perceptual detail than mental events (thoughts, imagination), whereas the latter may contain information about cognitive strategies.

To give an example from this literature, Johnson et al. (1988) asked participants to distinguish between memories of heard and imagined words (Figure 11.25). One group of participants heard some words in the experimenter's voice and were asked to imagine another set of words in the experimenter's voice. These participants made more source confusions than another group who heard words in the experimenter's voice and were asked to imagine another set of words in their own voice. Encoding of more perceptually distinct features can aid source monitoring (deciding whether a word was heard or imagined) even if the perceptual features are imagined.

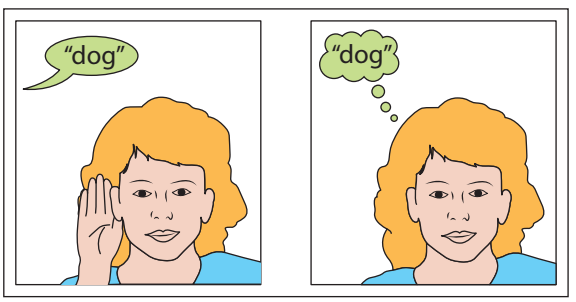


FIGURE 11.25: How can we distinguish between memories for heard words and memories for imagined words? Source monitoring involves an active evaluation of the quality and content of the retrieved information.

Information relating to source may be contained in regions throughout

the brain that processes perceptual, semantic, and affective information. Within the medial temporal lobes, research using fMRI suggests that the hippocampus (and parahippocampal cortex) may be differentially activated by source recognition and the perirhinal cortex by item recognition (Davachi et al., 2003).

Brain lesions to the prefrontal cortex also disrupt source monitoring. These patients have difficulties in putting memories in their spatial and temporal context despite having generally good recognition memory (e.g., Janowsky et al., 1989). Prefrontal lesions may also impair source memory for spatial context even when the patients claim to have subjective "remember" experiences (Duarte et al., 2005). Damage to the parietal lobes, by contrast, does not impair source monitoring, but these patients tend to lack confidence in their memory judgments (Simons et al., 2010) perhaps due to having lower imagery of remembered events.

Memory for temporal context

It may be that different regions within the PFC contribute to source memory in different ways. For instance, one claim is that the orbitofrontal cortex is particularly specialized for temporal context. Remembering when something happened (or which happened more recently) may require a different kind of cognitive mechanism, because memories do not come conveniently time-stamped. Evaluating temporal context may rely on other strategies such as memory strength or associations between temporally adjacent items. Patients with lesions in the orbitofrontal cortex may have problems in temporal source monitoring, but not spatial source monitoring or deficits in standard tests of memory recognition/recall (Duarte et al., 2010). Functional imaging suggests that the region is involved in successful *encoding* of temporal context but not necessarily its retrieval (Duarte et al., 2010).

Lesions in the orbitofrontal region are also associated with a neurological symptom called **confabulation** (Gilboa & Moscovitch, 2002). Confabulating patients generate false memories either spontaneously or when prompted. For example, when one patient was asked about the Falklands war, she spontaneously described a fictitious holiday to the islands (Damasio et al., 1985). She pictured herself strolling with her husband, and buying local trinkets in a store. When asked by the experimenter what language they speak there, she confidently replied, "Falklandese, what else?" One theory is that confabulation is related to temporal context confusion, such that confabulated memories represent blends of information from real memories (including, perhaps, memories for news and film clips) across different time periods (Schnider, 2003; Schnider & Ptak, 1999). Schnider (2003) argues that the deficient mechanism is one of inhibiting irrelevant memories rather than context retrieval per se. Evidence from this comes from a number of studies in which confabulators are compared with non-confabulating amnesics. The task of the patients is to detect whether a word or picture has previously been presented before in the current list (Figure 11.26). If patients producing

KEY TERM

Confabulation
A memory that is false and sometimes self-contradictory without an intention to lie.

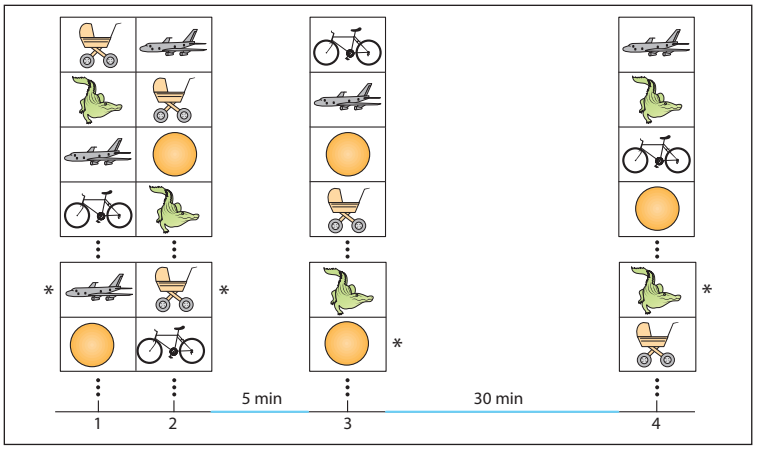


FIGURE 11.26: In the task devised by Schnider, participants must remember whether an item was previously presented in the *current* list (marked by *). However, some items are repeated between lists too (e.g., the crocodile appears on several lists) and confabulating patients have particular difficulties with these items.

From Schnider and Ptak (1999). Reproduced with permission from Springer Nature.

spontaneous confabulations are given a word that was on a previous list but that is new to the current list, then they incorrectly state that it was in fact on the current list. This may be consistent with a wider role of this region in tasks such as extinction learning (i.e., learning that a previously rewarded stimulus should no longer be responded to).

Evaluation

A useful metaphor for the functions of the prefrontal cortex in long-term memory is "working with memory." At encoding, this relates closely to the purported role of these regions in working memory: with ventrolateral regions supporting selection/maintenance and dorsolateral regions supporting manipulation (e.g., ordering to-be-remembered items). At retrieval, the prefrontal cortex may be involved in monitoring and evaluation of the contents of memory including confidence judgments, experiential states, and source monitoring.

SUMMARY AND KEY POINTS OF THE CHAPTER

- Traditionally, short-term memory (STM) has been considered as distinct from long-term memory (LTM), although an alternative view regards STM as the temporary activation of LTM. Working memory involves the manipulation of information held within STM and is linked to dorsolateral regions of the prefrontal cortex.
- Long-term memory can be divided into explicit and implicit memory (or declarative/non-declarative), according to whether the content of memory is amenable to conscious report. Explicit memory consists of knowledge of facts

(semantic memory) and events (episodic memory). Implicit memory consists primarily of skills and habits (procedural memory) and perceptual knowledge.

- Amnesia can arise from damage to medial temporal lobes, including the hippocampus. It results in selective impairment of declarative memory, leaving implicit memory intact. Both semantic and episodic memory is impaired in amnesia, although the extent of semantic memory impairment is variable.
- Amnesia is typically explained as a deficit in system consolidation (i.e., forming of permanent new connections across different brain areas) and produces difficulties in acquiring new declarative memories (anterograde impairment) and retrieving old memories that were not fully consolidated at time of injury (retrograde impairment). It is generally believed that the hippocampus has a time-limited role in consolidation that gives rise to a temporal gradient when damaged (remote memories are spared more than recent memories).
- Recognition memory is generally believed to have two components: recollection (context-dependent) and familiarity (context-independent).
- Although the medial temporal lobes are, collectively, involved in supporting declarative memory, there are important differences between these structures. While the hippocampus is linked to contextual (and particularly spatial) associations, the perirhinal cortex is linked to object memory, the entorhinal cortex to gist memory and the parahippocampal cortex to scene memory.
- Forgetting can occur because items are not processed deeply enough at encoding and/or because they fail to get consolidated. Forgetting can also occur because of retrieval failure. There is evidence that memory retrieval can actively inhibit other memories.
- The lateral frontal lobes have an important role to play in: (a) maintaining information in working memory; (b) selecting information in the environment to focus on (important for encoding); (c) providing cues and strategies to enable memory retrieval; and (d) evaluating the content of memories (as in “source monitoring”).

EXAMPLE ESSAY QUESTIONS

- Contrast the role of the hippocampus in memory with that of other structures in the medial temporal lobes.
- Is short-term memory distinct from long-term memory or just its temporary re-activation?
- What types of memory are typically impaired in amnesia?
- Are semantic and episodic memory separate memory systems?
- Does the hippocampus have a time-limited role in memory consolidation?
- What is the role of the frontal lobes in memory?

ONLINE RESOURCES

Visit the Instructor & Student Resources website at routledgelearning.com/wardcognitiveneuroscience for:

- Video interviews on key topics with leading psychologists, as well as a documentary clip featuring a densely amnesiac patient
- A lecture with author Jamie Ward on The Remembering Brain
- Links to online tests demonstrating implicit memory and testing your own memory capacity
- Multiple-choice questions and interactive flashcards to test your knowledge

CHAPTER 12

The speaking brain

CONTENTS

The ability to produce, perceive, and comprehend speech is a remarkable human achievement. In the most simplistic terms, spoken language is concerned with transferring ideas from one person's head to another person's head with the common physical link being the vibration of molecules in the air (Figure 12.1). It involves the transformation of thoughts into sentences and words and, ultimately, a series of articulatory commands sent to the vocal apparatus. These sound waves then produce mechanical changes on the cochlea (part of the inner ear) of the listener. These are perceived as speech, and the words, sentences, and meaning are inferred from this input. Speech recognition and speech production are often studied separately from each other, and it can be helpful to think about them as separate tasks. However, it is important to recognize that the driving force behind human language is to communicate ideas to the people around us. Outside of the laboratory, speech production normally only exists when someone else is around to engage in the complementary process of speech recognition. This social aspect of language implies that we are able to deduce what other people know, what they believe, and what they do not know.

DOI: 10.4324/9781003429975-12

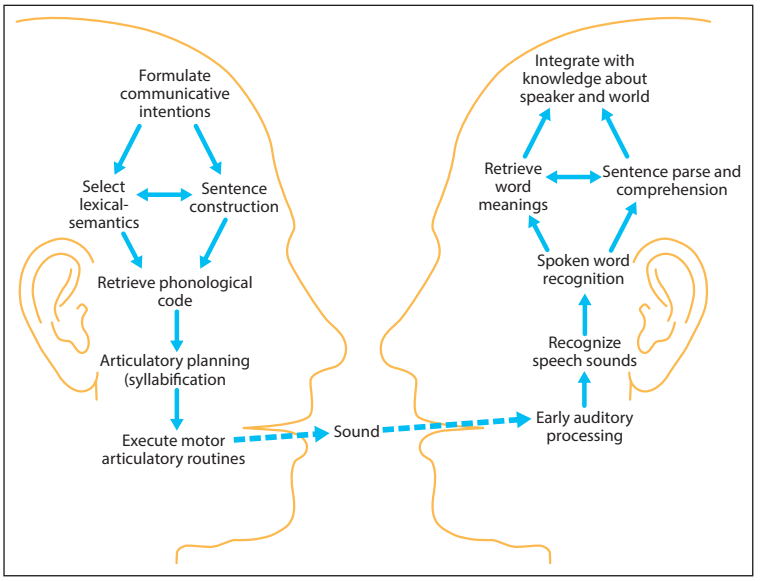


FIGURE 12.1: A simple schematic diagram showing some of the main stages in speech production (left) and speech comprehension (right).

ONLINE RESOURCES

Scan the QR code or visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience) to watch a TED talk by Uri Hasson titled "This is your brain on communication."

It is highly questionable whether the vocalizations of other animals could be said to be "true language" in this sense.

Chapter 8 considered the early auditory processing of speech. This chapter will consider how familiar spoken words are recognized and how the meaning of words and sentences are derived before, finally, considering the process of speech production.

DO NONHUMAN ANIMALS HAVE LANGUAGE?

The idea of being able to talk to the animals, Dr. Doolittle style, is a captivating one. Other species are clearly able to communicate with each other. For example, bees perform a dance that signals the location of nectar, and vervet monkeys produce calls when faced with a threatening stimulus. But are these communication systems related to human language? The question of animal language is an important one because it focuses the discussion on what language actually is and where it came from.

Many attempts at teaching language to other animals have relied on training them to associate symbols with objects and actions. The main difficulty with these studies is that, although animals are capable of learning associations, it is not clear that they have a conceptual level of understanding. For example, pigeons can be trained to respond in different ways, pecking once or twice, to pictures of trees or water (Herrnstein et al., 1977). But do they understand how trees relate to other concepts such as plants and bark, and could they use pecking to communicate the idea of a tree in the absence of a picture? If birds lack an equivalent of words, what some species of songbird have is the ability to learn to reproduce complex ordered sound sequences. This resembles syntax, at least superficial-

ly (Berwick et al., 2013). Bird song also appears to depend on their left hemisphere (Moorman et al., 2012) and has genetic counterparts in humans (Haesler et al., 2004).

What about closer evolutionary neighbors, such as the chimpanzee? The chimp, Washoe, was taught American Sign Language and learned around 200 signs (Gardner et al., 1989). Moreover, there was evidence of overgeneralizations (e.g., using "hurt" for tattoo), and the combining of words for unfamiliar objects (e.g., "water bird" for duck). The system was also spontaneously acquired by Washoe's adopted son. The problem with these studies is that many signs are iconic rather than arbitrary (e.g., "give" is represented by an inward hand motion), and it is not clear how often Washoe produced random or inappropriate word combinations. Some have argued that the ability to generate an infinite number of meaningful word combinations is the uniquely human component of language (Berwick et al., 2013).

FIGURE 12.2: The pygmy chimp Kanzi learned to communicate using written "lexigrams," shown in the colored insert. In what ways is this different from or similar to human language?

From Savage-Rumbaugh and Lewin (1994).

Savage-Rumbaugh and colleagues adopted a different approach with their bonobo or pygmy chimp, Kanzi (e.g., Savage-Rumbaugh et al., 1986). Kanzi learned how to use arbitrary written symbols to communicate and could select the symbols in response to human speech, as shown in Figure 12.2. There was evidence that the symbols were used flexibly (e.g., selecting "strawberry" to indicate wanting strawberries, the location of strawberries, or the object itself) and evidence of appreciation of word order (e.g., "Kanzi chase X" versus "X chase Kanzi"). This research has, however, been criticized on the grounds that Kanzi's utterances were mainly food requests that may have been learned through reward and that would not be found in a natural setting (Seidenberg & Petitto, 1987). Thus, while nonhuman animals may have some of the basic cognitive prerequisites for language, it is doubtful that they possess anything akin to the human capacity (Berwick et al., 2013).

SPOKEN WORD RECOGNITION

It is generally assumed that spoken word recognition entails matching some aspect of an acoustic form to a stored set of spoken words that comprise the set of known words in the speaker's vocabulary. It is often stated that the brain implements something akin to a dictionary (the mental lexicon; Figure 12.3) – that is, a store of all the known words, how they sound, their grammatical usage (noun, verb, etc.), their meaning, and so on. The store of speech sounds comprising words is known as the **phonological lexicon** (or speech input lexicon), and the matching process itself is called **lexical access**. This section considers a number of issues relating to

KEY TERMS

Phonological lexicon
A store of the abstract speech sounds that make up known words.

Lexical access
The process of matching a perceptual description of a word onto a stored memory description of that word.

FIGURE 12.3: It is often claimed that our brain contains a "mental lexicon," which, like a dictionary, specifies the properties of a word, such as how it is pronounced, its grammatical class (e.g., noun, verb), and its meaning(s).

rogerashford/iStock

lexical access from auditory, spoken word, inputs. First, what is the nature of the perceptual code that is used to access the stored set of words, and in what format are the stored speech forms themselves stored? Second, how is the matching process itself achieved? Are many different candidates considered together or one at a time? Is the process purely perceptual, or does the semantic context matter?

What are the access units for auditory word forms?

Linguists have traditionally placed great emphasis on the importance of phonemes in the representation of speech. Phonemes are categorical representations that distinguish between the sounds of different words. Thus, /r/ and /l/ are different phonemes in English but not Japanese. Even though /r/ and /l/ have certain acoustic and articulatory properties in common, they are considered as separate categories in languages that make this phonemic distinction. Some models of spoken word recognition also place great emphasis on the role of a phonemic code, as in the case of the motor theory of speech perception (Liberman & Mattingly, 1985; Liberman & Whalen, 2000). However, other cognitive neuroscientists have taken a more skeptical approach and have argued that phonemes may just be useful descriptions of the structure of language rather than something that is actually implemented in real cognitive/neural systems. For example, in some models, acoustic features of speech (e.g., voicing, stops, formant frequencies) are considered to access the spoken word forms directly without an intermediate phonemic description (Marslen-Wilson & Warren, 1994).

The evidence for a phonemic level in lexical access is equivocal. Some patients with acquired speech recognition problems are able to comprehend spoken words but are poor at explicitly discriminating between phonemes (e.g., are "ta" and "da" different?), whereas others show the opposite dissociation (Miceli et al., 1980). Indeed, the ability to explicitly segment speech into phoneme segments appears to be predicted by literacy levels, particularly for alphabetic scripts, rather than spoken language ability (Petersson et al., 2000). This suggests that

explicit phonemic awareness is not critical for speech recognition. In Hickok and Poeppel's (2004) model, explicit phoneme segmentation is captured by the dorsal route, whereas spoken word comprehension is performed by the ventral route. Recall from Chapter 8 that the ventral route is primarily concerned with speech comprehension, that is, the process of translating between an acoustic input and a semantic output, whereas the dorsal route is concerned with more motoric aspects of speech (as well as locating sound sources), that is, the process of translating an acoustic input into a motor output.

If not phonemes, then what are alternative perceptual access codes for spoken word recognition? Some researchers have argued that syllables may be critical (Mehler et al., 1981), whereas others have emphasized the importance of stress patterns (Cutler & Butterfield, 1992). In English, nouns tend to be stressed on the first syllable, and this can be used by the speech recognition system to infer likely word boundaries.

Neurobiological models of speech recognition are based on the idea that different neurons respond to acoustic information that varies on different time scales (Luo & Poeppel, 2012). In primate electrophysiology, some neurons respond preferentially to relatively rapid changes in the auditory signal (20–80 ms range), whereas others respond preferentially to changes occurring over medium (150–300 ms) and longer (500–1,000 ms) time scales (see DeWitt & Rauschecker, 2012). In human speech, these time scales may correspond approximately to phonemes, syllables and stress patterns, respectively. These rhythmic changes in the speech signal may induce corresponding rhythmic bursts of neural activity that can be observed in methods such as EEG/MEG as increased power in the gamma, theta, and delta range (fast, medium, and slow oscillations). These neural rhythms can then be used, in a top-down manner, to predict where boundaries in the speech signal are likely to occur, helping to segment speech into different-sized units (Giraud & Poeppel, 2012). This is illustrated in Figure 12.4. DeWitt and Rauschecker (2012) suggest, based on a meta-analysis of fMRI studies of speech recognition, that these different time scales are implemented in the auditory ventral stream in a hierarchical fashion from short-to-long durations and from posterior to anterior along the superior temporal lobes. Some aspects of speech rhythms are strongly conserved across languages (e.g., Zulu, Japanese, Spanish), such as the optimal tendency to produce syllables at a rate of about 5 Hz (Varnet et al., 2017). This probably reflects biomechanical constraints on the jaw. Although these regularities originate from the motor system, the auditory perceptual system is able to tune in to these rhythms and exploit them in speech recognition.

In addition to rhythmic regularities, speech perception makes use of the known words in its language in a top-down fashion. One example of this is referred to as the **Ganong effect** (Ganong, 1980) in which an ambiguous phoneme (e.g., "g" or "k") is more likely to be perceived as reflecting a real word (e.g., being perceived as "g" in an ambiguous GIFT/KIFT syllable but perceived as "k" in GISS/KISS). Localization of EEG signals suggests that this effect occurs midway along the auditory ventral stream (Bidelman et al., 2021) consistent with syllable-level effects.

KEY TERM

Ganong effect
The tendency to perceive an ambiguous speech sound as a phoneme that would complete a real word, rather than completing a nonword.

ONLINE RESOURCES

Watch helpful videos, such as a TED-Ed video on "How do our brains process speech?" and David Poeppel on "Rhythms of Speech and Rhythms of Brains," by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

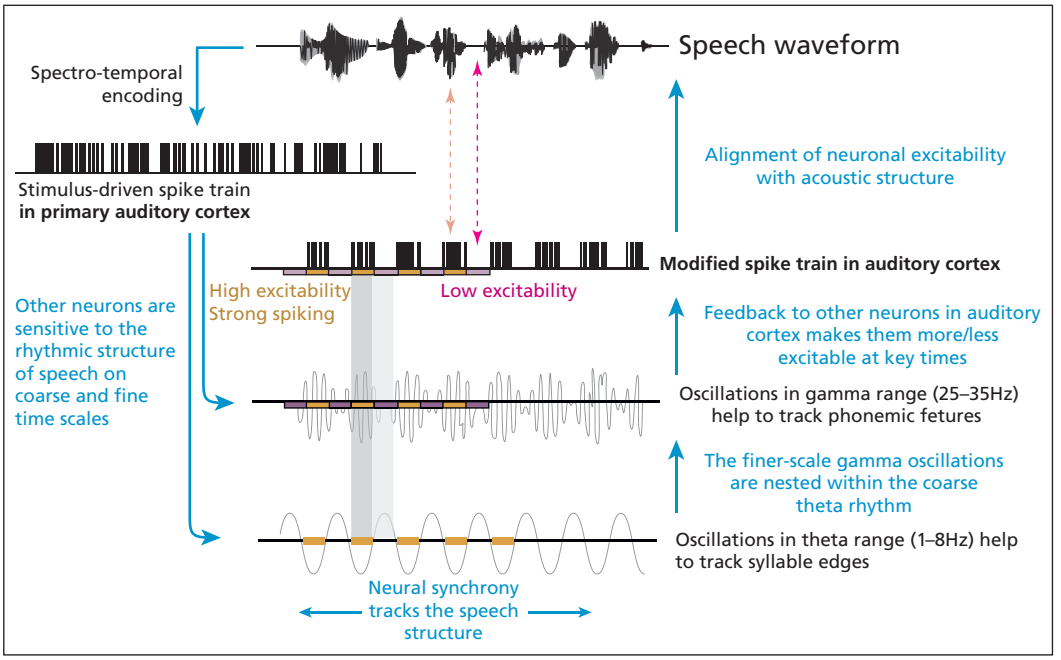


FIGURE 12.4: Neurons in the auditory cortex and the surrounding auditory ventral stream respond to the speech waveform in different ways. The early response in the primary auditory cortex tracks sudden changes in sound frequency and loudness, whereas other neurons track the more rhythmic qualities of speech that help to identify syllable and phonemic boundaries (needed for word recognition). They do this by firing in rhythm with the speech signal, and this, in turn, is fed back to other neurons in the auditory cortex which effectively amplifies the incoming signal when it matches the rhythm.

Adapted from Giraud and Poeppel (2012).

In summary, multiple features of the acoustic signal (varying in temporal duration, and psycholinguistic unit size) are likely to contribute to word recognition rather than being reliant on a single source of information (e.g., phonemic).

LINGUISTIC TERMINOLOGY MADE SIMPLE

Phoneme

A minimal unit of speech that serves to distinguish between meanings of words. In English, /r/ and /l/ are different phonemes because this sound difference can convey differences in word meaning (e.g., between "rip" and "lip"). In languages such as Japanese, this is not so and /r/ and /l/ are variants of a single phoneme.

Syllable

Clusters of phonemes that are centered on a vowel sound. The vowel forms the *nucleus* of the syllable. The vowel may optionally be preceded by consonant sounds (termed the syllable *onset*) and may optionally be followed by more consonants (termed the syllable *coda*). The vowel and coda collectively make up the *rime* of the syllable. The words "mark," "market," and "marquetry" have one, two, and three syllables, respectively.

Stress
An increase in the activity of the vocal apparatus of a speaker that aids segmentation of the speech stream into words.

Morpheme
The smallest meaningful unit in the grammar of a language. For example, "unladylike" has four syllables and three morphemes (un + lady + like). "Dogs" has one syllable but two morphemes (dog + s). Both "unladylike" and "dogs" are one word.

Word
Words occupy an intermediate position in size between a morpheme and a phrase. A word is sometimes defined as being the minimal possible unit in a reply.

Syntax
The rules (or grammar) that specify how words can be combined into sentences in a given language.

Semantics
Broadly defined as the meaning of linguistic expressions but also defined as the meaning of particular words (lexical-semantics) or the meaning of objects, words, and other types of stimuli (semantic memory).

Pragmatics
The way in which language is used in practice, such as implied or intended meaning (e.g., "Can't you read?" may be used as a rhetorical question that does not require an answer).

Prosody
Melodic aspects of spoken language such as stress, intonation (e.g., rising pitch to indicate a question), and emotion (e.g., slow and low to imply sadness).

Nouns
"The" words, which imply *things*, such as "the computer," "the idea."

Verbs
"To" words, which imply an *action*, such as "to buy," "to think," "to eat."

Adjectives
Words used descriptively such as "big," "soft," "easy."

Pronoun
A word that can substitute for a noun (e.g., "I," "you" and "him"). In the sentence "Mr. Rice spoke to Tom and offered him a job," "him" is the pronoun; it takes the place of "Tom."

Preposition
Indicates a connection, between two other parts of speech, such as "to," "with," "by," or "from."

Name/proper noun
A type of noun denoting a unique entity such as people and place names, e.g., "Donald Trump" or "Washington DC."

Function words (or closed class words)
Words that have little lexical meaning but instead serve to express grammatical relationships with other words within a sentence (e.g., pronouns, prepositions, "the," "and").

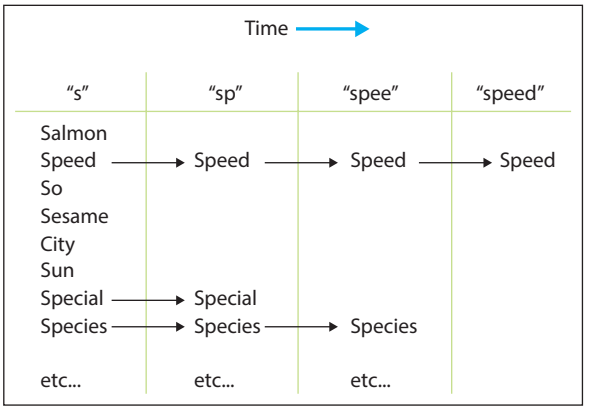


FIGURE 12.5: In the cohort model of spoken word recognition, all words that are initially consistent with the acoustic information become active in parallel. As more acoustic information is revealed, the size of the cohort dwindles until a unique match can be made.

The cohort model

Although the precise nature of the mechanism by which spoken word recognition takes place is still debated, there is general consensus that it involves competition between similar-sounding words (McQueen & Cutler, 2001). The most influential model in this area is the **cohort model** of Marslen-Wilson and Tyler (1980; Marslen-Wilson, 1987), shown in Figure 12.5. The acoustic information required to identify a word is revealed over time. The central idea of the cohort model is that a large number of spoken words are, in parallel, initially considered as candidates but that words get eliminated as more evidence accumulates. For example, on hearing the sound "e" all words beginning with this sound would become active. This is termed the cohort of words. But as more information is revealed (e.g., "ele"), then the cohort gets whittled down to fewer words (e.g., "elephant," "electricity") until a point is reached ("eleph") in which the evidence is consistent with only a single word. This is termed the **uniqueness point**. Thus the start of a word, particularly the first syllable, has an exaggerated importance. Indeed, listeners are better at detecting speech distortions when they occur prior to the uniqueness point, and the time taken to recognize a word depends on how early or late the uniqueness point occurs (Marslen-Wilson, 1987).

The uniqueness point is a structural property of the word, but do linguistic factors such as word frequency and imageability influence recognition? Considering word frequency, it is the case that not all candidates in a cohort behave equivalently. For example, the ambiguous onset "spee" is compatible with "speed," "speech," "species," and so on. However, studies of reaction time priming show that infrequent words (e.g., "species") get activated less (Zwitserlood, 1989). This suggests an early effect of word frequency. The imageability of a word also affects spoken word recognition but only for highly competitive cohorts (Tyler et al., 2000). **Imageability** is a semantic property of a word that relates to the extent to which a word's meaning can evoke sensory images. An fMRI study shows that imageability and degree of cohort competition interact in a posterior region of the superior temporal gyrus – a ventral stream region implicated in relatively early speech processing (Zhuang et al., 2011). Other fMRI research suggests that the superior temporal gyrus is activated more by words with a later uniqueness point (i.e., requiring more auditory processing), whereas the degree of activity in prefrontal cortex (including

KEY TERMS

Cohort model
In lexical access, a large number of spoken words are initially considered as candidates, but words get eliminated as more evidence accumulates.

Uniqueness point
The point at which the acoustic input unambiguously corresponds to only one known word.

Imageability
The extent to which a word can evoke a concrete image; e.g., "table" is high on this measure but "truth" is low.

Broca's area) was related to the size of the cohort (Zhuang et al., 2014). As such, selection from the cohort is determined both by perceptual and non-perceptual factors.

Word recognition in context: the N400

The cohort model was primarily developed to explain the recognition of single spoken words. However, words are normally spoken in the context of a discourse rather than in isolation. This raises the important question as to how these different aspects of spoken word recognition are related: that is, recognizing the form of a spoken word, retrieving its meaning, and linking word meaning to the wider context of the utterance.

One ERP component has been particularly informative for addressing this issue: the **N400**, so called because it reflects a negative peak at around 400 ms after the onset of a word (Kutas & Hillyard, 1980; for a review see Kutas & Federmeier, 2011). The amplitude of the N400 depends critically on whether a given word is appropriate to the wider context. Thus, the sentence "I take coffee with milk and dog" elicits a large N400 to the contextually anomalous word "dog" relative to the same sentence ending with the semantically appropriate word "sugar" (or a different sentence in which "dog" is an appropriate ending). The N400 is found either when a word is semantically anomalous, as in "the Dutch trains are sour" (trains cannot be tasted), or conflicts with known facts about the world, as in "the Dutch trains are white" (Dutch people know they are yellow) (Hagoort et al., 2004). This suggests that word-knowledge and world-knowledge are both brought to bear on this process rather than representing two separate processing stages (see Figure 12.6). Words need not be presented in sentence form for the N400 to be elicited. For example, given a semantically ambiguous word such as "bank," an N400 is elicited for the third word in triplets such as "river–bank–money," but not "finance–bank–money" (Titone & Salisbury, 2004). This result also suggests that the N400 reflects global context (operating over all three words) and not local context, given that the last two words are identical in both triplets.

KEY TERM

N400
An event-related component in EEG found when a word meaning appears out of context or unexpectedly.

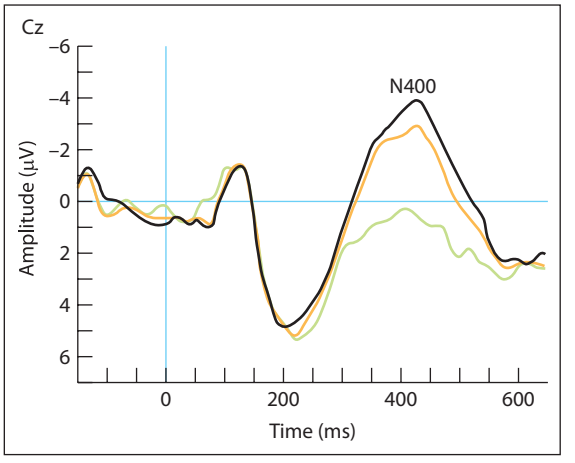


FIGURE 12.6: The N400 response to the critical word in three types of sentence: semantically coherent and correct ("the Dutch trains are *yellow*"; green line), semantically coherent but incorrect ("the Dutch trains are *white*"; brown line), semantically incoherent ("the Dutch trains are *sour*"; black line).

From Hagoort et al. (2004). Reprinted with permission from AAAS.

The N400 is found for written words presented one at a time as well as spoken words (and, indeed, for other meaningful stimuli besides words). As such, it is not critically dependent on auditory perceptual processes. Nevertheless,

the N400 tends to emerge earlier for spoken words than written words (Holcomb & Neville, 1990). This is perhaps surprising given that spoken words are heard piecemeal over time. It suggests that the semantic context interacts with lexical access even before the spoken word can be uniquely discriminated. Several studies support this interpretation. Van den Brink et al. (2001) compared sentences with highly probable endings ("It was a pleasant surprise to find that the car repair bill was only 17 *dollars*") to those with contextually inappropriate endings including those that shared initial (e.g., "dolphin") or final (e.g., "scholar") phonemes. In this example, "scholar" is linked to an earlier onset of the N400 than "dolphin," reflecting the mismatch between the heard and expected initial phonemes. Finally, van den Brink et al. (2006) varied the uniqueness point of the critical spoken word. Despite the fact that words with an early uniqueness point could be identified 100 ms faster than the other words, the N400 did not shift in time. Thus, the language system does not have to "wait" for the uniqueness point to be reached before it can generate an N400 and, hence, lexical access (relating to uniqueness point) and contextual integration (relating to N400) are not two separate and discrete stages in speech recognition.

Evaluation

The auditory speech signal is processed by neurons in the superior temporal cortex (auditory ventral stream) at different temporal scales that correspond, roughly, to the linguistic units of phonemes, syllables, and stress patterns. All of these units may play a role in spoken word recognition, that is, selecting one word from amongst competing alternatives. This competitive process not only involves selecting amongst similar-sounding words, but is also constrained by prior information (e.g., how common a word is) and current context (e.g., how likely a word is based on the semantic theme) as a result of interactions between the auditory system and other key brain regions involved in language.

SEMANTIC MEMORY AND THE MEANING OF WORDS

On encountering a word such as "lion," one is able to retrieve many associated properties, such as the fact that it is an animal, has four legs, is a native of Africa, and is a carnivore. Collectively, such properties, or features, are considered to comprise the meaning of the word. These features are assumed to be linked together via a network. For example, the word "lion" may connect with features such as animal, carnivore, etc.; the feature "animal" may connect with eats, breathes, reproduces, etc.; "breathes" connects with lungs, and so on. This network enables generalizations and novel inferences to be made. A question such as "does a giraffe have

kidneys?" can be answered with a high degree of confidence despite the fact that this semantic proposition has almost certainly never been encountered before! According to most theories, this same knowledge base is consulted irrespective of whether the spoken word is heard, the written word is seen, or if a lion itself is seen, heard, or merely thought about. The fact that semantic memory has a network structure, rather than being a single localized entity, has made it a particular challenge to study. As one review has put it: "The search for the neuroanatomical locus of semantic memory has simultaneously led us nowhere and everywhere" (Thompson-Schill, 2003).

Although all models propose that concepts are composed of a network of constituent features, models of semantic memory differ in terms of the following:

- How are the features organized: hierarchical versus non-hierarchical?
- What format do the features take? Are they abstract or grounded in sensorimotor information?
- Is category information (e.g., "animal") represented in addition to feature-level information (e.g., "has eyes"), or are categories purely emergent properties of features?

These different issues are discussed in the later sections, which also introduce different models of semantic memory and its neuroanatomical basis. This chapter does not consider the *learning* and acquisition of semantic memories, and its relationship to episodic memory, which was covered in Chapter 11, "The remembering brain."

Is semantic memory organized hierarchically?

The early influential model of Collins and Quinlan (1969), shown in Figure 12.7, assumed a hierarchical network organization

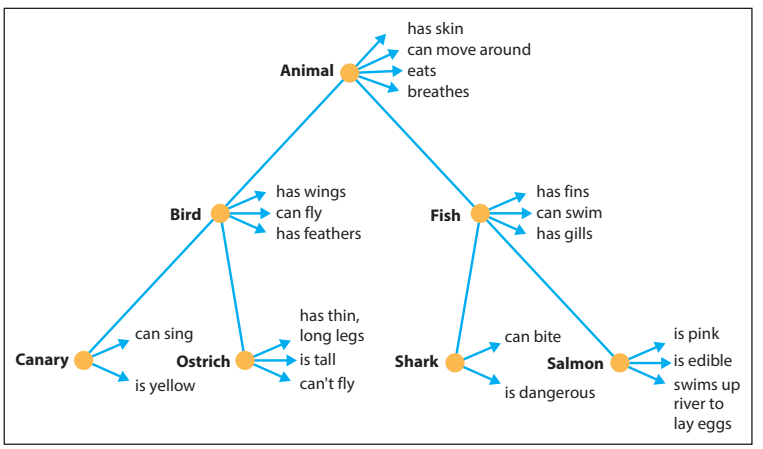


FIGURE 12.7: In the Collins and Quinlan (1969) model, semantic features are organized hierarchically with superordinate information accessed first. Subsequent models have retained the idea that knowledge may consist of a network of interconnected features but do not make the assumption of hierarchical organization.

Reprinted from Collins and Quinlan (1969). © 1969, with permission from Elsevier.

from superordinate (animal, mode of transport, etc.) to ordinate (bird, fish, car, van, etc.) to subordinate (canary, ostrich, Ferrari, etc.). There is some evidence that supports the hierarchical nature of the model. Participants are faster at classifying a robin as a bird than an animal, because the latter requires going further up in the hierarchy (which takes additional processing time). However, there are also problems with the model. For example, not all concepts have clear hierarchies (e.g., the difference between truth, justice, and law). Second, apparent effects of distance within the hierarchy could also be explained by how frequently two words or concepts co-occur (Wilkins, 1971). For example, robin and bird may co-occur together more than robin and animal.

Although this model was not derived from neuroscientific findings, there is some evidence that these different kinds of superordinate and subordinate information have different neural substrates (broadly consistent with this aspect of the model). The lateral temporal lobes are widely recognized as having an important role in semantic memory. Rogers et al. (2006) found that different parts of the lateral temporal lobes were activated in fMRI depending on the specificity of the information. There was a posterior-to-anterior gradient from less specific information (e.g., animal), intermediate specificity (e.g., bird), to more specific information (e.g., robin). This may explain why some studies of lexical-semantics have highlighted posterior temporal regions (Hickok & Poeppel, 2004), whereas others implicate more anterior temporal regions (Mummery et al., 2000). Both could be correct, depending on the type of information (superordinate, subordinate) that needs to be accessed. Patients with damage to the anterior temporal lobes, such as in semanic dementia, tend to retain the ability to make superordinate classifications (e.g., "animal," "bird") but struggle with item and subordinate level classifications (e.g., "robin," "Labrador") (Rogers & Patterson, 2007). This supports the evidence from functional imaging that more anterior regions of the temporal lobes are activated by more finer-grained semantic judgments (e.g., Rogers et al., 2006).

Some kinds of knowledge can only be meaningfully represented at the subordinate level; for instance, **proper names** such as "Justin Bieber," "Paris," and "Lassie" all denote specific entities in contrast to words (common nouns) such as "popstar," "city," and "dog" that could denote any number of entities. The specificity of proper names together with other factors such as lower lexical frequency may render them particularly hard to retrieve from the lexicon (Bredart, 2017). Impaired naming of proper names (both people and places), relative to naming other categories, has been linked to the left anterior temporal lobe (e.g., Tranel, 2009), and fMRI studies of healthy participants reveals activity in the left anterior temporal lobe when retrieving a name to a face relative to retrieving

KEY TERM

Proper name/proper noun
A type of noun denoting a unique entity such as people and place names, for example, "Donald Trump" or "Washington DC."

the occupation from the same face (Tsukiura et al., 2002). The latter was linked to more posterior temporal lobe activity in the right hemisphere. In summary, the evidence from proper names is consistent with a hierarchical arrangement from general to specific along the temporal lobes.

Is semantic memory amodal or grounded?

The fact that the same semantic memory can be accessed from multiple kinds of sensory input (e.g., the written and spoken word "lion," the roar or sight of a lion, etc.) has traditionally been taken to imply that semantic memory itself is not tied to particular sensory channels but is, instead, considered to be **amodal** or abstract. The notion that semantic memory is based on amodal representations (or "symbols") has dominated cognitive psychology for almost a century. For instance, the semantic features in the Collins and Quinlan (1969) model are regarded as amodal symbols. So the feature of salmon, "is pink," should be understood as representing information that is *about* color rather than the alternative claim that the information is stored using a visually based code.

The problem with defining words in terms of other words – like a dictionary – is that it is an entirely circular process. The "mental lexicon" metaphor falls into the same trap. When looking up a dictionary definition of, say, "power" one may get "strength or force exerted" and when looking up "force" one gets the definition "power made operative against resistance" and "strength" defined as "a source of power or force." In short, it is impossible to get a satisfactory definition for any given word without knowing the meaning of some other words in advance. This is termed the **symbol grounding problem** in linguistics.

One way of breaking the circularity is if there are some concepts that are not defined in terms of each other but are "grounded" by universals in the environment and our interactions with them (such as shared perceptual and motor experiences). So for instance, the meaning of a word such as "power" could be grounded by the strength of actions generated by our motor system (but could then be extended, by analogy, to the "power" of a light bulb), and "sweet" and "green" could be grounded by our perceptual experiences of the world (but could be extended, by analogy, so that a concept like revenge can also be "sweet"). In this view, conceptual knowledge is derived from the associated sensorimotor experiences rather than some abstract definition, although the latter could be represented within semantic memory too. Grounded concepts could either be learned or innate, with some theories advocating one position or the other (see Barsalou, 2008). Certain abstract concepts may also be grounded in the same way. For instance, the proposal that the meaning of numbers has a spatial component (see Chapter 13) can be regarded as an

ONLINE RESOURCES

Check out the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience) for current controversies on the nature of semantic memory including talks by Lawrence Barsalou and Karalyn Patterson.

KEY TERMS

Amodal
Not tied to one or more perceptual systems.

Symbol grounding problem
The problem of defining concepts without assuming some preexisting knowledge.

KEY TERM

Embodied cognition
The idea that the body (its movement, or internal state) can be used in cognition (e.g., to understand words, or social situations).

example of grounding, as can the proposal that emotions can be defined in terms of bodily feelings (see Chapter 16). The term **embodied cognition** is used to refer to the use of the body (its movement, or internal state) to represent meaning and can be considered as a sub-field within grounded cognition (Barsalou, 2008; Wilson, 2002).

In fully grounded models of semantic memory (Allport, 1985; Martin, 2007), the collection of different semantic features that make up a concept reside solely in the different information channels from which they were acquired. An example is shown in Figure 12.8. So, for instance, the semantic memory of a telephone would reside partly in auditory regions (for what it sounds like), visual regions (for what it looks like), action-related regions (for how to use it), and so on. The different domains of knowledge would be interconnected as a network such that activating one property (e.g., the sound of a telephone) triggers activity in other parts of the network (e.g., its associated actions and appearance) – a process termed pattern-completion. In these accounts, retrieving information from semantic memory involves many of the same processes that are involved in mental imagery. There is evidence consistent with this. For instance, on encountering a sentence such as "The ranger saw the eagle in the sky," participants are subsequently faster at naming a picture of an eagle (priming) but, crucially, they are even faster at naming a picture of an eagle with outstretched wings than one that is perched with folded wings (Zwaan et al., 2002).

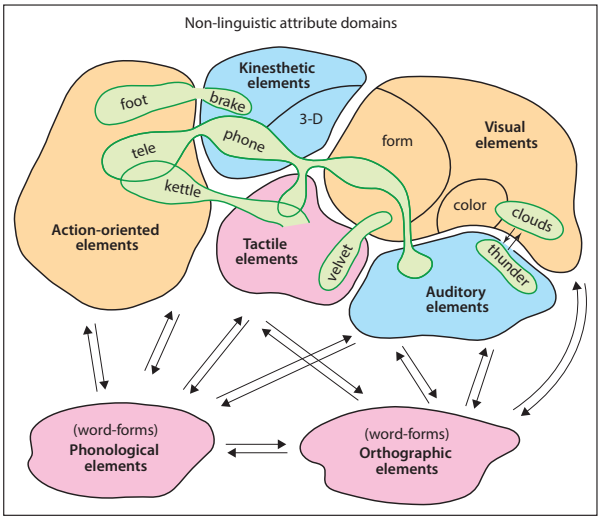


FIGURE 12.8: In Allport's (1985) model, concepts are distributed over many different domains of knowledge.

Reprinted from Allport (1985). © 1985, with permission from Elsevier.

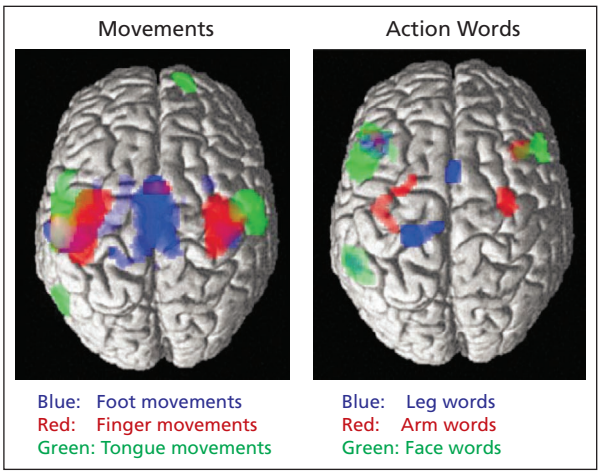


FIGURE 12.9: Spoken verbs such as "kick," "pick," and "lick" activate regions that overlap with or are next to the corresponding part of the motor cortex – foot, fingers, and tongue.

(Hauk et al., 2004)

Action-based concepts, according to a grounded/embodied semantics viewpoint, should depend on parts of the brain representing the body and motor production which are primarily located in the parietal and frontal cortices. In support of this, lesion studies suggest a critical role of left parieto-frontal regions involved in both semantic knowledge of actions and tools as assessed using pictures (Tranel

et al., 2003). Moreover, fMRI shows that spoken verbs such as "lick," "pick," and "kick" activate regions that overlap with, or are next to, the corresponding part of the motor cortex – mouth, fingers, and legs (Hauk et al., 2004). This is shown in Figure 12.9. Although actions are more closely associated with the grammatical category of verbs, the relationship is not exact (e.g., "hammer" and "mug" are nouns with strong action-based connotations). TMS research has shown that retrieval of action words relative to non-action words is affected by stimulation of motor areas irrespective of whether the words are nouns or verbs (Oliveri et al., 2004).

There is also evidence for the importance of sensory regions in semantic knowledge. Concepts which load heavily on auditory features (e.g., "telephone") activate auditory association cortex more than concepts that load heavily on visual or motoric features (Kiefer et al., 2008). Odor-related words ("garlic," "cinnamon," "jasmine") activated primary olfactory cortex more than control words (Gonzalez et al., 2006). Making color judgments about words (e.g., TAXI-yellow?) activates brain regions involved in color perception (Simmons et al., 2007).

The idea that semantic memory is grounded solely in sensory and motor systems of the brain has, however, received criticism. For example, Mahon and Caramazza (2008) assume that the core system within semantic memory is amodal but that modality-specific representations are evoked more as a downstream by-product. So for example, the core semantic representation of an "eagle" would *not* include perceptual image(s) of its appearance, but such images could (in a non-obligatory way) be generated by the particular demands of the task. This spreading activation may provide a "dressing" to conceptual processing that enriches it with detail, but they argue that the amodal system is needed to maintain invariance of concepts in the face of significant variability in superficial details. For instance, the word/concept "dog" can be instantiated from Chihuahua through to Rhodesian Ridgeback, and both are perceptually very similar to a "wolf" which is a different conceptual entity altogether. So the amodal system would bind together entities that are superficially very different (e.g., the wide variety of dog breeds).

Some models assume an importance for both grounded and amodal semantic representations. The **hub-and-spoke model** would be an example of this (Patterson et al., 2007), as illustrated in Figure 12.10. The model stores semantic information in various regions involved in sensory and bodily processes (the spokes), but these connect to a central, amodal, semantic system (the hub). Patterson et al. (2007) explain semantic dementia in terms of damage to the hub. This condition is linked to atrophy of the anterior temporal lobes/temporal poles (Mummery et al., 2000) and appears to affect semantic memory relatively selectively (sparing other cognitive functions) and globally (affecting almost all domains of knowledge). Why is an amodal hub needed at all? According to this

KEY TERM

Hub-and-spoke model
A model of semantic memory that contains both amodal concepts (the "hub") and semantic features that are grounded in the sensory, motor, and bodily cortex (the "spokes").

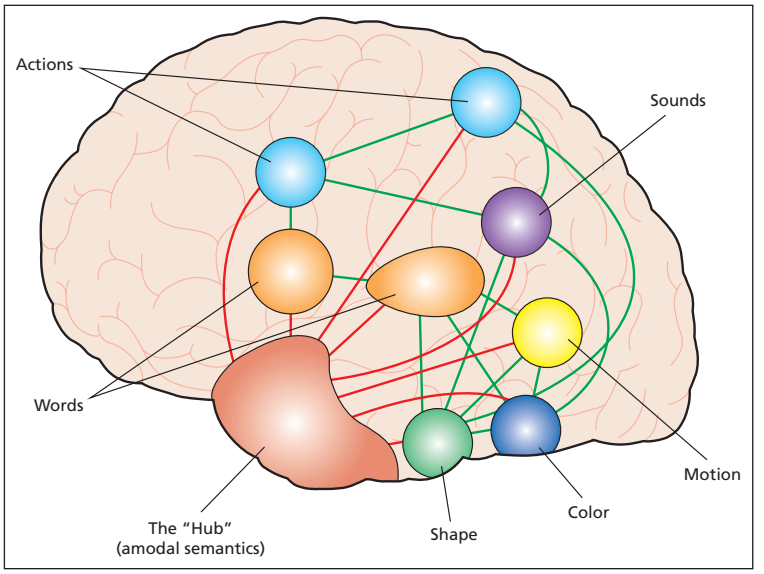


FIGURE 12.10: The hub-and-spoke model is a hybrid model of semantic memory which contains both amodal representations (assumed to lie in the anterior temporal lobes; the "hub") and representations that are grounded in sensory and motor systems (the "spokes").

Adapted from Patterson et al. (2007).

model, the hub enables exceptional items to be categorized (e.g., penguin, ostrich) and enables superficially different entities to be grouped together (e.g., a prawn and scallop as seafood).

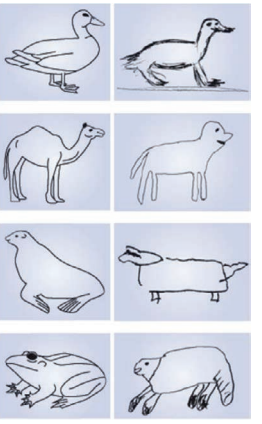
Evidence for the hub-and-spoke model comes from the fact that patients with semantic dementia are able to categorize pictures relatively accurately when the exemplars are typical (e.g., categorizing a dog as an animal) but struggle with atypical category members (e.g., failing to categorize an ostrich as a bird; Patterson, 2007). This is shown in Figure 12.11 for copying pictures after a delay and naming pictures. When asked to select semantic features, they are biased toward choosing the typical category answer. For instance, they may match green with carrot because most vegetables are green (Rogers et al., 2007). In short, patients with semantic dementia are able to make category distinctions based on feature probabilities (represented in the spokes), but not based on conventional knowledge which incorporates exceptions-to-the-rule and learned taxonomies.

Category specificity in semantic knowledge: innate or emergent property?

The final section considers whether different kinds of (superordinate) semantic categories have different neural substrates in the

brain. For instance, do animals and tools rely on different neural substrates within the semantic memory network and, if so, why? There are three possibilities: category groupings are explicitly learned, categories are learned via statistical regularities, or categories are hardwired. It is to be noted that this debate, concerning conceptual knowledge, is different to that about visual recognition of different classes of objects although, under some accounts, they are related (e.g., if concepts rely on a visual code).

Two publications in the early 1980s triggered an enduring debate on the neural organization of semantic categories (for a review, see Capitani et al., 2003). Warrington and McCarthy (1983) documented a patient with acquired brain damage who had preserved knowledge for animals, foods, and flowers relative to inanimate objects. The following year, Warrington and Shallice (1984) reported four patients with the opposite profile. These patients were impaired at comprehending pictures and words, in naming pictures, and matching pictures and words. To account for this pattern, Warrington and Shallice (1984) proposed the **sensory–functional distinction**. They suggested that certain categories may depend critically on certain types of knowledge: animals and fruit and vegetables may be defined more by their sensory properties (color, shape, four legs, etc.), whereas inanimate objects, particularly tools, may be defined by their functions. This is illustrated in Figure 12.12.



Item	Sept 1991	Mar 1992	Sept 1992	Mar 1993
Bird	–	–	–	Animal
Chicken	–	–	Bird	Animal
Duck	–	Bird	Bird	Dog
Swan	–	Bird	Bird	Animal
Eagle	Duck	Bird	Bird	Horse
Ostrich	Swan	Bird	Cat	Animal
Peacock	Duck	Bird	Cat	Vehicle
Penguin	Duck	Bird	Cat	Part of animal
Rooster	Chicken	Chicken	Bird	Dog

FIGURE 12.11: *Top*: when shown a picture and asked to reproduce it after a delay of only a few seconds, patients with semantic dementia tend to reproduce typical features of the category (e.g., four legs, tails) but omit atypical features of the particular exemplar (e.g., the hump, flippers). *Bottom*: when naming animals, they also tend to generate more typical category members as their impairment progresses with time.

From Patterson et al. (2007). Reproduced with permission from Springer Nature.

In this sensory-functional model, categories are emergent properties that come about because similar concepts tend to share similar features. For instance, animals tend to have lots of features that tend to co-occur such as presence of eyes, mouth, self-initiated movement, and so on. Man-made objects, on the other hand, tend to have distinctive relations between their shape and function (e.g., sharp edges and cutting). Computational simulations of semantic features of objects and animals tend not to result in a uniform network but rather a "lumpy" structure in which some features tend to be closely con-

KEY TERM

Sensory–functional distinction
The hypothesis that semantic features are clustered in the brain according to what they are used for and what their physical properties are.

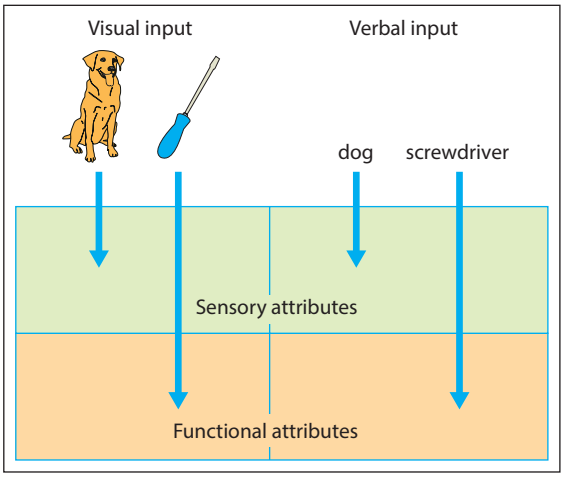


FIGURE 12.12: It has been argued that semantic memory may be organized along the lines of functional versus sensory features, rather than categorically along the lines of animals, tools, food, etc.

From Humphreys and Forde (2001). © Cambridge University Press. Reproduced with permission.

nected with each other but hardly connected at all to other sets of features in the network (Devlin et al., 1998; Tyler & Moss, 2001). Subsequent models, already discussed previously, moved away from the notion that the features are divided into a sensory–functional dichotomy to more fine-grained sets of features (such as action-based, shape-based, movement-based, and so on) but retained the basic assumption that categories (animals, tools, food, etc.) are an emergent property reflecting their different weightings on these features.

There are, however, alternative claims. Caramazza and Shelton (1998) put forward an evolutionarily based proposal that at least some categories are hardwired. The categories proposed were animals, plant life (e.g., fruit and vegetables), conspecifics (other humans), and possibly tools. In addition to this list, it is often argued that the representation of number knowledge is a true categorical distinction reflecting some innate abilities (Dehaene et al., 2003). Although these claims are not straightforward to test, there is at least some evidence that is more consistent with this view than the rival claim that these categories are an emergent property of the kinds of features they possess. In neuropsychological studies, patients with animate category-specific deficits are not necessarily impaired at answering sensory relative to functional questions about animals or objects (e.g., Lambon Ralph et al., 1998). Also some brain-damaged patients have been reported with relatively selective deficits to one category such as food (e.g., Samson & Pillon, 2003). However, in these cases there is often still some degree of impairment in other categories (e.g., animals).

A similar semantic network in congenitally blind people has also been used to argue that the structure of semantic knowledge is innate rather than dependent on experience (in this case, visual experience). Different regions of temporal cortex show selective fMRI activity for naming tools versus animals in both sighted (Beauchamp et al., 2002) and congenitally blind participants (Mahon et al., 2009), as well as responding to tool movement versus human movement in the sighted (Beauchamp et al., 2002). These results could be taken as evidence for hardwiring of these categories (Mahon et al., 2009), but it is also possible that the organization of "visual" cortex in blind

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people is influenced by other kinds of experience (e.g., shape information via touch).

Evaluation

Semantic memory is represented in the brain as a network of information which has made it a particular challenge to study. The network includes regions involved in action and perception (grounded semantics) that are useful for representing the sensory and motor aspects of concepts. The lateral temporal lobes may have a particular role in linking different features of the network, with a posterior-to-anterior shift in the specificity of the representations (broadly from superordinate to subordinate). One claim is that the anterior temporal lobes are an amodal hub that is particularly important for storing atypical information (e.g., birds that don't fly).

KEY TERMS

Wernicke's aphasia
A type of aphasia traditionally associated with damage to Wernicke's area and associated with fluent but nonsensical speech and poor comprehension.

Broca's aphasia
A type of aphasia traditionally associated with damage to Broca's area and linked to symptoms such as agrammatism and articulatory deficits.

LOOKING BACK ON NINETEENTH-CENTURY MODELS OF SPEECH AND APHASIA

Paul Broca (1861) is credited with providing the first scientific evidence that specific cognitive functions can be localized in the brain, although this idea had been around for some time (e.g., in the earlier phrenology movement). His patient, Leborgne, lost the ability to produce speech and his utterances consisted of "tan, tan, tan." Broca concluded that there is a dedicated language center in the brain.

Wernicke (1874) documented a different type of aphasia in which the patient was fluent but had difficulties comprehending speech. He divided the spoken forms of words into separate input and output centers termed "auditory images" and "motor images," respectively.

Damage to the auditory images was assumed to impair speech perception and was associated with **Wernicke's aphasia**. Damage to the motor images was assumed to impair speech production and was associated with **Broca's aphasia**. Perhaps the most influential model of speech and aphasia to derive from the classical nineteenth-century research is that of Lichtheim (1885). His basic idea survived at least 100 years in various guises (Goodglass & Kaplan, 1983). Lichtheim maintained Wernicke's distinction between auditory and motor centers and argued that they are linked by two routes: both directly and indirectly via a concept center (equivalent to semantic memory). This is shown in Figure 12.13. These separate routes were based on Lichtheim's observations that some aphasic patients have repetition disorders but adequate comprehension.

In some respects, the Lichtheim model still has a contemporary resonance. For example, the notion of separate speech input and output lexicons is still incorporated in most models (Shallice, 1988), as is the notion that there are both semantic and

auditory-verbal routes to repetition (Butterworth & Warrington, 1995). The most significant challenges to the Lichtheim model have come from the observation that Broca's and Wernicke's aphasia are not well characterized as selective disorders of output and input. Broca's aphasics often have problems in comprehension as well as production (Caramazza & Zurif, 1976). Wernicke's aphasics also have difficulties in output as well as input. They tend to produce made-up words or neologisms: "A bun, bun (BULL) . . . a buk (BULL) is cherching (CHASING) a boy or skert (SCOUT) . . ." (Ellis et al., 1983). In fact, some have argued that these are meaningless syndromes that have no real modern-day relevance (Caramazza & Badecker, 1991). Furthermore, the functions associated with the regions termed Broca's area and Wernicke's area tend to be manifold and do not always map onto the functions that one would expect from the aphasic subtypes. Articulation deficits are not associated with damage to Broca's area (Dronkers, 1996); this suggests it is not a speech motor store. Wernicke's area comprises a number of functional regions involved in perception of non-speech as well as speech (Wise et al., 2001) and involved separately in comprehension and in acoustic/phonological analysis (Robson et al., 2012).

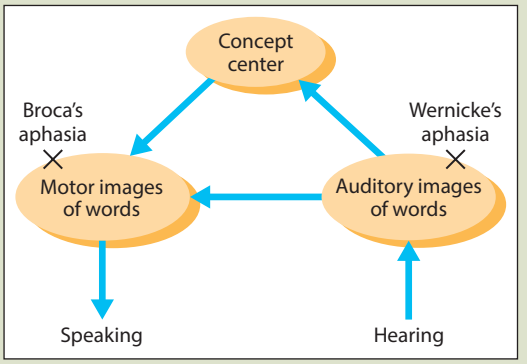

FIGURE 12.13: The Lichtheim model of speech and aphasia links together Wernicke's and Broca's area via direct and indirect routes.

UNDERSTANDING AND PRODUCING SENTENCES

Words not only carry information about meaning (semantics), but they also carry information about syntactic roles (grammatical classes such as nouns and verbs). The syntactic properties of words will determine the order and structure of the words within a sentence, that is, **syntax**. This enables the listener to figure out who is doing what to whom. Consider the three sentences next. Sentences A and B have different meanings but the same syntax, whereas sentences A and C have the same meaning but different syntax:

KEY TERM

Syntax
The order and structure of the words within a sentence.

A The boy hit the girl.
B The girl hit the boy.
C The girl was hit by the boy.

In general, empirical evidence suggests that processing the meaning of sentences uses similar neural resources to processing the meaning of single words (Friederici, 2012). However, there is far stronger

evidence to suggest the processing of *syntax* of sentences is, at least partially, separable from the processing of semantics and also from other general resource demands such as working memory. This evidence is considered next.

The role of Broca's area in sentence processing

The standard nineteenth-century view of Broca's aphasia was in terms of a loss of motor forms for speech which, therefore, affected speech production more than speech comprehension (see the accompanying Box for further historical details). This idea endured until the 1970s where it was replaced with an alternative proposal; namely, that there is a dedicated syntactic processor that is involved in both sentence comprehension and sentence production and that this is associated with the syndrome of Broca's aphasia (and/or with damage to Broca's area). The two main lines of evidence to support this alternative view were the symptom of agrammatism in these patients and also evidence that – under some circumstances – sentence comprehension was also impaired in these patients.

The symptom of **agrammatism**, meaning "loss of grammar," was a typical feature of patients classified with Broca's aphasia. The presenting symptoms are halting, telegraphic speech production that is devoid of function words (e.g., of, at, the, and), bound morphemes (e.g., –ing, –s), and often verbs. For example, given the Cookie Theft picture (see Figure 12.14) to describe, one patient came out with "cookie jar . . . fall over . . . chair . . . water . . . empty . . ." (Goodglass & Kaplan, 1983). This symptom is more consistent with the notion of a syntactic disorder than with a loss of motor programs for speech.

KEY TERM

Agrammatism
Halting, "telegraphic" speech production that is devoid of function words (e.g., of, at, the, and), bound morphemes (e.g., –ing, –s), and often verbs.

With regards to sentence comprehension, many seemingly complex sentences such as "The bicycle that the boy is holding is broken" can be comprehended just from the content words and with minimal knowledge of syntax (bicycle . . . boy . . . hold . . . broke). It was only when these patients were given sentences in which syntax was crucial to comprehension that disorders became apparent. For example, "The boy is eating the ice-cream" is semantically constrained by the fact that ice-creams do not eat boys, whereas a sentence such as "The boy is chasing the girl" cannot be unambiguously interpreted by the semantics of constituent words alone. Caramazza and Zurif (1976) showed that Broca's aphasics are impaired on the latter type of sentence only, as shown in Figure 12.15.

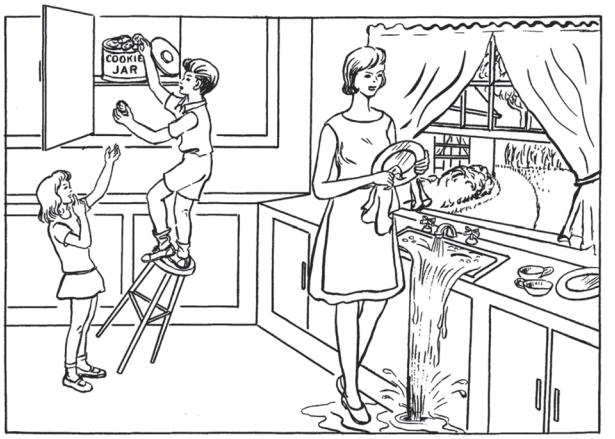

FIGURE 12.14: Sentence production abilities in aphasia have been assessed by giving patients complex pictures such as the "cookie theft" to describe.

From Goodglass and Kaplan (1972).

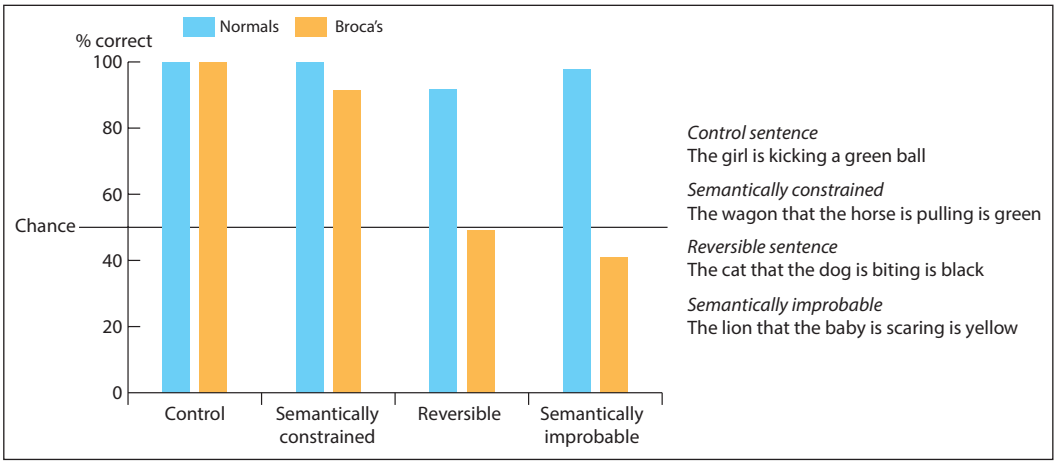

FIGURE 12.15: In a group study of Broca's aphasics, Caramazza and Zurif (1976) found that participants had particular problems in comprehending sentences on a picture-sentence matching task when the subject and object of the verb were determined from syntax and not from semantics.

There are several important caveats to the aforementioned lines of evidence: some of them are methodological and some are theoretical. Given the paucity of appropriate imaging techniques in the 1970s and 1980s, the diagnosis of Broca's aphasia depended on a checklist of symptoms (such as agrammatic speech) rather than on the basis of brain damage localized to Broca's region. This generated a rather muddied picture that has only been clarified in recent times. First, it led to the erroneous assumption that agrammatic symptoms necessarily arose from damage to that region. Other studies that carefully map lesion location support the conclusion that parts of Broca's area are important for sentence comprehension (Tyler et al., 2011). However, it is not the only part of the brain important for syntax. Damage to the temporal lobes has been found to be at least as important in sentence comprehension as Broca's area (Dronkers et al., 2004). Patients with lesions in this area often have difficulties with a wide range of sentences (including semantically reversible sentences; Thothathiri et al., 2012), but do not necessarily have difficulty in comprehending single words. In fact, they often meet the checklist-based diagnostic criteria of Broca's aphasia. Thus, sentence processing is composed of different mechanisms supported by different regions: a key fact that was missed by earlier lines of research. These regions are summarized in Figure 12.16.

The contemporary view of Broca's area is that it is multi-functional and can be divided into (at least) two functional subdivisions. The posterior division consists of BA44 (extending into the premotor area, BA6), and the anterior division consists of BA45 (extending into BA47).

BA44 is often considered to be involved in processing of hierarchical structures and sequencing of behavior in general

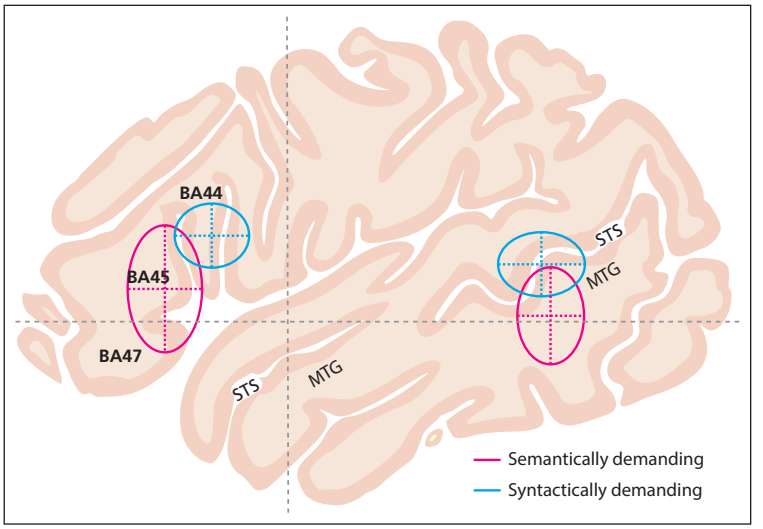

FIGURE 12.16: Areas of the brain important for sentence processing. Results of this meta-analysis of fMRI studies show different frontal and temporal regions that respond more to the syntactic demands of a sentence (in blue) or the semantic demands of a sentence (in red). The regions of BA44 and BA45 are both part of Broca's area, whereas the regions STS (superior temporal sulcus) and MTG (middle temporal gyrus) are in the posterior temporal lobe.

From Hagoort and Indefrey (2014).

(Friederici, 2011, 2012; Newman et al., 2003). This includes, but is not limited to, the syntactic dependency of words in sentences. It is also often assumed to be involved in higher-level motor planning of speech linked to the audio-motor dorsal route of speech perception (Hickok & Poeppel, 2004) or, possibly, a mirror system for speech and other gestures (Rizzolatti & Arbib, 1998). It is higher-level insofar as it does not contain the actual motor programs for speech (Broca's original proposal). One specific suggestion as to how this region might operate is that it generates predictive (top-down) signals to other parts of the brain (in the case of sentences, to the temporal cortex) as to what kind of word is expected (e.g., a noun versus a verb) as well as monitoring (bottom-up) whether the prediction was obtained (Friederici, 2012).

With regards to syntax itself, Friederici et al. (2006b) found increasing activity in BA44 with increasing syntactic complexity; the latter being defined according to whether the word orderings were typical or atypical syntactic constructions in German (Figure 12.17). In a related study, artificial grammars were constructed using nonsense syllables and artificial syntactic structures, rather than using real words and naturally occurring syntax (Friederici et al., 2006a). So instead of using grammatical categories (such as nouns and verbs), arbitrary categories were created (e.g., category A versus category B), and different syntactic rules learned concerning the order in which A and

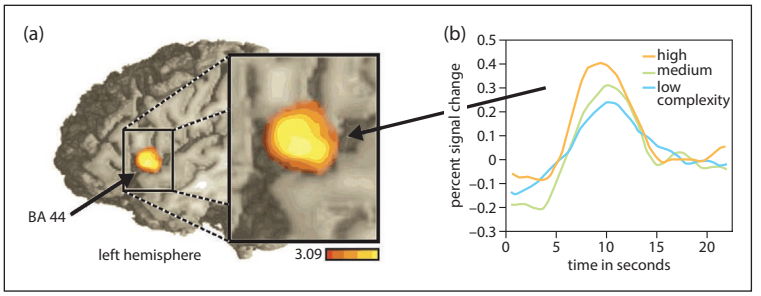

FIGURE 12.17: Processing of sentences, comprising real words, shows increasing activity in a region of Broca's area according to the degree of syntactic complexity.

Adapted from Friederici et al. (2006b).

B may occur (with rules differing in terms of hierarchical complexity). After exposure to grammatical sequences (a learning phase), participants judged whether a sequence was grammatical/ungrammatical (a test phase). Grammaticality judgments at test were linked to activity in BA44 and the degree of activity modulated by syntactic complexity.

The anterior portion of Broca's area (BA45, extending into BA47) is often considered to have rather different functions: specifically relating to working memory and the control of semantic memory. These are clearly important functions for sentence processing but are not directly related to syntax per se. In fMRI studies, judging a word's grammatical class activates BA44 but judging its concreteness (a semantic property) activates the more anterior BA45 region (Friederici et al., 2000). Applying TMS over Broca's region can produce a double dissociation between the processing of meaning (synonym judgments) versus phonology (deciding if two words sound the same) when two written words are presented, with impaired semantic judgments linked to more anterior stimulation (Gough et al., 2005).

Is syntax independent from semantics?

Evidence from patients with acquired brain damage points to some separation between syntax and semantics. Patients with semantic dementia gradually lose the meaning of individual words, but they still produce sentences that are grammatical, albeit lacking in content (e.g., "I've been worried to death thinking, trying, I am going to try and think with you today . . . I think of things, I can't often say . . . er . . . say what to say"; Hodges et al., 1994). Comprehension tests on semantic dementia patients also suggest that they can decide whether a sentence is grammatical or not even if it contains words that they apparently do not understand (e.g., is the following grammatical: "Are the boys fix the radio?"; Rochon et al., 2004). However, some aspects of syntax may depend on the integrity of the semantics of particular words; for example,

when a word is grammatically singular but conceptually plural (e.g., "the *label* on the bottles" refers to more than one label; Rochon et al., 2004).

In normal sentence comprehension, the process of assigning a syntactic structure to words is termed **parsing**. One key debate in the literature concerns the extent to which parsing is based solely on the syntactic properties of words (structure-driven parsing; Frazier & Rayner, 1982) or is additionally influenced by semantic properties of words (discourse-driven parsing; MacDonald et al., 1994). Evidence in favor of single initial computation of sentence structure comes from **garden-path sentences**, in which the early part of a sentence biases a syntactic interpretation that turns out to be incorrect. The classic example of this is given by Bever (1970):

> The horse raced past the barn fell.

In this example, the word "fell" comes as a surprise unless one parses the sentence as "The horse {THAT} raced past the barn {WAS THE ONE THAT} fell." The fact that there is any ambiguity at all suggests that not all possible sentence constructions are considered (consistent with a structure-driven parse). However, in some instances semantics does appear to bias the way that the sentence is parsed (consistent with a discourse-driven parse). For example, being led up the garden path can often be avoided if the ambiguous sentence is preceded by supporting context (Altmann et al., 1994). Consider the following sentence:

> The fireman told the man that he had risked his life for to install a smoke detector.

This sentence is less likely to lead down the garden path if preceded by context such as this (Altmann et al., 1994):

> A fireman braved a dangerous fire in a hotel. He rescued one of the guests at great danger to himself. A crowd of men gathered around him. The fireman told the man that he had risked his life for to install a smoke detector.

On balance, it seems that the setting up of a sentence structure is, to some degree, dependent on both syntactic and contextual factors. Some researchers have taken this evidence as far as to state that syntactic and semantic processes are completely unified (McClelland et al., 1989). However, studies of brain-damaged individuals (see previous) and imaging/ERP methods (see next) speak against such a strong interpretation. It appears that certain aspects of syntax and lexical-semantics can be dissociated from each other.

There is an event-related brain potential (ERP) that is associated with processing syntactic anomalies such as the unexpected word in a garden-path sentence or an overtly ungrammatical sentence

KEY TERMS

Parsing
The process of assigning a syntactic structure to words.

Garden-path sentences
A sentence in which the early part biases a syntactic interpretation that turns out to be incorrect.

KEY TERM

P600
An event-related brain potential (ERP) typically associated with the processing of grammatical anomalies.

(Gouvea et al., 2010). It is termed the **P600** because it is a positive deflection occurring at around 600 ms after word onset. This can be contrasted with N400, introduced earlier, which has been linked to the processing of semantic anomalies (irrespective of whether it is in a sentence context). More generally, the N400–P600 distinction supports the idea that syntax and semantics are separable. The P600 is still found when contrasting ungrammatical relative to grammatical sentences even when both are semantically meaningless (Hagoort & Brown, 1994) such as "The boiled watering can *smokes* the telephone in the cat" (grammatical) versus "The boiled watering can *smoke* the telephone in the cat" (ungrammatical) – see Figure 12.18. The most common cognitive interpretation of the P600 is that it reflects syntactic reanalysis of the sentence. However, it can also be found for (non-garden path) grammatical sentences that are difficult to parse suggesting it is involved in syntactic analysis generally rather than reanalysis in particular (Kaan et al., 2000).

Functional imaging studies suggest somewhat different roles for the anterior and posterior temporal cortex and Broca's area in sentence processing. This may reflect differences between semantics and syntax, and also the interface between them. Pallier et al. (2011) presented sentences of increasing structure made up of either content words (which have lexical-semantics) or nonwords (e.g., "I tosieve that you should begept . . ."). The anterior temporal cortex responded to the presence of word meaning (relative to nonwords) but not the size of the syntactic structure. Both Broca's area and the posterior superior temporal sulcus showed the opposite

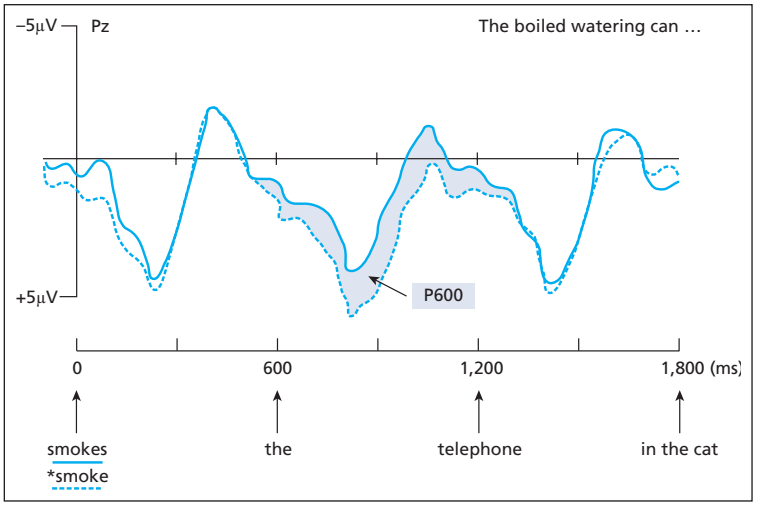

FIGURE 12.18: The P600 is found ~600 ms after a syntactically anomalous (or hard-to-process) word is presented. In this example the P600 is greater for "smoke" than "smokes" in the sentence "The boiling watering can smokes/smoke the telephone in the cat."

From Hagoort (2008). Used with permission of The Royal Society. Permission conveyed through Copyright Clearance Center, Inc.

profile. They argued that the posterior temporal lobes may be the integration site for semantics (originating in the anterior temporal regions) and syntax (within Broca's region). Other fMRI studies show that Broca's area is active when processing hierarchical/syntactic relationships among nonlinguistic symbols (Bahlmann et al., 2008) but that the posterior temporal lobes are only activated when the stimulus material is related to language. This supports the view that this is a syntax-semantics integration site (see Friederici, 2012).

Is syntax independent from working memory?

Increasing syntactic complexity tends to be linked to greater working memory loads. As such, distinguishing between syntax and working memory is not straightforward. It has even been claimed that the only contribution of Broca's area to sentence comprehension is its role in working memory (Rogalsky & Hickok, 2011).

Brain-damaged patients with phonological short-term memory deficits (markedly reduced digit span) can produce and comprehend many sentences adequately (Caplan & Waters, 1990; Vallar & Baddeley, 1984), suggesting a dissociation between the two, but others show clear deficits when syntactically complex sentences are presented (Romani, 1994). In the study by Romani (1994) the comprehension problems were not found when reading text (enabling reinspection to correct parsing) but were found for spoken sentences and when written words were presented one by one (which prevent reinspection and, hence, reanalysis of syntax).

In an fMRI study, Makuuchi et al. (2009) independently manipulated working memory and syntactic complexity (Figure 12.19). The working memory manipulation related to the number of intervening items between the subject of the sentence and the associated verb, whereas the syntax manipulation consisted of the presence/absence of hierarchical syntactic structure (embedding). The effect of syntactic complexity was found in the posterior portion of Broca's area (BA44). The effect of working memory was found in an adjacent, but distinct, region of Broca's area and was also linked to activity in the parietal lobes. Such frontoparietal systems are characteristic of working memory systems in general. Analysis of the functional connectivity between the two frontal regions (i.e., the extent to which their activity is correlated) revealed greater cooperation when processing the demanding embedded sentences.

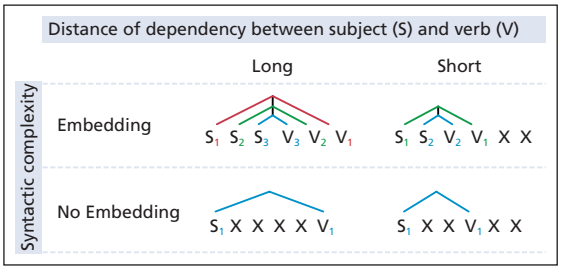

FIGURE 12.19: The experimental design of Makuuchi et al. (2009) varied working memory (short or long distance between a verb and its subject) and syntactic complexity (presence or absence of embedding). An example sentence for a long embedded sentence is "Maria (S1), die (S2) Hans, der (S3) gut aussah (V3) liebte (V2) Johann geküsst hatte (V1)" (translated as "Maria who loved Hans who was good looking kissed Johann"). An example of a long non-embedded sentence is "Achim (S1) den großen Mann gestern am späten Abend gesehen hatte (V1)" (translated as "Achim saw the tall man yesterday late at night").

Evaluation

Broca's region appears to serve multiple functions in sentence processing. It is involved in processing hierarchical dependencies between words in a sentence (e.g., syntactic trees). However, this may be a more general function that is not specific to language. In addition, it is important for verbal working memory, which is needed for processing longer and more complex sentences. It is also important for placing words into context by retrieving or manipulating information in semantic memory. Again, this function is not specific to sentence processing – it is useful for memory (deep encoding) and reasoning (problem solving). Although Broca's region is important for sentence processing, it is not the only region of the brain to be so. It works in concert with other regions of the brain notably the anterior and posterior temporal lobes that are important for processing the meaning of words and sentences. Evidence for the partial separation of syntax and semantics comes from: patient studies (showing dissociations in ability); human electrophysiology (showing temporal dissociations such as the N400 and P600 components); and fMRI (showing different but overlapping neural substrates).

RETRIEVING AND PRODUCING SPOKEN WORDS

Speech production, in natural situations, involves translating an intended idea into a sentence structure and retrieving and producing the appropriate words. To study this process in the laboratory, one standard method has been to study the retrieval of single words in isolation upon presentation of a picture or word definition. Both of these tasks are assumed to initiate semantic processes. A number of broad questions will be considered in this section. How many stages are there in retrieving spoken words, and are the stages discrete or interactive? What type of information is retrieved – syntactic, semantic, morphological, syllabic, phonemic, and so on?

The type of information that needs to be retrieved in speech production is normally divided into three kinds. First, one must select a word based upon the meaning that one wishes to convey. This process is called **lexicalization**. This process is heavily constrained by knowledge of the listener (related to pragmatics). For example, the words "it," "horse," "stallion," and "animal" could, to some extent, all be used to convey the same concept. Second, at least in the context of producing sentences, the grammatical properties of a word must be retrieved and specified. This includes grammatical class (e.g., noun, verb, adjective) and, in many languages, the gender of the word. Finally, the actual form of the word in terms of its constituent syllables, phonemes, and articulatory patterns needs to be retrieved. There is general consensus across different models that these are the kinds of information that need to be retrieved. However, individual models differ in terms of the nature of the mechanisms (e.g., whether different stages interact).

KEY TERM

Lexicalization
In speech production, the selection of a word based on the meaning that one wishes to convey.

DIAGNOSING DEMENTIA VIA DIFFERENCES IN LANGUAGE USE

Alzheimer's disease is known to affect memory and result in word-finding difficulties, but could this be turned around and used diagnostically? The speech and writing of some famous individuals, before and after dementia, provide some initial clues. Iris Murdoch's last novel, *Jackson's Dilemma*, was completed just before her diagnosis of dementia and departed significantly in style from her previous novels. Compared to her earlier works, the use of syntax and overall structure did not change, her vocabulary had changed such that she had a more restricted range of words, particularly relying more on higher-frequency words than before (Garrard et al., 2005).

FIGURE 12.20: Iris Murdoch, 1919–1999.

Machine learning (artificial intelligence) methods can capture these kinds of discriminating linguistic features either from elicited speech, such as describing the Cookie Theft picture (Orimaye, Wong et al., 2017), or from spontaneous speech in free conversation (Horigome et al., 2022). This occurs with relatively high levels of accuracy (90 percent in Horigome et al., 2022) and without the need for before versus after snippets of speech from the same individual.

Studies of speech errors

Observations of everyday speech errors have been useful in constraining theories of word retrieval (Garrett, 1992). Speech errors tend to swap words for words, morphemes for morphemes, phonemes for phonemes, and so on. This provides evidence for the psychological reality of these units. Considering the word level, it is possible to substitute words of similar meaning as in a semantic error, such as saying "dog" for cat. One variant of this error is the **Freudian slip**. Freud believed that speakers repress their true thoughts during conversation, and these could be revealed by inadvertent speech errors (Ellis, 1980). For example, the former British Prime Minister, Tony Blair, mistakenly referred to "weapons of mass *distraction*" (rather than destruction) in a parliamentary debate on the 2003 invasion of Iraq. It is also the case that word substitutions tend to preserve grammatical class, such that nouns swap for nouns, and verbs for verbs, as in the example "guess whose *mind* came to *name*?" (Garrett, 1992). Moreover, affixation of morphemes may occur independently of retrieval of word stems

KEY TERM

Freudian slip
The substitution of one word for another that is sometimes thought to reflect the hidden intentions of the speaker.

KEY TERMS

Malapropisms
A speech error that consists of a word with a similar phonological form to the intended word.

Spoonerisms
A speech error in which initial consonants are swapped between words.

Inner speech
Use of words or images without audible or physical speaking.

Tip-of-the-tongue phenomenon
A state in which a person knows, conceptually, the word that he or she wishes to say but is unable to retrieve the corresponding spoken form.

Anomia
Word-finding difficulties.

(Fromkin, 1971), as illustrated by the example "I random*ed* some sampl*y*" (instead of "I sampled some randomly"). In this instance, the suffix morphemes (–ed, –y) were stranded while the stem morphemes (random, sample) swapped.

A final type of word error is where the error has a similar phonological form to the intended word (e.g., historical → "hysterical") (Fay & Cutler, 1977). These are also called **malapropisms** after the character Mrs. Malaprop (in Sheridan's play *The Rivals*, 1775), who made many such errors. These errors are typically used to support the notion that there is competition between similar words during normal word retrieval, rather than a single word selected immediately. Sometimes the exchange will be between phonemes, and it is generally the case that the exchanged phonemes will occupy the same position in the word (e.g., first consonants swap with each other, vowels swap with each other; Dell et al., 1997). One example of this is **spoonerisms**, in which initial consonants are swapped (e.g., "you have *h*issed all my *m*ystery lectures"). Errors in **inner speech** (saying things in one's head) tend to involve word-level exchanges but not exchanges between similar phonemes, suggesting that inner speech is not a full mental simulation of the speech production process (Oppenheim & Dell, 2008).

Another common, naturally occurring disruption of speech production is the **tip-of-the-tongue phenomenon** (Brown, 1991; Brown & McNeill, 1966). In a tip-of-the-tongue state the person knows, conceptually, the word that he or she wishes to say, but is unable to retrieve the corresponding spoken form for output. It generally produces a "feeling of knowing" and can be intensely frustrating. These states can be elicited by giving people definitions or pictures of relatively infrequent words. For example, "a navigational instrument used in measuring angular distances, especially the altitude of the sun, moon and stars at sea" (the answer being *sextant*). Although the word may be elusive, other types of information may be available. For example, speakers of languages such as Italian often know the gender of a word (Vigliocco et al., 1997), and speakers often know the approximate length of the word or the number of syllables (Brown & McNeill, 1966). These results suggest that words are not retrieved in an all-or-nothing manner but, rather, that different aspects of a word can become available at different stages and relatively independently from each other.

Patients with **anomia** as a result of brain damage have severe word-finding difficulties. This is strongly reminiscent of the normal tip-of-the-tongue state, but in pathological proportions. This symptom can arise from two very different types of impairment. First, it may be a result of a semantic difficulty that results in a failure to distinguish between different concepts and, consequently, a difficulty in specifying the precise word to be retrieved (Caramazza & Hillis, 1990b). Second, other patients may know exactly which word they want to produce but are unable to retrieve the associated phonological information to articulate it (Kay & Ellis, 1987).

Different stages in spoken word retrieval

The most influential models of spoken word retrieval divide the process of getting from a conceptual level of representation to a phonological word form into two steps. Further stages may be involved in translating this into motor commands. Consider the model put forward by Levelt and colleagues (for reviews, see Levelt, 1989, 2001), shown in Figure 12.21. The first stage of their model involves retrieving a modality-independent word-level entry that specifies the syntactic components of the word (e.g., its grammatical class). These are termed **lemma** representations. Thus, this first stage involves lexicalization together with retrieval of syntactic features. The second stage involves retrieval of what they term a **lexeme** representation. Retrieval of the lexeme makes available the phonological code that drives articulation. This lemma–lexeme division accounts for some of the key findings in the speech production literature. First, it offers an account of the tip-of-the-tongue phenomenon by postulating that the lemma may be activated but the lexeme is not active (or is not fully active). Second, it offers a way of distinguishing between words with identical forms that differ in meaning (e.g., "bank" as in money or river) and/or grammatical class (the "watch"/to "watch"). These stimuli have different lemmas but a single lexeme.

KEY TERMS

Lemma
A modality-independent, word-level entry that specifies the syntactic components of the word.

Lexeme
The phonological code that drives articulation.

Levelt's model proposes that these two stages are discrete, such that lexeme retrieval does not begin until lemma selection is complete. Most other models assume interactivity such that multiple kinds of information (semantic, lexical, phonological) are active simultaneously with selection of the "winning" spoken output arising via a competitive process. This process has often been simulated in neural network models. Dell's (1986) model of speech production is shown in Figure 12.22 and also consists of two stages that interact in both a bottom-up and top-down manner. This can explain the presence of *mixed errors* that are both semantically and phonologically similar to the intended word (Dell & Reich, 1981). Examples of these include saying "rat" for cat, and "oyster" for lobster. If it were coincidental, then we would have to assume that "rat" is a semantic error for cat that just so happens to sound like it. However, these errors occur too often to be coincidences (Dell & Reich, 1981), and it suggests, instead, that having similarity at two levels (semantic, phonological) biases the selection process. In tip-of-the-tongue states it is sometimes possible to know the first phoneme without knowing grammatical gender (lexeme access without lemma access), and vice versa, suggesting that different kinds of

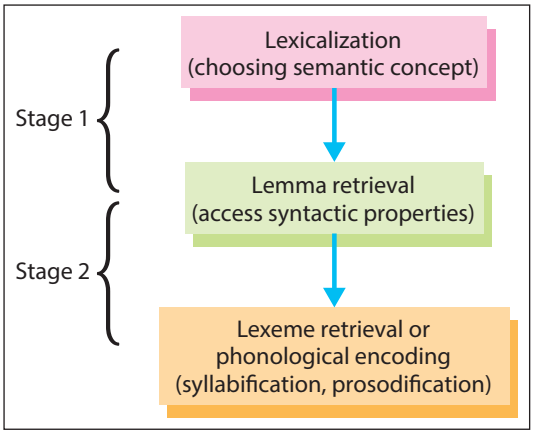

FIGURE 12.21: In Levelt's model, word retrieval takes place in two stages. The stages are discrete such that the second stage does not begin until the first stage is complete, and so phonological factors cannot influence word selection.

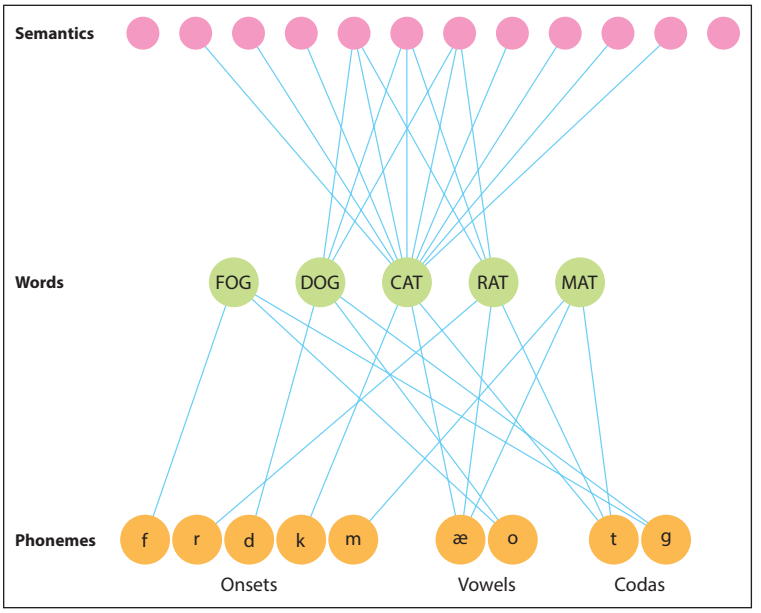

FIGURE 12.22: Dell's model contains three layers that are fully interactive: a layer of semantic features, a layer of words (or lemmas) and a phonological layer (in this version, it consists of different parts of the syllable). Mixed errors, such as cat → "rat," arise because of similarity both at the semantic and the phonological level. Models that do not allow interactive activation from phonology up to words have difficulty accounting for such errors.

information can be accessible without one depending on the other (more consistent with the Dell, 1986, approach). The network can also be "lesioned" by adjusting the weights (i.e., strength of the connections) between the different levels in order to model speech production impairments in aphasia (e.g., Dell et al., 2007). Lesioning the semantic-lexical weights can mimic errors in picture naming (a task in which semantic knowledge is essential), and lesioning the lexical-phonemic weights can mimic errors in repetition (a task in which semantics isn't necessary).

More recent models of speech production have combined the interacting stages approach with neuroscientific models. Walker and Hickok's (2016) model of speech production, which they term SLAM (semantic-lexical-auditory-motor) is based on the dual route model of speech of Hickok and Poeppel (2004). The Hickok and Poeppel (2004) model was initially put forward primarily as a model of speech *perception* with a ventral stream for comprehending speech (auditory to lexical to semantic) and a dorsal stream involved in tasks such as speech repetition and auditory short-term memory (auditory to motor). Walker and Hickok (2016) argue that speech production effectively makes use of the ventral stream in reverse (semantic to lexical to auditory) followed by the dorsal stream to generate the motor output. The idea that speech *production* uses auditory processes is

perhaps counterintuitive. However, it is consistent with the notion of inner speech, and there is some empirical evidence for this assumption. Silent speech production does activate the auditory cortex (Callan et al., 2006), and the severity of speech motor impairments in aphasia are linked to damage of the auditory-motor dorsal route whereas tasks such as picture naming (involving both semantics and speech production) appear to depend on the functioning of both routes (Fridriksson et al., 2018). The theoretical motivation for having the intermediate auditory stage is to be able to predict, and hence monitor, the sensory outcomes of motor actions. This constitutes a "forward model" as discussed previously in Chapter 10 in the context of action predictions.

Articulation: closing the communication loop

This chapter began with a simple model of spoken language in which ideas are shared between a speaker and a listener. Having started at the speech perception end of this loop and considered semantic and syntactic processes, and word retrieval, the final stage to be considered is articulation itself.

As noted earlier, phonemes can be described in terms of a limited set of articulatory gestures such as voicing (i.e., vibration of vocal cords) and place of articulators (e.g., tongue against teeth

ONLINE RESOURCES

Watch informative videos, such as Greg Hickok on "Evolution of Dual Stream Models for Language" and Sophie Scott on "The Neural Basis of Vocal Communication," by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

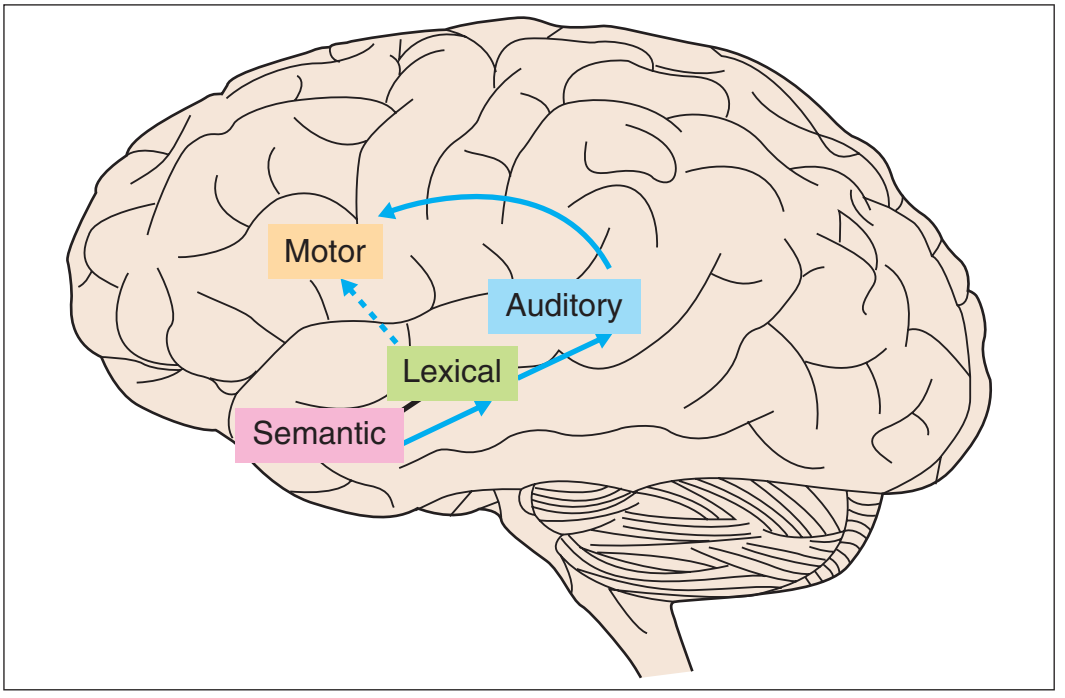

FIGURE 12.23: The SLAM model of speech production has four main stages from semantics -> lexical -> auditory -> motor (noting that the initial letters spell SLAM). As an extension of the Hickok and Poeppel (2004) model, this involves running the auditory ventral stream in reverse followed by the dorsal stream for generating the speech output. A less dominant pathway may link lexical and motor aspects of speech (shown here as a dotted arrow).

or against palate). However, in spite of this, many believe that the phoneme is not the basic unit of articulation. Others have argued that the basic unit of articulation is the syllable – at least for common syllables that may function as overlearned motor patterns (Levelt & Wheeldon, 1994). In connected speech there must be a mechanism that segments the phonological code into syllables across adjacent morphemes and adjacent words. This process has been called *syllabification*. For example, the phrase "he owns it" consists of three syllables ("he," "own," "zit"), in which the final consonant of the word "owns" becomes the onset of the following syllable. Repetition priming studies with fMRI reveal different neuroanatomical basis for syllable-level effects (e.g., in ventral premotor) versus phoneme-level effects (e.g., in basal ganglia) (Peeva et al., 2010).

As with all forms of voluntary movements, speech production ultimately depends upon the primary motor cortex (M1) to initiate movement of the mouth, jaw, and tongue. A region of M1 has also been identified by fMRI that responds selectively to movement of the glottal folds of the larynx relative to the other articulators (Brown et al., 2008). Flinker et al. (2015) explored the timing of activity in three key regions (motor cortex, Broca's area, and auditory cortices in the superior temporal gyrus) using direct electrophysiological recordings in humans undergoing brain surgery for epilepsy. The task of repeating speech involves both speech perception and speech production and, during this task, activity cascaded from auditory regions to Broca's area, to motor regions, although the activation wasn't in discrete stages (e.g., Broca's area became active before activity in auditory areas had finished). This is shown in Figure 12.24. Broca's area was not activated during the speech production phase consistent with the contemporary view that it does not contain actual motor programs. However, it may still be important for preparing speech production. It was activated more for unfamiliar syllables (nonwords) relative to words, suggesting it is involved in structuring novel speech elements. Other research shows that facilitatory forms of TMS over Broca's area improves the accuracy of repetition of foreign (i.e., meaningless) speech (Restle et al., 2012). In the Flinker et al. (2015) study, the auditory cortex was activated both in speech perception and speech production. The latter occurs because participants can hear their own voice, but note that hearing one's own voice produced far less activation than hearing other people speak. This is because auditory monitoring processes enable us to predict the sensory consequences of our own speech and hence dampen them (Hickok, 2012); this is the same reason why we find it hard to tickle ourselves. Mirror neurons that have both sensory (including auditory) and motor components may also be important in this process of predicting the sensory outcomes of motor acts (Guenther & Vladusich, 2012).

Although the primary motor cortex is essential for producing speech, other brain regions may be involved in coordinating that process. Damage to these regions produces poorly articulated speech. Patients with articulation disorders typically have damage to the basal ganglia and/or the insula cortex (Dronkers, 1996). Damage to the insula can result in difficulties in shaping the vocal tract, known

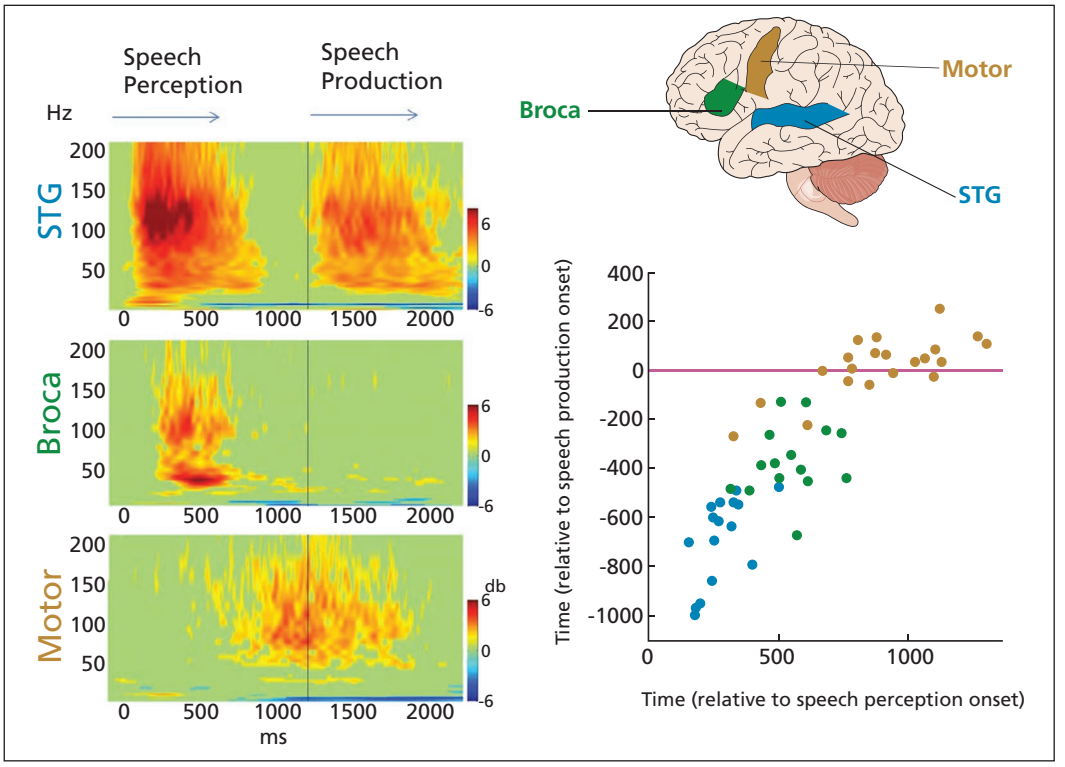

FIGURE 12.24: Electrical activity (measured in terms of rate of change of local electrical fields, Hz) during speech repetition follows a temporal pattern from auditory regions (STG) to Broca's area, to motor cortex. The figures on the left show mean electrical activity, and the figure on the right shows the peak of electrical activity over different electrodes (each dot is an electrode).

as **apraxia for speech** (Dronkers, 1996). People with apraxia for speech know what it is that they want to say and have normal muscle tone of the speech articulators, but distort the production of consonants, vowels, and prosody. This is sometimes perceived by others as sounding like a foreign accent (Moen, 2000). By contrast, damage to the cerebellum and basal ganglia can result in impaired muscular contractions known as **dysarthria** (Kent et al., 2001).

KEY TERMS

Apraxia for speech
Difficulties in shaping the vocal tract.

Dysarthria
Impaired muscular contractions of the articulatory apparatus.

SUMMARY AND KEY POINTS OF THE CHAPTER

- Speech perception exploits the rhythmic nature of the input signal by having a wavelike neuronal response profile which corresponds roughly to different parts of speech (phonemes, syllables, stress patterns).
- Recognizing spoken words involves a process of competition and selection between similar-sounding words, as in the "cohort model."
- The meaning of words may be represented as a network of distributed semantic features, but there is controversy

as to how these features are internally organized and whether the features are amodal or are part of a wider network that supports perception and action.
- Deficits in syntax (word order) can occur largely, although perhaps not completely, independently from deficits in semantics (word meaning) and vice versa. However, there is little evidence for a single "syntax module" that is disrupted in aphasic disorders, such as agrammatism or that arises specifically from lesions to Broca's area.
- Producing spoken words involves retrieving different kinds of information: semantic, grammatical, and phonological. Evidence from tip-of-the-tongue, anomia, and everyday speech errors suggests that some information can be retrieved in the absence of other types of information.
- Speech production is likely to involve many of the neural substrates of speech perception (perhaps used in reverse) with speech itself generated by the motor cortex.

EXAMPLE ESSAY QUESTIONS

- How is auditory input mapped onto our stored knowledge of spoken words?
- Does speech perception use mechanisms involved in speech production?
- How do studies of the N400 and P600 shed light on the cognitive architecture of language processing?
- Does semantic memory depend on brain systems specialized for perception and action?
- What is the role of Broca's region in language?
- Do models of word retrieval require discrete stages corresponding to semantics, grammar, and phonology?

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CHAPTER 13

The literate and numerate brain

CONTENTS

Literacy and numeracy provide cognitive neuroscience with important examples of "expert systems." These depend significantly on formal training and cultural inventions (e.g., writing, algebra) but they also only exist because the (human) brain provides a suitable scaffold for these skills in the first place. Literacy is too recent an invention to have evolved specific neural substrates, having first emerged around 5,000 years ago. There would also have been no formal numerical notation before this time, although early counting systems existed. Archaeological evidence suggests that Cro-Magnon man, around 30,000 years ago, kept track of the phases of the moon by making collections of marks on bones (Marshack, 1991). Universal literacy has only occurred in Western societies over the last 150 years, and levels of literacy in developing countries have only changed substantially over the last 40 years (UNDP, 2011).

Learning to read and write, and use number symbols, may involve the construction of a dedicated neural and cognitive architecture in the brain. But this is likely to be derived from a core set of other skills that have developed over the course of evolution. In general support of this view, we find that different individuals (across diverse cultures) acquire networks for literacy and numeracy in roughly the same place in the brain (which would not be expected if they could simply

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KEY TERM

Neuronal recycling
A tendency to reuse parts of the brain that evolved for evolutionary older functions (e.g., visual recognition) for culturally modern ones (e.g., reading).

be slotted in using any "spare" neurons). This has been referred to as **neuronal recycling** (Dehaene & Cohen, 2007). In literacy, the basic neuronal scaffolding includes visual recognition, manipulation of sounds, and learning and memory. In numeracy, these skills are needed too, but one additional claim is that there is a special system for number meaning within the parietal cortex that predates skilled numeracy (e.g., it is found in human infants and many other animals). Recall from Chapter 12 that semantic memory consists of a distributed network with different pockets of specialization and a hub within the temporal lobes for most words but perhaps not numbers (Cappelletti et al., 2002). One curious consequence of this is that reading the similar words FIVE and FIRE might lead to the activation of different neural networks within that system.

This chapter begins by considering the visual recognition of letters, digits, and words within the visual ventral stream and considers how and why this region becomes specialized for this kind of material. The middle sections then consider how written words are read aloud and understood by connecting with various aspects of the language system. Evidence from different languages and scripts will be considered as well as from impaired reading following acquired brain damage and in developmental dyslexia. The final part of the chapter contrasts symbolic processing of numbers (e.g., written digits) with nonsymbolic aspects of number (e.g., different sized collections of objects) to illustrate how our culturally acquired systems interface with older (in evolutionary terms) cognitive capacities for basic numeracy.

THE ORIGINS AND DIVERSITY OF WRITING SYSTEMS

Writing has its historical origins in early pictorial representation (Figure 13.1). The point at which a picture ceases to be a picture and becomes a written symbol may relate to a transition between attempting to depict an object or concept rather than representing units of language (e.g., words, phonemes, morphemes). For example, although Egyptian hieroglyphs consist of familiar objects (e.g., birds, hands), these characters actually denote the sounds of words rather than objects in themselves. As such, this is a true writing system that is a significant step away from the pictorial depictions of rock art.

Different cultures appear to have made this conceptual leap independently of each other (Gaur, 1987). This explains some of the great diversity of writing systems (see Figure 13.2). The earliest writing system emerged between 4,000 and 3,000 BCE, in what is now southern

FIGURE 13.1: The diversity of written language.

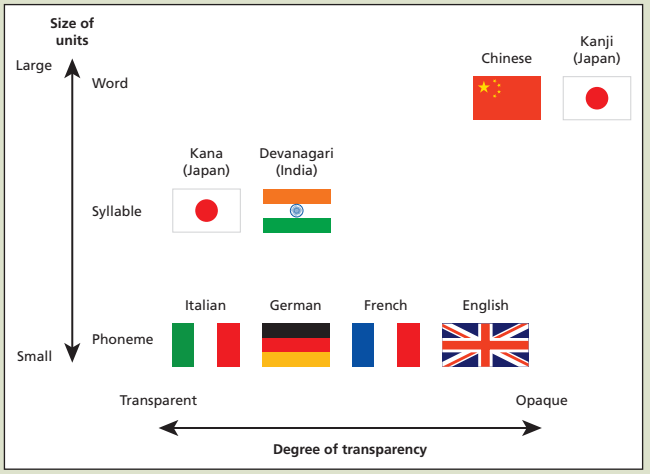

FIGURE 13.2: Writing systems can be classified according to the size of the linguistic unit denoted (phoneme, syllable, word) and the degree of regularity (or transparency) between the written and spoken forms.
From Dehaene (2010, p. 117).

Iraq, and was based on the one-word–one-symbol principle. Scripts such as these are called **logographic**. Modern Chinese and Japanese **Kanji** are logographic, although they probably emerged independently from the Middle Eastern scripts. Individual characters may be composed of a number of parts that suggest meaning or pronunciation, but the arrangement of these parts is not linear like in alphabetic scripts.

Other types of script represent the sounds of words. Some writing systems, such as Japanese **Kana** and ancient Phoenician, use symbols to denote syllables. Alphabetic systems are based primarily on mappings between written symbols and spoken phonemes. All modern alphabets are derived from the one used by the Phoenicians; the Greeks reversed the writing direction to left–right at some point around 600 BC.

The term **grapheme** is normally used to denote the smallest meaningful unit of written language, analogous to the term "phoneme" in spoken language. In languages such as English, this corresponds to individual letters (Henderson, 1985), although the term is also often used to refer to letter clusters that denote phonemes (e.g., in the latter definition, the word THUMB would have three graphemes: TH, U, and MB, corresponding to the phonemes "th," "u," and "m").

It is important to note that not all alphabetic scripts have a very regular mapping between graphemes and phonemes. Such languages are said to be **opaque**. Examples include English and French (consider the different spellings for the words COMB, HOME, and ROAM). Not all irregularities are unhelpful. We write CATS and DOGS (and not CATS and DOGZ) and PLAYED and WALKED (not PLAY*ED* and WALK*T*), to preserve common morphemes for plural and past tense, respectively. However, other irregularities of English reflect historical quirks and precedents (Scragg, 1974). For example, KNIFE and SHOULD would have been pronounced with the "k" and "l" until the seventeenth century. Moreover, early spelling reformers changed spellings to be in line with their Greek and Latin counterparts (e.g., the spelling of DETTE was changed to DEBT to reflect the Latin "*debitum*"). Other languages, such as Italian and Spanish, have fully regular mappings between sound and spelling; these writing systems are said to be **transparent**. Different writing systems can be conceptualized in terms of both the size of the linguistic unit and the degree of transparency, as shown in Figure 13.2.

KEY TERMS

Logographs
Written languages based on the one-word–one-symbol principle.

Kanji
A Japanese writing system based on the logographic principle.

Kana
A Japanese writing system in which each character denotes a syllable.

Grapheme
The smallest meaningful unit of written language.

Opaque orthography
A system of written language with an irregular (or semi-regular) correspondence between phonemes and graphemes.

Transparent orthography
A system of written language with a regular correspondence between phonemes and graphemes.

Word superiority effect
It is easier to detect the presence of a single letter presented briefly if the letter is presented in the context of a word.

Lexical decision
A two-way forced-choice judgment about whether a letter string (or phoneme string) is a word or not.

VISUAL RECOGNITION OF LETTERS, WORDS, AND NUMBERS

Interactions between parts and wholes

One of the earliest findings in the study of visual word recognition was the fact that there is little processing cost, in terms of response times, for recognizing long relative to short words (Cattell, 1886). Of course, reading a long word out loud will take longer than reading a short word aloud, and the time between seeing a word and *saying* the word is also related to word length (Erikson et al., 1970). But the actual *visual* process of recognizing a word as familiar is not strongly affected by word length. This suggests a key principle in visual word recognition – namely, that the letter strings are processed in parallel rather than serially one by one.

Visual word recognition also appears to be greater than the sum of its parts (i.e., its constituent letters) insofar as patterns across several letters are also important. If one is asked to detect the presence of a single letter (e.g., R) presented briefly, then performance is enhanced if the letter is presented in the context of a word (e.g., CARPET) or a nonsense letter string that follows the combinatorial rules of the language (e.g., HARPOT), compared with a random letter string (e.g., CTRPAE) or even a single letter in isolation (Carr et al., 1979; Reicher, 1969). This is termed the **word superiority effect**. It suggests that there are units of representation corresponding to letter clusters (or known letter clusters comprising words themselves) that influence the visual recognition of letters and words. Intracranial EEG recordings suggest that word and word-like stimuli are distinguished from consonant strings after around 200 ms in the mid-fusiform cortex (Mainy et al., 2008). Scalp EEG recordings reveal a similar picture but suggest an interaction between visual processes and lexical-semantic processes such that stimuli with typical letter patterns can be discriminated at around 100 ms (e.g., SOSSAGE compared with SAUSAGE), but with words differing from nonwords at 200 ms (Hauk et al., 2006). This latter effect was interpreted as top-down activity from the semantic system owing to the EEG source being located in language rather than visual regions.

The word superiority effect implies that there is a role of top-down information in visual word recognition, as summarized in Figure 13.3. That is, stored knowledge of the structure of known words can influence earlier perceptual processes (McClelland & Rumelhart, 1981; Rumelhart & McClelland, 1982). One commonly used task to investigate word recognition is **lexical decision** in which participants must make a two-way forced-choice judgment about whether a letter string is a word or not. Nonwords (also called pseudo-words) are much faster to reject if they do not resemble known words (Coltheart et al., 1977). For example, BRINJ is faster to reject than BRINGE. According to many models of word recognition, the task of lexical decision is performed by matching

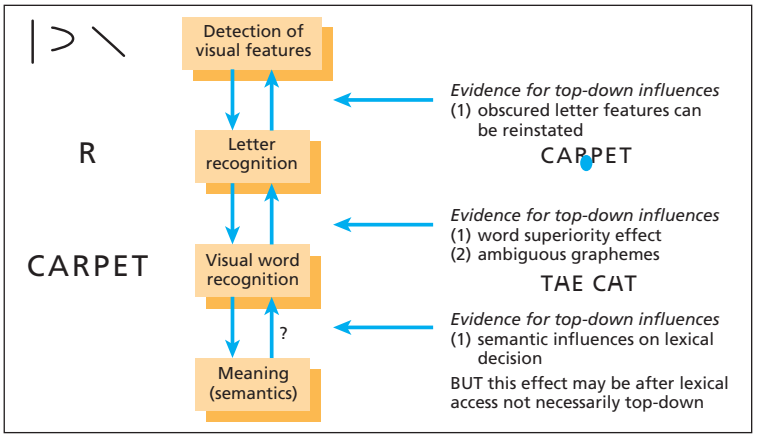

FIGURE 13.3: A basic model of visual word recognition showing evidence in favor of top-down influences.

the perceived letter string with a store of all known letter strings that comprise words (e.g., Coltheart, 2004a; Morton, 1969). This store is referred to as the **visual lexicon** (also the orthographic lexicon). Under this account, there is no reason to assume that meaning or context should affect tasks such as lexical decision. However, such effects have been reported and provide evidence for semantic influences on word recognition. Lexical decision, during fMRI, activates a wider network of regions involved in language and semantic memory (Binder et al., 2003) and lexical decisions for semantically related word pairs (e.g., BREAD and BUTTER) are performed faster than unrelated pairs (Meyer & Schvaneveldt, 1971).

Digits (e.g., 5) are visually comparable to letters (e.g., S), but they function more like a Chinese logograph in that they represent a single concept/word rather than attempting to map on to a part of spoken language (e.g., phoneme or syllable). Similarly, the relationship between parts and wholes in multi-digit numbers (e.g., 5213) captures something important about its meaning – the **place value system** – that does not have a counterpart in written words. The place value notation means that the quantity is determined by its place in the written string – thus the "2" in 12, 20, and 285 all mean something different (2, 20, and 200 respectively). Moreover, when reading aloud in English, the written digit 2 can be verbally rendered as "two," "twelve" or "twenty" depending on the context in which it is used. The same cannot always be said of other languages. Chinese children must learn the numbers up to 10, but thereafter it is easy (Figure 13.4). Thus, 12 is literally translated as "ten-two" in Chinese and 21 is "two-ten-one." Not surprisingly, Chinese-speaking children outperform their English-speaking counterparts when learning to count (Miller & Stigler, 1987). However, the overall writing system in China poses a general disadvantage when it comes to literacy learning.

KEY TERMS

Visual lexicon
A store of the structure of known written words.

Place value system
A system of writing numbers in which the quantity is determined by its place in the written string.

FREE
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ONLINE RESOURCES

Visit the demo test library (www.testable.org/ward) to test yourself on the word superiority effect and lexical decision.

FIGURE 13.4: Why do Chinese-speaking children find learning to count easier than speakers of many other languages?

kiankhoon/iStock

The visual word form area (VWFA)

Within the brain, the visual system may implement an interactive hierarchy from simple features to increasingly complex ones, as shown in Figure 13.5. However, the question as to what sits at the top of the hierarchy is a matter of debate. A neuron that responds to a particular word would be equivalent to a grandmother cell, but it is also possible that words emerge from the distributed co-activation of letters or letter clusters.

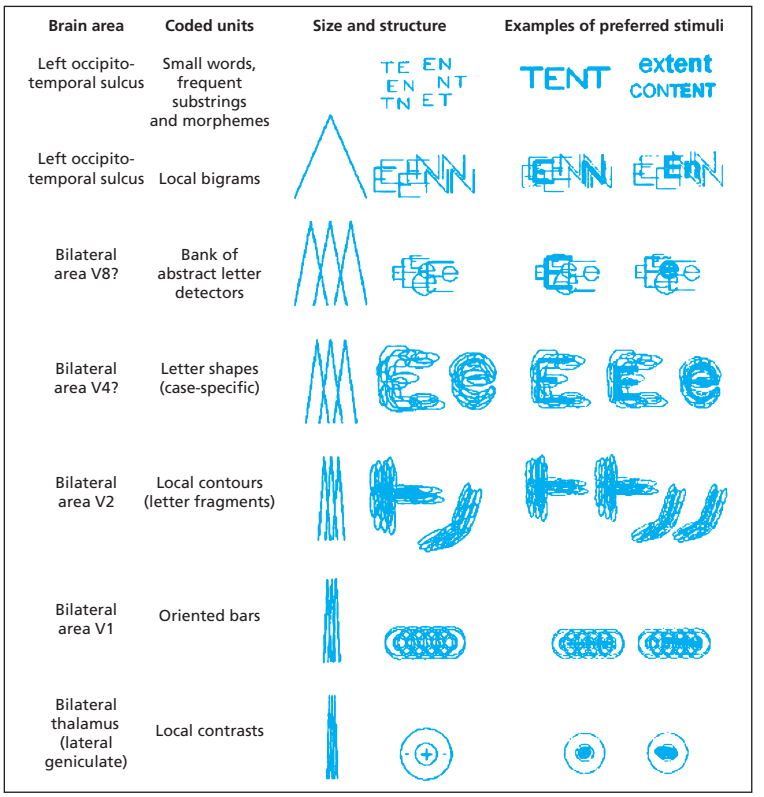

FIGURE 13.5: Visual word recognition can be considered as a hierarchy that progresses from relatively simple visual features (e.g., based on processing of contrast and line orientation), to shape recognition, to culturally tuned mechanisms that, for instance, treat *E* and *e* as equivalent. It is still debated as to what sits at the very top of the hierarchy: it may consist of whole words (i.e., a lexicon) or common letter patterns.

From Dehaene et al. (2005). Trends in Cognitive Science.

CHARACTERISTICS OF THE VISUAL WORD FORM AREA

- Responds to learned letters compared with pseudo-letters (or false fonts) of comparable visual complexity (Price et al., 1996b).
- Repetition priming suggests that it responds to both upper- and lower-case letters even when visually dissimilar (e.g., "a" primes "A" more than "e" primes "A") (Dehaene et al., 2001).
- Subliminal presentation of words activates the area, which suggests that it is accessed automatically (Dehaene et al., 2001).
- Electrophysiological data comparing true and false fonts suggest that the region is activated early, at around 150–200 ms after stimulus onset (Bentin et al., 1999).

The VWFA is located in the left mid-occipitotemporal gyrus (also called the fusiform gyrus), shown in Figure 13.6. Some of the response characteristics of this region to visual stimuli are listed above. Meaningless shapes that are letter-like do not activate the region. This suggests that the neurons have become tuned to the visual properties of known letters and common letter patterns (Cohen et al., 2002). This particular region of the brain lies along the visual ventral stream (Chapter 7), and neurons in this region are known to respond to particular visual features (e.g., shapes, junctions) and have large receptive fields (i.e., do not precisely code for location of objects).

The VWFA also responds to nonwords made up of common letter patterns as well as to real words, although the degree of this activity may be task dependent (e.g., reading versus lexical decision; Mechelli et al., 2003). The responsiveness to nonwords has cast some doubt over whether this region is actually implementing a visual lexicon (i.e., a store of known words). One reason a neural implementation of a visual lexicon could respond to nonwords, at least to some degree,

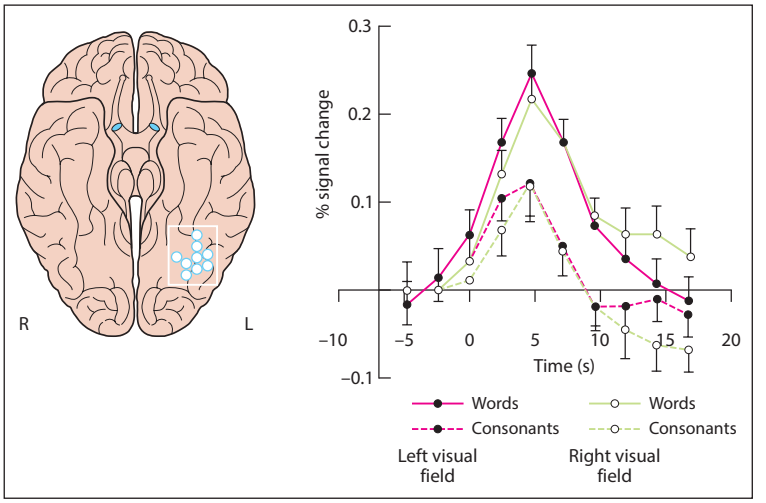

FIGURE 13.6: The visual word form area is located on the rear undersurface of the brain, primarily in the left hemisphere. It responds to written words more than consonant strings, and irrespective of whether they are presented in the left or right visual field.

Reprinted from McCandliss et al. (2003). © 2003, with permission from Elsevier.

as well as real words is because nonwords can only be classified as such after a search of the visual lexicon has failed to find a match (Coltheart, 2004a). Thus, a neural implementation of a visual lexicon could be activated by the search process itself, regardless of whether the search is successful or not (i.e., whether the stimulus is a word or nonword). Dehaene and colleagues (2002) initially argued that the VWFA contains a prelexical representation of letter strings, whether known or unknown. Subsequent evidence led them to refine this to include several different-sized orthographic chunks including words themselves (Dehaene & Cohen, 2011). For instance, the BOLD activity in the VWFA is unaffected by the length of real words suggesting that the letter pattern might be recognized as a single chunk (Schurz et al., 2010). The same isn't found for nonwords which implies that their processing is not holistic. Moreover, BOLD activity in the VWFA differentiates real words from the same-sounding nonwords (e.g., taxi versus taksi; Kronbichler et al., 2007). This suggests that word-based activity is indeed related to the letter pattern rather than phonology.

Given that visual recognition of letters and words is a culturally dependent skill, why should it be the case that this same part of the brain becomes specialized for recognizing print across different individuals and, indeed, across different writing systems (Bolger et al., 2005)? Possible answers to this question come from studies examining the function of the VWFA in illiterate people and also in people who do not read visually (Braille readers). Dehaene et al. (2010) compared three groups of adults using fMRI: illiterates, those who became literate in childhood, and those who became literate in adulthood. They were presented with various visual stimuli such as words, faces, houses, and tools. Literacy ability was correlated with increased activity of the left VWFA, and there was a tendency for literacy to reduce the responsiveness of this region to faces (which displaced to the right hemisphere). The basic pattern was the same if literacy was acquired in childhood or adulthood. Subsequent studies have explored this further in children. Voxels in the fusiform gyrus are differentially sensitive to faces and letters using fMRI even before children learn to read (Cantlon et al., 2011; Dehaene-Lambertz et al., 2018). This doesn't mean that literacy is innate, only that letters can tap into certain core visual mechanisms. As the child learns to read these initial biases become even more selective: so, a voxel that initially responded strongly to letters and less strong to faces will continue to respond strongly to letters but now only very weakly to faces (the non-preferred category is diminished).

To what extent is the VWFA strictly "visual"? An fMRI study of congenitally blind individuals found that they activated the left VWFA when reading Braille relative to touching other kinds of object (Reich et al., 2011). Thus, the VWFA is not strictly visual but may preferentially process certain types of shape. The idea that shape is important comes from studies of "reading" with Morse code. In Morse code, letters are represented as a series of auditory dots and dashes (i.e., short and long tones). For instance, the letter "A" is dot-dash. However, Morse code readers don't activate the

VWFA (Maier et al., 2004), unlike Braille readers. This suggests that the VWFA doesn't represent all letter codes but may be more specialized for shape (from visual letters and Braille but not Morse). The tendency for it to be predominantly left-lateralized may arise from the need for it to establish close ties with the language system (i.e., another non-visual factor). Indeed literates, relative to illiterates, show greater top-down activation of the VWFA in response to processing speech (Dehaene et al., 2010). Further evidence that the laterality of the VWFA is dependent on the location of the speech system comes from studies of left-handers. Whereas right-handers tend to have left lateralization for speech production, left-handers show more variability (some on the left, others on the right or bilateral). In left-handers, the lateralization of the VWFA tends to correlate with the dominant lateralization of speech observed in the frontal lobes (Van der Haegen et al., 2012). This again suggests that the development of a putatively "visual" mechanism is linked to important non-visual influences.

Other researchers have argued that the existence of the visual word form area is a "myth," because the region responds to other types of familiar stimuli, such as visually presented objects and Braille reading, and not just letter patterns (Price & Devlin, 2003, 2011). These researchers argue that this region serves as a computational hub that links together different brain regions (e.g., vision and speech) according to the demands of the task. This, of course, is not completely incompatible with the view described by others: that is, that the region becomes progressively tuned to certain stimuli more than others and interacts with the language system (bidirectionally). In support of this, Saygin et al. (2016) scanned children twice with fMRI, once at age 5 (before they could read) and again at age 8 years. Individual differences in the location of the VWFA at age 8 could be predicted by how this region structurally connected (using DTI) with language regions of the brain at age 5. Thus, the specialization of the VWFA emerges both from its visual responsiveness (in sighted people) and by virtue of it being a connecting hub to other regions.

Pure alexia or "letter-by-letter" reading

In addition to the aforementioned neuroimaging evidence, it has also been argued that damage to the VWFA region produces a specific difficulty with reading – namely, pure alexia or letter-by-letter reading (Pflugshaupt et al., 2009). Imagine that a patient comes into a neurological clinic complaining of reading problems. When shown the word CAT, the patient spells the letters out "C," "A," "T" before announcing the answer – "cat." When given the word CARPET, the patient again spells the letters out, taking twice as long overall, before reading the word correctly. While reading is often accurate, it appears far too slow and laborious to be of much help in everyday life. Historically, this was the first type of acquired dyslexia to be documented, and it was termed **pure alexia** to emphasize the fact that reading was compromised without

KEY TERM

Pure alexia
A difficulty in reading words in which reading time increases proportionately to the length of the word.

impairment of spelling, writing, or verbal language (Dejerine, 1892). It is also sometimes called "letter-by-letter reading" (Patterson & Kay, 1982), although not all patients with pure alexia use the strategy of reading single letters aloud.

The defining behavioral characteristic of pure alexia is that the patients have a relatively selective problem in reading words (but not in speaking per se or all aspects of vision), such that reading time increases proportionately to the length of the word (the same is true of nonwords). This is illustrated in Figure 13.7 (left). This is consistent with the view that each letter is processed serially in these patients rather than the normal parallel recognition of letters in visual word recognition. However, patients with pure alexia tend to be quite heterogeneous in their exact profile on behavioral tests. Some pure alexic patients have problems in visual recognition of individual letters (although letters are still recognized better than words) that can be made worse by perceptual distortions of the text (e.g., script or "joined-up" writing is harder to read than print) (Warrington & Shallice, 1980). For other patients their problem seems to reflect a breakdown of abstract orthographic knowledge that is not strictly visual. For example, some patients are impaired at deciding whether two letters of different case (e.g., "E," "e") are the same, but can detect real letters from made-up ones, and real letters from their mirror image (Miozzo & Caramazza, 1998). This heterogeneity may reflect differences in lesion location within a hierarchically organized system of visual/orthographic information in and around the VWFA (Purcell et al., 2014), such as that illustrated earlier in Figure 13.5. Disruption of information flow at various stages, from early visual to word-specific levels, can result in cessation of parallel letter reading and adoption of letter-by-letter strategies (Behrmann et al., 1998; Bowers et al., 1996). These latter models have typically used "interactive activation" accounts in which there is a cascade of bottom-up and top-down processing, such that a problem at one level propagates to other levels. Another line of evidence suggests that the flow of information from lower to higher levels is reduced rather than blocked. Many pure alexic patients are able to perform lexical decisions or even semantic categorizations (animal versus object) for briefly presented words that they cannot read (e.g., Bowers et al., 1996). For this to occur, one needs to assume that there is some

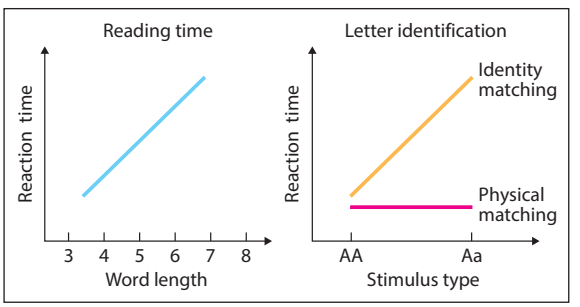

FIGURE 13.7: In pure alexia (or letter-by-letter reading), reading time is slow and laborious and is strongly affected by word length (see graph on the left). Patients often have difficulty in determining whether two letters are the same when they differ by case (e.g., slow at judging that A–a have the same identity, but not at judging that A–a are physically different; see graph on the right). The disorder results in a difficulty in parallel processing of abstract letter identities, but it is still debated whether the primary deficit is visual or reading-specific.

Data adapted from Kay and Hanley (1991).

partial parallel processing of the letter string that is able to access meaning and lexical representations, but that is insufficient to permit conscious visual word recognition (Roberts et al., 2010).

Number form area (NFA)?

Anderson et al. (1990) report a brain-damaged patient who could still read and write numbers, but not letters or words, and Cipolotti (1995) reports the opposite dissociation. These results are surprising given the visual and motoric similarity of letters and numbers (e.g., 5 and S). However, this division is supported by neuroimaging evidence. Shum et al. (2013) found a distinct region of fusiform cortex that responded to Arabic numerals (e.g., 2) more than letters, false fonts or even written number names (e.g., TWO). This has been termed the **number form area (NFA)**. Functional connectivity of this region, assessed with resting state fMRI, shows that it connects with bilateral intra-parietal sulcus in contrast to the nearby VWFA (responding more to letters), which connects with left-hemisphere language regions (Abboud et al., 2015). This region is shown in Figure 13.8. That is, the specialization of certain neurons to cultural symbols doesn't just reflect their perceptual properties (e.g., shape) but reflects the optimization of connectivity to other regions that are part of the relevant network. Words and numbers project to somewhat different networks because of their different properties: differences in meaning and difference in structure (e.g., alphabetic scripts can be decoded into phonemes).

KEY TERM

Number form area (NFA)
A region of fusiform cortex that responds, in brain imaging, to numerals more than letters.

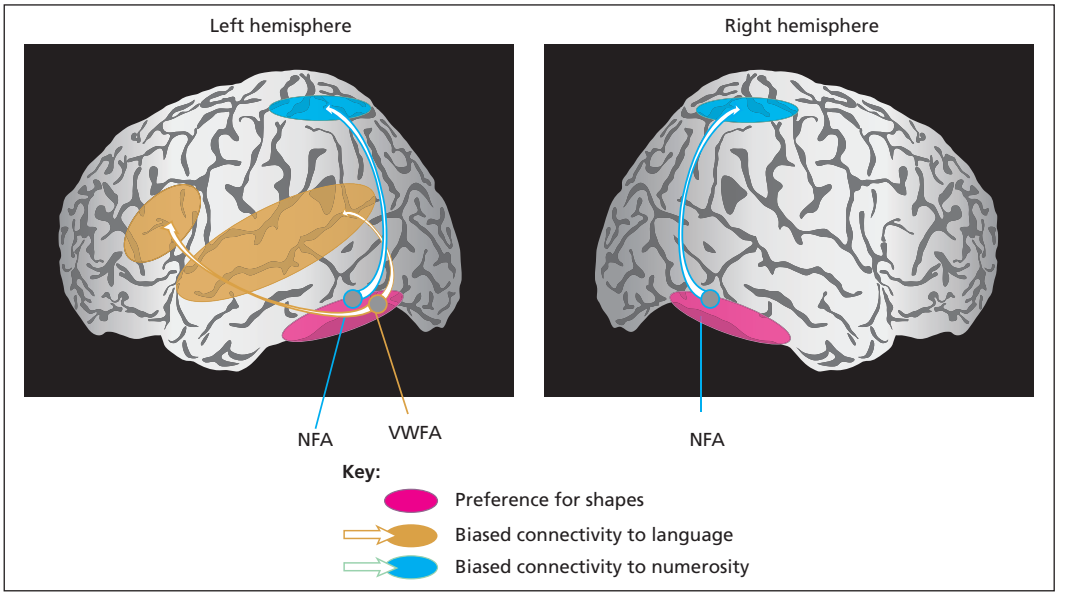

FIGURE 13.8: The number form area (NFA) and visual word form area (VWFA) lie close to each other in the fusiform cortex (specialized for shape) but have different patterns of connectivity.

Adapted from Hannagan et al. (2015).

Evaluation

There is good evidence that there is a region within the mid-fusiform cortex that responds relatively more to word and word-like stimuli than other kinds of visual object. Although located within the "visual" ventral stream, neither its precise function nor anatomical location are strictly visual. Instead, it is a region that connects vision to the wider language network and also shape perception from other senses (including touch). Numbers have a preferential connection to parietal cortex rather than the language network. Whether the VWFA stores known words (i.e., implements a visual lexicon) in addition to letter patterns remains a matter of debate as the presence of word-specific effects could be related to top-down effects (e.g., from the semantic system) rather than reflecting a store of word forms.

SKILLED READING: FROM SPELLING TO SOUND AND MEANING

There are, broadly speaking, two things that one may wish to do with a written word: understand it (i.e., retrieve its meaning from semantic memory) or say it aloud (i.e., convert it to speech). Are these two functions largely separate or is one dependent on the other? For instance, does understanding a written word require that it first be translated to speech (i.e., a serial architecture)? This possibility has sometimes been termed **phonological mediation**. A strict model of that kind would make it impossible to understand **homophones** (words with the same phonology but different spelling, e.g., ROWS and ROSE), which is not the case. It is even the case in acquired aphasic patients who make phonemic errors during reading and naming can still sometimes differentiate the meaning of pairs of words such as ROWS and ROSE (Hanley & McDonnell, 1997). The alternative proposal is that understanding written words and transcoding text into speech are two largely separate, but interacting, parallel processes. The evidence largely supports the latter view and has given rise to so-called dual-route architectures for reading, which is discussed in this section.

KEY TERMS

Phonological mediation
The claim that accessing the spoken forms of words is an obligatory component of understanding visually presented words.

Homophone
Words that sound the same but have different meanings (and often different spellings), for example, ROWS and ROSE.

Dual-route models

The most influential models of reading aloud are based on a dual-route model of reading initially put forward by Marshall and Newcombe (1973) but developed further by others (in particular see Coltheart et al., 2001). The standard dual-route model is shown in Figure 13.9. The key features of this model are (1) a semantically based reading route in which visual words are able to access semantics directly and (2) a phonologically based reading route that uses known regularities between spelling patterns and phonological patterns (e.g., the letters TH are normally pronounced as "th") to achieve reading. This route is also called grapheme–phoneme conversion. The key aspect of the model is that the different routes may be preferentially

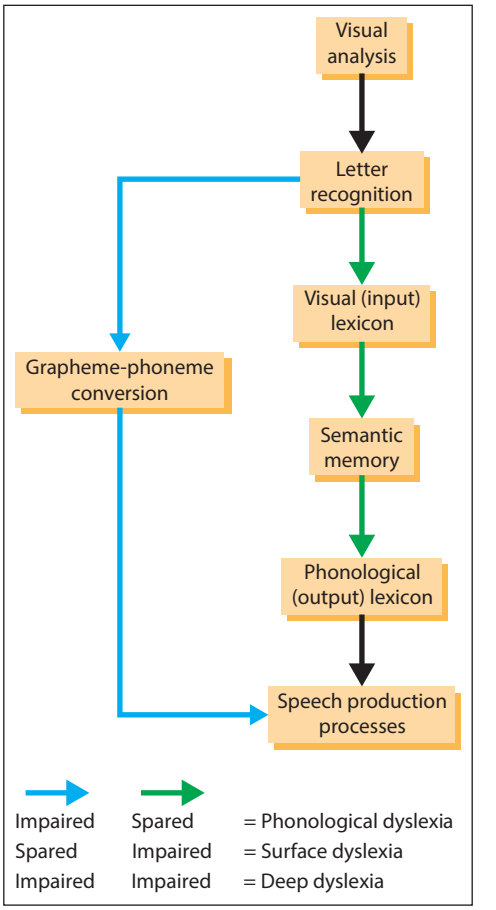

FIGURE 13.9: A dual-route model of reading. The standard lexical–semantic and grapheme–phoneme conversion routes are shown in green and red, respectively. Grapheme–phoneme conversion is a slower route that can accurately read nonwords and regularly spelled words. The lexical–semantic route is faster and can read all known words (whether regular or irregularly spelled) but is more efficient for common, high-frequency words.

used for different kinds of orthographic stimuli, although skilled reading will ultimately derive from the combination of both. The grapheme–phoneme conversion route is essential for reading nonwords, which, by definition, do not have meaning or a stored lexical representation. Known words, by contrast, do have a meaning and can be read via direct access to the semantic system and the stored spoken forms of words. Of course, many of these words could also be read via grapheme–phoneme conversion, although in the case of words with irregular spellings it would result in error (e.g., YACHT read as "yatched" instead of "yot"). The extent to which each route is used may also be determined by speed of processing – the direct semantic access route is generally considered faster. This is because it processes whole words, whereas the grapheme–phoneme conversion route processes them bit by bit. The semantic route is also sensitive to how common a word is – known as word frequency (and not to be confused with "frequency" or pitch in the auditory sense). Reading time data from skilled adult readers are broadly consistent with this framework. High-frequency words (i.e., those that are common in the language) are fast to read, irrespective of the sound–spelling regularity. For low-frequency words, regular words are read faster than irregular ones (Seidenberg et al., 1984).

Profiles of acquired central dyslexias

The dual-route model predicts that selective brain damage (in skilled readers) to different components comprising the two routes should have different consequences for the reading of different types of written material. Indeed, this appears to be so. Some patients are able to read nonwords and regularly spelled words better than irregularly spelled words. The latter tend to be pronounced as if they were regular (e.g., DOVE pronounced "doove" like "move," and CHAOS pronounced with a "ch" as in "church"). These patients are called **surface dyslexics** (e.g., Shallice et al., 1983). Within the dual-route system it may reflect reliance on grapheme–phoneme

KEY TERM

Surface dyslexia
Ability to read nonwords and regularly spelled words better than irregularly spelled words.

conversion arising from damage to the semantic system (Graham et al., 1994) or visual lexicon itself (Coltheart & Funnell, 1987). This enables nonwords and regularly spelled words to be read accurately. The lexical-semantic route in Figure 13.9 may still have some level of functioning that supports high-frequency words. As such, these patients typically show a frequency × regularity interaction. That is, high-frequency words tend to be read accurately no matter how regular they are, but low-frequency words tend to be particularly error-prone when they are irregular.

KEY TERMS

Phonological dyslexia
Ability to read real words better than nonwords.

Deep dyslexia
Real words are read better than nonwords, and semantic errors are made in reading.

Another type of acquired dyslexia has been termed **phonological dyslexia**. These patients are able to read real words better than nonwords (Beauvois & Derouesne, 1979). When given a nonword to read, they often produce a real word answer (e.g., CHURSE read as "nurse"), and more detailed testing typically reveals that they have problems in aspects of phonological processing (e.g., auditory rhyme judgment) but that they can perceive the written word accurately (e.g., Rapcsak et al., 2009). As such, these patients are considered to have difficulties in the phonological route (grapheme–phoneme conversion) and are reliant on the lexical-semantic route. Given that these patients have problems in phonological processing as well as reading, one can debate whether these deficits should be labeled as reading-specific at all (Woollams, 2014). This is reminiscent of the debate about the nature and location of the VWFA. It is likely that the brain architecture for reading will impinge on other core skills: in this case, the location of grapheme–phoneme conversion depends on neural resources for manipulating speech sounds.

Another type of acquired dyslexia exists that resembles phonological dyslexia in that real words are read better than nonwords, but in which real word reading is more error-prone and results in a particularly intriguing type of error – a semantic error (e.g., reading CAT as "dog"). This is termed **deep dyslexia** (Coltheart et al., 1980). The patients also have a number of other characteristics, including a difficulty in reading low imageability (e.g., truth) relative to high imageability (e.g., wine) words. The most common way of explaining deep dyslexia is to assume that *both* reading routes are impaired (Nolan & Caramazza, 1982). The lexical–semantic route is degraded such that similar concepts have effectively become fused together and cannot be distinguished from one another, and the absence of grapheme–phoneme conversion prevents an alternative means of output.

Does brain imaging support the dual-route model?

The initial motivation for postulating two routes for reading was cognitive rather than anatomical. Nevertheless, functional imaging may provide an important source of converging evidence to this debate – at least in principle (e.g., Cattinelli et al., 2013). Of course, functional imaging measures the activity of regions only in response to particular task demands, and so it does not provide any direct

evidence for actual anatomical routes between brain regions.

Aside from the fusiform region (or VWFA) already considered, a number of other predominantly left-lateralized regions are consistently implicated in fMRI studies of reading and reading-related processes such as lexical decision. These include the inferior frontal cortex (including Broca's area); the inferior parietal lobe; and several anterior and mid-temporal lobe regions (see Figure 13.10). These are considered in turn.

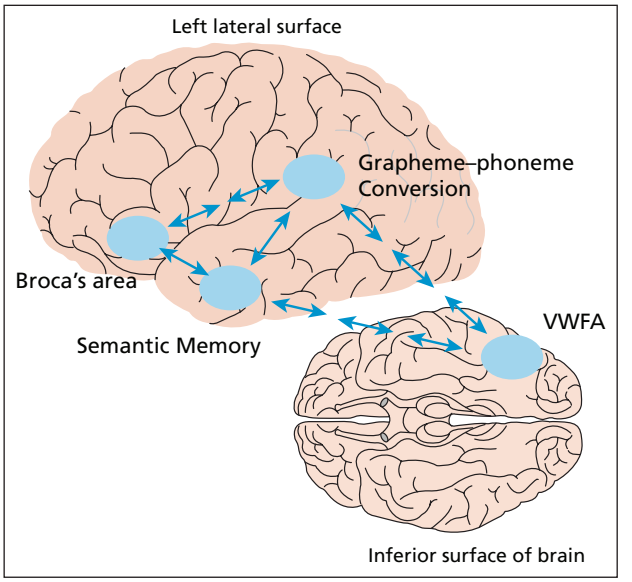

FIGURE 13.10: Key areas identified in brain imaging studies and their possible functions. Note that the anatomical routes (and intermediate processing stages) are largely unknown and are shown here as illustrative possibilities. The role of the inferior frontal lobe (Broca's area) in reading is uncertain but may contribute to both semantically based reading and reading via phonological decoding. It may also bias the reading strategy that is adopted (according to the task).

Inferior frontal lobe (Broca's area, BA44 and BA45)

This region is implicated in fMRI studies of reading, as well as in language processing in general (see Chapter 12). Some have suggested that the inferior frontal lobe does not have a core role to play in single word reading but is instead related to general task difficulty (Cattinelli et al., 2013). However, others have suggested that it has a specific role in converting graphemes to phonemes (Fiebach et al., 2002) as this region is activated more by low-frequency words with an irregular spelling (Fiez et al., 1999). These words are the hardest to read via grapheme–phoneme conversion, and the assumption is that more cognitive effort manifests itself as greater BOLD activity. An alternative way of interpreting increased activity for low-frequency irregular words is by assuming that a greater BOLD response for these items provides evidence for more semantic support being offered by this region (rather than reflecting the grapheme–phoneme conversion routine working harder). Indeed, some studies have made this alternative claim (Jobard et al., 2003). It is possible that both claims could be true if different subregions were contributing to both reading routes. Heim et al. (2005) suggest that BA45 is involved in semantic retrieval (e.g., during lexical decision), but BA44 supports grapheme–phoneme conversion. Patients with damage to the wider inferior frontal region make more errors on nonwords than real regular words, but additionally struggle with low-frequency irregular words (Fiez et al., 2006). That is, the pattern is neither a specific profile of surface dyslexia nor of phonological dyslexia but a mix of the two. This suggests that the region does indeed serve multiple functions during reading rather than being specifically tied to one process/route.

Inferior parietal lobe

The inferior parietal lobe consists of two anatomical regions: the supramarginal gyrus, which abuts the superior temporal lobes, and the angular gyrus, lying more posteriorly. Both have long been linked to language. The angular gyrus has been linked to verbal working memory (Paulesu et al., 1993) and binding semantic concepts (Binder & Desai, 2011). The supramarginal gyrus was historically linked to Wernicke's area and phonological processing in particular. For instance, it contains the planum temporale, which is implicated in developmental dyslexia and phonological awareness (see the later section). With particular reference to reading, it has been suggested that the left supramarginal gyrus is implicated in grapheme–phoneme conversion. It tends to be activated more by nonwords than words, and evidence from intracranial EEG (Juphard et al., 2011) and fMRI (Church et al., 2011) suggest that reading of longer nonwords is linked to longer duration of EEG activity and increased BOLD signal. These findings suggest piecemeal processing of letter strings rather than holistic recognition. An excitatory (rather than inhibitory) TMS protocol over this region facilitates nonword reading (Costanzo et al., 2012), whereas inhibitory TMS impairs phonological (but not semantic) judgments about written words (Sliwinska et al., 2012). Finally, patients with semantic dementia hyper-activate this region, relative to controls, when attempting to read low-frequency irregular words (Wilson et al., 2012). These words tend to be regularized by these patients (e.g., SEW read as "sue"), suggesting that they, but not controls, may utilize this region to read these words (i.e., to compensate for their inability to read the words using semantics).

Anterior and mid-temporal lobe

These regions of the brain are strongly implicated in supporting semantic memory (see also Chapter 12). Within models of reading, one would therefore expect that they would contribute to the reading-via-meaning route (i.e., mapping orthography to phonology via semantics). The mid-temporal cortex is a region that tends to be activated, during fMRI, in semantic relative to phonological processing of written words (Mechelli et al., 2007). Gray matter volume in this region, and the anterior temporal pole, measured by VBM correlates with ability in reading of irregular words in aphasic patients (Brambati et al., 2009). Finally, patients with semantic dementia, who invariably present with surface dyslexia, have lesions in this area (Wilson et al., 2009) and are forced to use an alternative route (grapheme-phoneme conversion) for much of their reading.

In summary, the evidence from functional imaging suggests that different brain regions are involved in reading via grapheme–phoneme conversion (left supramarginal gyrus) and reading via meaning (anterior and mid-temporal lobes). This evidence

generally supports the dual-route notion but does not – at present – discriminate well between different versions of it. Other regions (e.g., left inferior frontal lobe) have an important role in reading but serve an unclear function as they do not clearly map onto a construct within current cognitive models of reading.

Is the same reading system universal across languages?

The dual-route model is an attractive framework for understanding reading in opaque languages such as English, in which there is a mix of regular and irregular spelling-to-sound patterns. But to what extent is this model likely to extend to languages with highly transparent mappings (e.g., Italian) or, at the other extreme, languages that are logographic rather than alphabetic (e.g., Chinese)? The evidence suggests that the same reading system is indeed used across other languages (Rueckl et al., 2015), but the different routes and components may be weighted differently according to the culture-specific demands.

Functional imaging suggests that reading uses similar brain regions across different languages, albeit to varying degrees. Italian speakers activate more strongly areas involved in phonemic processing when reading words, whereas English speakers activate more strongly regions implicated in semantic retrieval (Paulesu et al., 2000). Studies of Chinese speakers also support a common network for reading Chinese logographs and reading Roman-alphabetic transcriptions of Chinese (the latter being a system, called pinyin, used to help in teaching Chinese; Chen et al., 2002). Reading Chinese logographs may make more demands on brain regions involved in semantics than reading English (Chee et al., 2000), and this reveals itself behaviorally in studies showing that reading logographs is more affected by word imageability than reading English words (Shibahara et al., 2003). Imageability refers to whether a concept is concrete or abstract, with concrete words believed to possess richer semantic representations. Thus, it appears that Chinese readers may be more reliant on reading via semantics. One possible consequence of this is that the reading system is more bilateral in the Chinese brain, compared to reading systems with stronger phonological decoding (Perfetti et al., 2013).

Cases of surface dyslexia have been documented in Japanese (Fushimi et al., 2003) and Chinese (Weekes & Chen, 1999). Reading of Chinese logographs and Japanese Kanji can be influenced by the parts that comprise them. These parts have different pronunciations in different contexts, with degree of consistency varying. This is broadly analogous to grapheme–phoneme regularities in alphabetic scripts. Indeed, the degree of consistency of character–sound correspondence affecting reading of both words and nonwords is particularly apparent for low-frequency words. The results suggest that there are non-semantic routes for linking print with sound even in scripts that are not based on the alphabetic principle. Conversely,

phonological dyslexia has been observed in these scripts, adding further weight to the notion that the dual-route model may be universal (Patterson et al., 1996; Yin & Weekes, 2003). Similarly, surface dyslexia (Job et al., 1983) and phonological dyslexia (De Bastiani et al., 1988) have been observed in Italian, even though this reading system is entirely regular and could, in principle, be achieved by grapheme–phoneme correspondence alone. As with English and Chinese, Italian also shows a word frequency × regularity interaction for reading aloud in skilled adult readers (Burani et al., 2006).

Evaluation

The dual-route model of reading presently remains the most viable model of reading aloud. It is able to account for skilled reading, for patterns of acquired dyslexia and for differences in regional activity observed in functional imaging when processing different types of written stimuli. The model also extends to written languages that are very different from English.

KEY TERM

Developmental dyslexia
Problems in literacy acquisition that cannot be attributed to lack of opportunity, or basic sensory deficits.

DEVELOPMENTAL DYSLEXIA

Developmental dyslexia is defined as problems in literacy acquisition (reading and/or spelling) that cannot be attributed to lack of opportunity or other known causes (e.g., deafness, brain injury). Reading ability varies on a continuum so estimates of prevalence depend on a judgment of severity, but it is estimated at around 5–12 percent in the USA and affecting men more than women (Katusic et al., 2001). Some reading systems are also easier to acquire than others (e.g., transparent alphabets v. Chinese logographs), which also means that the degree of impairment needed for diagnosis is language specific.

With regards to reading different kinds of stimuli, there is heterogeneity in what can be accurately read. For instance, some English-speaking developmental dyslexics may have particular problems in reading words with irregular spellings but are relatively good at reading nonwords (developmental surface dyslexia), and others may have particular problems with nonwords (developmental phonological dyslexia) (Castles & Coltheart, 1993). However, most developmental dyslexics do not fall neatly into either of these two categories (Manis et al., 1996). This is to be expected if there is disruption in the system before specialization emerges: a problem in one part of the network will tend to disrupt the development of other parts of the reading network (e.g., Harm & Seidenberg, 2004). By contrast, damage to the system after specialization (acquired dyslexia) may result in more distinct patterns of reading behavior. This has made it particularly challenging to identify the core deficit in developmental dyslexia. To give one concrete example, developmental dyslexics show less activation of the

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VWFA to words relative to normal readers (McCandliss & Noble, 2003), but this could potentially be just restating the initial problem in "neuro" terms (i.e., dyslexics are less expert at reading) rather than offering an actual explanation of the cause.

Broadly speaking, the core cognitive deficits in developmental dyslexia have been linked to problems in either the visual domain or the auditory domain, with the latter being the dominant view (Goswami, 2015). To be clear, people with developmental dyslexia do not present with overt problems in hearing or seeing (e.g., due to difficulties with the eyes or ears). Instead, these difficulties may reflect individual differences in high-level functioning that arise through differences in brain development which, in turn, may be driven by genetic differences (Scerri & Schulte-Koene, 2010). These differences will not be specific to reading (because reading is a cultural invention) and should be present in dyslexics before they learn to read.

To consider visually based explanations first, one theory states that developmental dyslexia is caused by a deficit of the magnocellular visual pathway (e.g., Stein & Walsh, 1997). Recall from Chapter 7 that this pathway, originating subcortically, is involved in the fast detection of visual information (including motion) and low-resolution visual information. It has been implicated in reading because of its role in the allocation of visuo-spatial attention including eye movements (via the visual dorsal stream) and may account for symptoms such as text appearing jumbled. Gori et al. (2016) conducted a number of studies showing support for this theory: developmental dyslexics have problems in motion perception; and motion perception ability in pre-literate children predicts future reading development (independently of phonological skills). Other evidence shows that the capacity for attending to multiple objects (e.g., letters) at the same time is reduced in developmental dyslexia (Bosse et al., 2007). However, others have argued that this ability is a consequence of skilled reading rather than a precursor to it (Goswami, 2015).

With regards to auditory processing, the dominant theory is that developmental dyslexia is linked to problems in **phonological awareness**: that is, in the ability to explicitly segment a speech stream into units such as syllables, rimes and phonemes. The term "explicit" is important because natural speech perception segments the acoustic input into different units automatically and effortlessly, but tasks that require an awareness of these units may depend on other mechanisms (Ramus & Szenkovits, 2008). These tasks include counting syllables, detecting phonemes or creating spoonerisms (e.g., "fuzzy duck" → "ducky fuzz"). Developmental dyslexics tend to be impaired in these tasks across all languages in which they have been tested (Ziegler & Goswami, 2005). In terms of brain mechanisms, they may depend on the auditory dorsal stream for speech segmentation, in contrast to the auditory ventral stream for speech comprehension (Hickok & Poeppel, 2004). This auditory dorsal stream includes the left temporoparietal

KEY TERM

Phonological awareness
The ability to explicitly segment a speech stream into units such as syllables, rimes and phonemes.

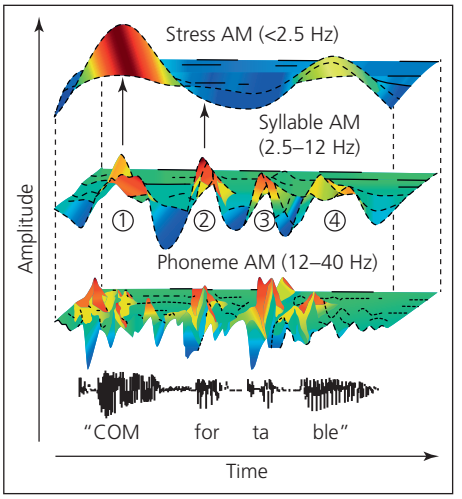

FIGURE 13.11: The acoustic speech signal can be considered as a summation of several frequency bands fluctuating in intensity (amplitude) over time (AM = amplitude modulation). The ability to detect amplitude rises, at certain frequencies, may be related to phonological awareness which, in turn, is important for reading development.

area (planum temporale), which is anatomically more symmetrical in developmental dyslexics (Galaburda et al., 1985). The normal pattern is for it to be larger in the left hemisphere of non-dyslexics. More recent research shows that the degree of asymmetry is correlated with phonological awareness abilities (Eckert et al., 2001), and these phonological awareness abilities in children predict the degree of activation of the VWFA to nonwords (Shaywitz et al., 2002). This is a good example of how differences in one part of the reading network can impact on other parts. Whether other kinds of auditory problems underpin difficulties in phonological awareness remains to be fully explored. One theory is that developmental dyslexics have particular problems in detecting certain auditory "edges" that occur at stress and syllable boundaries (Goswami, 2015), as shown in Figure 13.11. This implies that they would also have problems in certain non-speech tasks such as musical rhythm.

Less transparent reading systems (e.g., English and French) are harder to acquire than transparent ones (e.g., Italian), and rates of developmental dyslexia are higher in countries who speak those languages (Lindgren et al., 1985). Notwithstanding these cultural differences, there might be common differences (e.g., phonological awareness) that explain reading difficulties across all cultures. Paulesu et al. (2001) compared English, French, and Italian dyslexics and normally reading controls matched for IQ and education level. The English and French dyslexics had received a formal diagnosis. Given that it is very unusual for Italian adults to receive a diagnosis of dyslexia, a large sample was screened, and those falling in the bottom 10 percent of a number of speed-reading tasks were considered dyslexic. (Note: the Italian "dyslexics" were better readers than their English and French counterparts given the nature of their reading system, but were nevertheless poor readers with respect to their Italian controls.) All three groups of dyslexics showed evidence of poor performance in a number of verbal skills, suggesting a core deficit in this area. Brain activity when reading, measured using PET, was consistently reduced in the left posterior temporal region in dyslexics relative to controls, suggesting a common neural mechanism independent of the reading system involved (Figure 13.12).

Evaluation

The defining problem of developmental dyslexia is in reading (and spelling), but the core problem is likely to lie in some other, more generic, cognitive processes that are important for the development

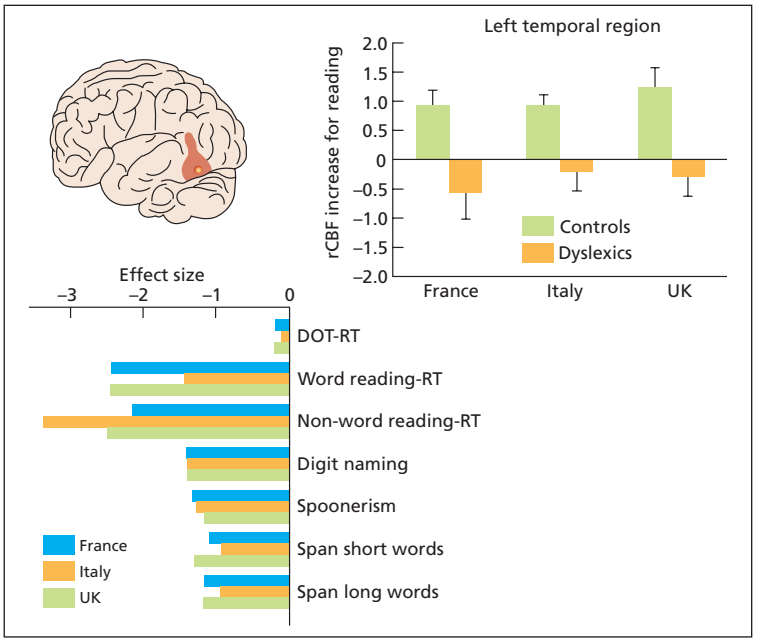

FIGURE 13.12: English, French, and Italian dyslexics show less activation in a left temporal region relative to controls. English, French, and Italian dyslexics show normal reaction time to a dot appearing but have difficulties on word and nonword reading and other nonreading tasks including digit naming, spoonerisms ("lucky duck" to "ducky luck"), and span tasks (repeating lists of short or long words).

From Paulesu et al. (2001). Reprinted with permission from AAAS.

of skilled literacy. Candidate mechanisms are in high-level visual processes and in phonological awareness (explicit segmentation of spoken language and possibly other sounds), with most evidence concentrated on the latter. There is heterogeneity in the profile of developmental dyslexia that may be indicative of different causes, which may also affect different aspects of literacy (e.g., ability to read nonwords). As noted later, similar debates also exist about the root causes of developmental difficulties in numeracy (dyscalculia) although one claim here is that there is a specialized mechanism, honed by language and culture, for understanding numbers.

SYMBOLIC AND NONSYMBOLIC NUMBER COGNITION

The basic principles discussed previously with regards to the acquisition of skilled literacy (i.e., building on other cognitive abilities and neural specializations) also applies to skilled numeracy. Becoming skilled at mathematics in the modern world requires learning of arbitrary notations and their meaning (e.g., 5, 6, +, –, ∏, √), as well as specific procedures (e.g., for calculating the circumference of a circle). These can be referred to as symbolic number cognition. Over and above this acquired knowledge, humans and other species appear to have a more basic set of numerical abilities that enable them to estimate quantity and perform basic calculations. This is our nonsymbolic number cognition that many theories regard as a start-up kit for the culturally acquired symbolic aspects of number. It consists of a

rough sense of how much and how many (together with a more precise sense of number for small quantities). It is to be noted that a basic level of numerical competence is found in almost all individuals. Some people with a condition known as **dyscalculia** (or acalculia) lack a basic understanding of numbers. This difficulty may be a result of brain damage (i.e., numerical competence is lost) or may be of developmental origin (i.e., numerical competence is never fully gained). The study of dyscalculic individuals has led to important insights into numerical cognition.

The meaning of numbers has been variously referred to as magnitude, quantity (Dehaene, 1997), or numerosity (Butterworth, 1999). A telephone number is a number (or, rather, a numerical label), but it is not a quantity. The phone number 683515 is not larger than the phone number 232854. Number meaning is also assumed to be independent of the format used to denote it (e.g., 3, III, "three," "*trois*" or three fingers). Integer numbers or whole numbers are properties of a collection. **Counting** involves putting each item in the collection in one-to-one correspondence with a number or some other internal/external tally ("one, two, three, four, five, six – there are six oranges!") (Gelman & Gallistel, 1978). Most fractions can be explained in terms of collections. Thus 6/7 refers to 6 parts of a collection of 7. Other types of number (e.g., zero, infinity, negative numbers) are harder to grasp and are learned later, if at all.

This section will start off by considering nonsymbolic aspects of number to illustrate how, in the next section, this influences the nature of symbolic number cognition (i.e., involving digits or number words). The remaining sections will consider the neural basis of number meaning and the Triple-Code model of numerical cognition.

KEY TERMS

Dyscalculia
Difficulties in understanding numbers; calculation difficulties.

Counting
The process of putting each item in a collection in one-to-one correspondence with a number or some other internal/external tally.

FIGURE 13.13: An understanding of numbers is crucial for many day-to-day activities.

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WHAT IS THE RELATIONSHIP BETWEEN NUMBERS AND SPACE?

Why is it that number meaning is located in the parietal lobes (rather than any other region of the brain)? One speculation is that an understanding of number/quantity may have evolved out of spatial processes, which are located in adjacent if not overlapping regions of the parietal cortex (Hubbard et al., 2005). One strong theoretical position is that number meaning is itself represented using some sort of spatial code like a "mental number line" (Dehaene, 1997; Moyer & Landauer, 1967). A weaker proposal is that number and space are distinct entities that, nonetheless, tend to interact with one another (Walsh, 2003). Whatever the mechanism, there are several key lines of evidence for number–space associations:

- When people are asked to make judgments about numbers (e.g., odd/even judgments), they are faster with their left hand for small numbers, but faster with their right hand for larger numbers – the **SNARC effect** (spatial numerical association of response codes; Dehaene et al., 1993). This is shown in Figure 13.14. The direction of the number–space association may be influenced by reading direction and counting habits (Shaki et al., 2012). Bilateral TMS over the posterior parietal lobe reduces the SNARC effect (Rusconi et al., 2007).
- Generating "random" numbers while turning the head from side to side is associated with smaller numbers, on average, generated from left turns (Loetscher et al., 2008).
- An Amazonian tribe (the Munduruku) with very limited number vocabulary and no formal mathematical education understand number–space mappings (Dehaene et al., 2008). When given a line (with endpoints marked as array sizes of 1 or 10 dots), they map the position of intermediate numbers (e.g., six dots) using a logarithmic scale. In a Western sample, education leads to linearization of number–space associations for small numbers (1–10), but not larger numbers (1–100).
- Patients with visuo-spatial neglect (but who are not dyscalculic) show spatial biases in number bisection (e.g., "what number is midway between 11 and 19? . . . 17") as if they are ignoring the left side of number space (Zorzi et al., 2002).
- Some people report habitually visualizing numbers in particular visuo-spatial configurations, normally oriented from left to right. These are called number forms or number–space synesthesia, and their functioning is linked with activity in the intraparietal sulcus and prefrontal cortex assessed with fMRI (Tang et al., 2008).

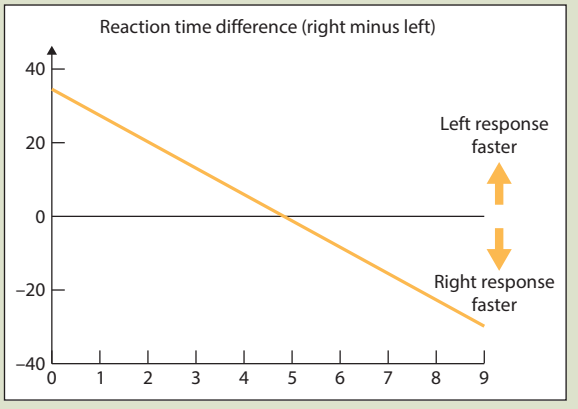

FIGURE 13.14: People are faster at making judgments about small numbers with their left hand and faster at making judgments about large numbers with their right hand.
Adapted from Dehaene et al. (1993).

KEY TERM

SNARC effect
If people are asked to make judgments about numbers (e.g. odd/even judgments), they are faster with their left hand for small numbers but faster with their right hand for large numbers.

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Processing nonsymbolic numbers: collections and quantities

Experimental studies involving judgments of the size of collections typically use arrays of dots and can be broadly divided into two domains: those that require an exact assessment of number (e.g., "there are 8") versus those that require a relative, or approximate, assessment of number (e.g., "there are about 8," "there are more blue dots than yellow dots"). These different kinds of task may recruit different kinds of cognitive processes and different brain mechanisms.

Considering relative assessments of number, a standard paradigm is to present two arrays of dots and instruct/train participants to respond to either the larger or smaller set. The two arrays can either be presented one after the other, or at the same time (e.g., in different colors) as shown in Figure 13.15. Typically, the size of the dots is varied so that the two arrays are equated for factors such as overall surface area (i.e., so the judgment is based on discrete quantities rather than a continuous quantity). The advantage of this paradigm is that it can be adapted for use in a wide variety of animals, from fish (Agrillo et al., 2012) to primates (Washburn & Rumbaugh, 1991), and also humans at all stages of development (Xu & Spelke, 2000). One common finding is that the ability to perform the task decreases with increasing set sizes, even when the ratio is constant. Thus, it is harder to discriminate sets of 20:30 dots than sets of 10:15 even though the ratio is 2:3 in both cases. The standard explanation is that the system for processing numbers is less precise (or less efficient) the larger the set size that is considered. In addition, larger ratios are also easier to discriminate (e.g., 2:5 relative to 2:3). Individual differences in performance on this task (in ninth-grade children) are correlated with math achievement in school and extend back to kindergarten (Halberda et al., 2008). Moreover, the ability to discriminate which of two sets is larger is worse in children with developmental dyscalculia (Piazza et al., 2010). As such, this basic numerical system may act as a start-up kit for culturally embedded mathematics.

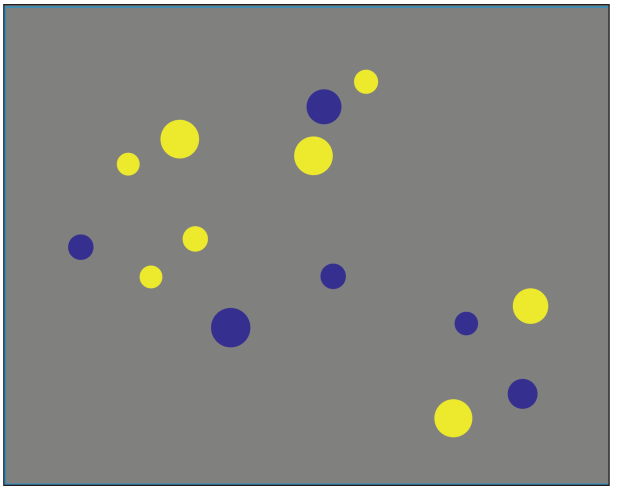

FIGURE 13.15: Which set is larger: blues or yellows? When presented too briefly to count (200 ms), then schoolchildren differ in their ability to perform the task and this correlates with SAT (Standard Assessment Test) scores in mathematics.
Adapted from Halberda et al. (2008).

The alternative approach is to require participants to determine exact quantities: for instance to state how many dots are present, or to respond when exactly N dots are present (the latter being more appropriate for other species). These tasks require matching of a stimulus to some internal standard of number (linguistic or non-linguistic). In humans, when participants are asked to state (verbally) the size of a collection, then there appears to be a difference between small numbers (up to 3 or 4)

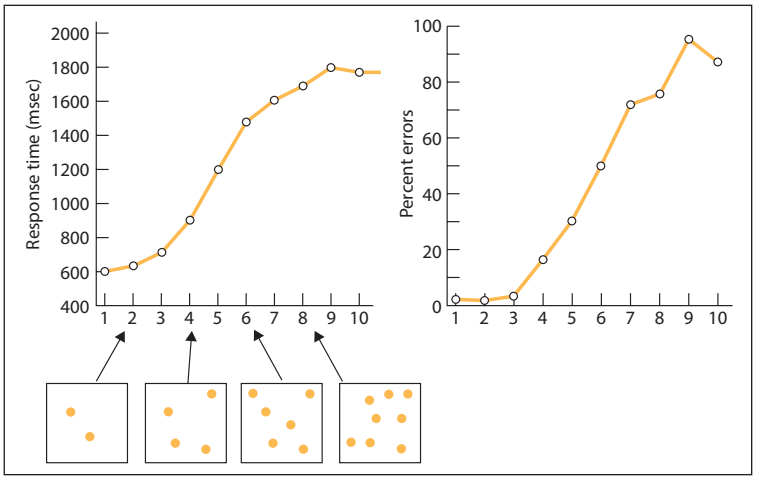

FIGURE 13.16: The ability to state how many objects are in an array may occur automatically for small arrays (< 4; called subitizing) but occurs serially for larger arrays (> 4; called counting). In this version of the experiment the arrays were presented briefly (200 ms).

and larger numbers (beyond 4). Specifically, people are just as fast when there are 1, 2, 3, or 4 items in an array (i.e., no decrease in efficiency with increasing size of number), but above that they slow down proportionally to the number of items in the collection (Mandler & Shebo, 1982), as shown in Figure 13.16. This has typically been explained in terms of two separate mechanisms: (1) a rapid ability to enumerate, in parallel, a small collection of objects that is independent of language (termed **subitizing**) and (2) a slower, serial, mechanism that is dependent on language (counting) or resorting to approximation. The claim is not that collections above 4 cannot be processed without language, but, rather, that numbers above 4 can only be processed approximately rather than exactly in the absence of language (Dehaene, 1997) (for a different view see Gelman & Butterworth, 2005). Subitizing reflects a separate mechanism that doesn't simply reflect the general advantage for small numbers (Revkin et al., 2008) and has been linked to different neural substrates, namely, within the visual ventral stream rather than parietal cortices (Vuokko et al., 2013).

KEY TERMS

Subitizing
The capacity to enumerate an exact quantity of objects without counting them.

Distance effect
It is harder to decide which of two numbers is larger when the distance between them is small (e.g., 8–9 relative to 2–9).

Processing number symbols: digits and words

Symbolic, or linguistic, representations of number consist of words and digits (e.g., 7 or "seven"). Although these are superficially very different to collections of dots, there is evidence that similar kinds of cognitive processes are used for symbols as for dots. Moyer and Landauer (1967) conducted a seminal study investigating how symbolic number magnitude is represented. Participants had to judge which of two numbers was numerically larger (e.g., 5 compared with 7). They noted two important effects on the pattern of response times. The **distance effect** refers to the fact that it is much easier (i.e., faster

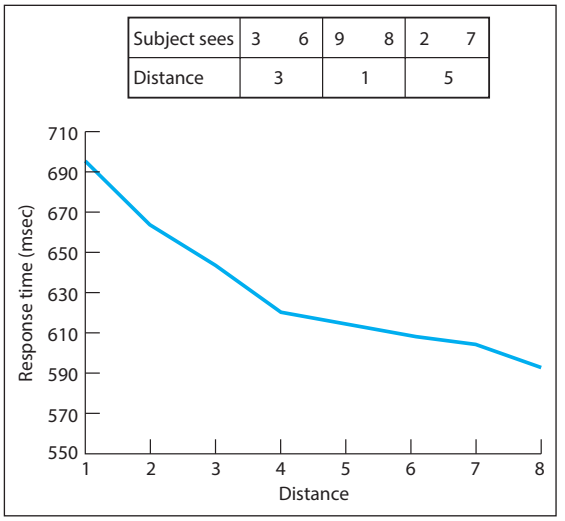

FIGURE 13.17: The ability to discriminate between two numbers increases as the numerical distance between them increases – the so-called distance effect.

From Butterworth (1999). © Palgrave-Macmillan. Reproduced with permission of the author.

response time) to decide which number is larger when the distance between two numbers is large (e.g., 2 or 9) relative to small (e.g., 8 or 9) – see Figure 13.17. This suggests that number magnitude is retrieved, rather than, say, the relative order of numbers (since 2 and 8 both come before 9). The **size effect** refers to the observation that it is easier to judge which of two numbers is larger when the numbers are small (e.g., 3 or 5) compared with when they are large (e.g., 7 or 9), even when the distance between them is equal. This, of course, resembles the findings with dot arrays described earlier. The result implies that the mental representations of larger numbers are less robust (or "fuzzier") even in the symbolic domain.

Other studies suggest that symbolic and nonsymbolic representations of number converge on to a single (abstract) number meaning system. Koechlin et al. (1999b) asked participants to decide whether a stimulus was greater than or less than 5. The stimulus consisted of Arabic numerals (e.g., 7), number words (e.g., SEVEN), or dot patterns (which participants were asked to estimate, not count). Crucially, before each trial a very brief (66 ms) additional stimulus was presented that the participants could not consciously report seeing – a prime. The prime was either greater or less than 5. If the prime and stimulus were on the same side of 5, then performance was enhanced. The fact that this occurs rapidly across different codes suggests that these codes access a single system for number meaning.

Finally, some cultures do not have a large range of number words. In certain Amazonian and Australian Aboriginal societies, there are no number names beyond around 3 (e.g., "1, 2, many") as shown in Figure 13.18. To what extent can they process larger numbers for which there is no symbolic representation? The Munduruku, in Amazonia, are able to divide a large collection into half by placing items into two piles one at a time (McCrink et al., 2013). They can also compare approximate sizes of collections as well as a Western control group (e.g., 20 compared with 15), and perform exact arithmetic on small numbers (e.g., 3 stones minus 1 stone = 2 stones) but *not* exact arithmetic on larger numbers, for which they lack a number name (Pica et al., 2004). Thus, when adding 5 stones and 7 stones they might choose an answer that is approximately 12 (e.g., 11, 12, or 13) but not a distant number (e.g., 8 or 20). Thus, although symbolic and nonsymbolic representations of number are normally closely tied, they are not equivalent and can serve different functions in numerical cognition. Symbolic representations permit exact and approximate quantification, whereas nonsymbolic representations permit approximate quantification (except for small numbers).

KEY TERM

Size effect
It is easier to state which number is larger when the numbers are small (e.g., 2 and 4) relative to large (e.g., 7 and 9) even when the distance between them is the same.

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ONLINE RESOURCES

Test yourself at the distance and size effects with digits (www.testable.org/ward) and symbols (panamath.org).

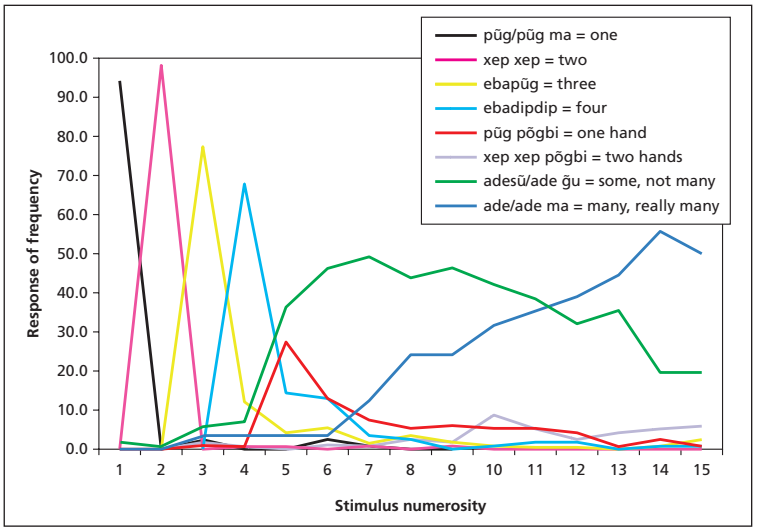

FIGURE 13.18: The number naming system of the Munduruku in Amazonia becomes very imprecise for numbers larger than 4. How does this affect their ability to understand numbers?

From Pica et al. (2004).

Neural substrates of number meaning

Evidence from electrophysiological single-cell recordings in nonhuman primates has revealed the existence of neurons that are tuned to the number of objects. These neural representations may enable core numerical abilities in many species and, in humans, may become linked to (and modified by) symbolic representations of number (Nieder & Dehaene, 2009). One type of neuron responds more strongly the more objects that there are (Roitman et al., 2007). Another type, so-called **number neurons**, appear to be selectively tuned to particular numbers; for instance responding to 4 objects more than to 3 or 5 (for a review see Nieder, 2013).

KEY TERM

Number neurons
Neurons that respond preferentially to particular set sizes.

The standard procedure used in these studies involves recording from neurons while the monkey performs a number discrimination task of deciding whether two consecutively presented arrays contain the same number of dots. One important finding is that the degree of response selectivity of the neuron is related to numerical size, and this may be the neural basis of the size effect in response time studies that has already been discussed (Nieder & Miller, 2004). For example, a neuron that responds maximally to four dots will respond very little to three or five dots (a selective response), but a neuron tuned to detect ten dots will respond quite strongly to nine or eleven dots (a less selective response) – see Figure 13.19. The number neurons tended to be found in both regions of the parietal lobes (notably the intraparietal sulcus, IPS) and the prefrontal cortex in the macaque. Some number neurons maintain the same tuning preference irrespective of whether dots were presented simultaneously, as an array, or after sequential presentation, one by one (Nieder et al.,

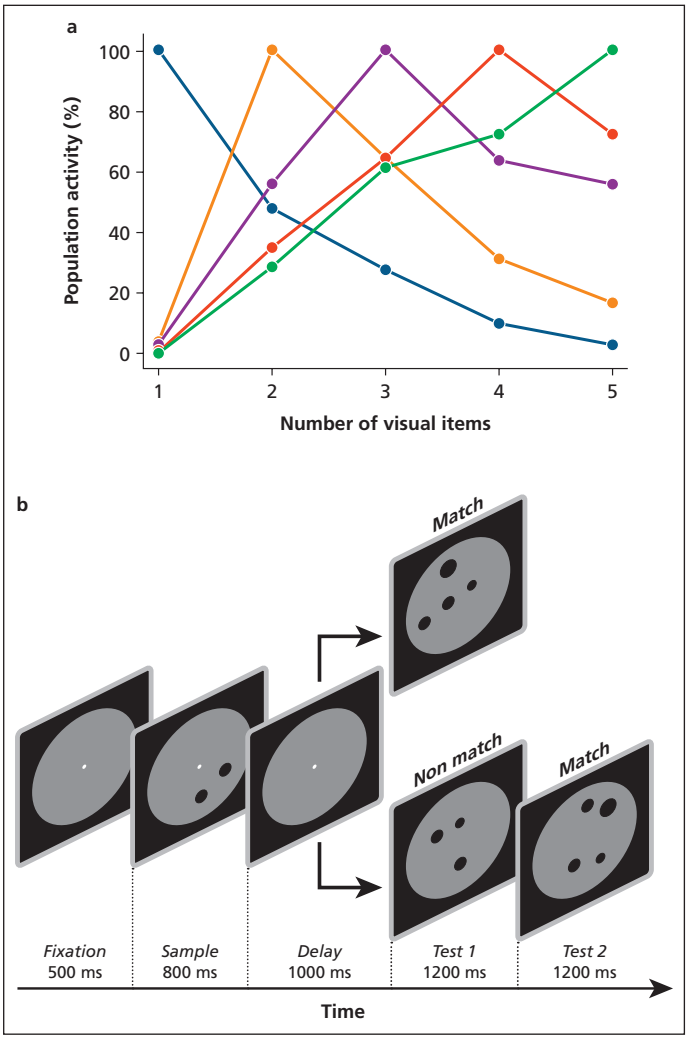

FIGURE 13.19: Top: the relative level of activity of number neurons that are selectively tuned to respond to between one and five items. Notice how the tuning to smaller numbers is more precise (narrower curves). Bottom: A typical experiment in which a monkey must decide whether two sets of dots are matched in quantity or not. The activity of individual neurons is recorded during the task. From Nieder (2013).

2006). Certain number neurons may also respond to a particular number of sounds as well as visual stimuli (Nieder, 2012). Diester and Nieder (2007) trained monkeys to associate dot arrays with written digits and found number neurons that responded both to a particular set size and its corresponding symbol. Interestingly, these neurons tended to be in the prefrontal cortex rather than the intraparietal sulcus. In human fMRI, a frontal-to-parietal shift in BOLD activity is found contrasting children and adults when performing magnitude comparisons on pairs of digits (Ansari et al., 2005). That is, children tend to activate the prefrontal cortex more in this task, whereas adults tend to activate the intraparietal sulcus more. One possibility is that the intraparietal sulcus contains the core number meaning system (present from an early age and in other species) that, in humans, becomes progressively tuned to symbolic representations of numbers via education and/or language.

Evidence from adult human functional imaging also points to the particular importance of the intraparietal sulcus. This region is

more active when people perform calculations relative to reading numerical symbols (Burbaud et al., 1999) and in number comparison relative to number reading (Cochon et al., 1999). The degree of activation of the region shows a distance effect for both digits and number words (Pinel et al., 2001) and is sensitive to subliminal priming when the "unseen" prime and seen stimulus differ in quantity (Dehaene et al., 1998b). This suggests that the region is the anatomical locus for many of the cognitive effects already discussed. Most of the studies cited previously used Arabic numbers or number names. Another study with dot patterns showed habituation of the neural response to the number of items in an array, analogous to behavioral studies of human infants (Piazza et al., 2004). The same region of the brain is activated by numbers across different cultures and writing systems (Tang et al., 2006). Both the intraparietal sulcus and frontal regions show fMRI adaptation effects when the same number is repeated and irrespective of notation (Piazza et al., 2007).

Dyscalculia also tends to be linked to dysfunction of the parietal lobes. Acquired dyscalculia has, for a century, been linked to left-hemispheric lesions (Gerstmann, 1940; Grafman et al., 1982), which more recent studies have localized to the left intraparietal region (Dehaene et al., 1998a). However, studies of structural differences in developmental dyscalculia point to differences in the left and/or right intraparietal sulcus (Isaacs et al., 2001; Rotzer et al., 2008). Moreover, evidence from TMS (Cohen Kadosh et al., 2007) and brain imaging (Pinel et al., 2001) suggests that the right parietal lobe also plays an important role in normal number processing. These regions are shown in Figure 13.20.

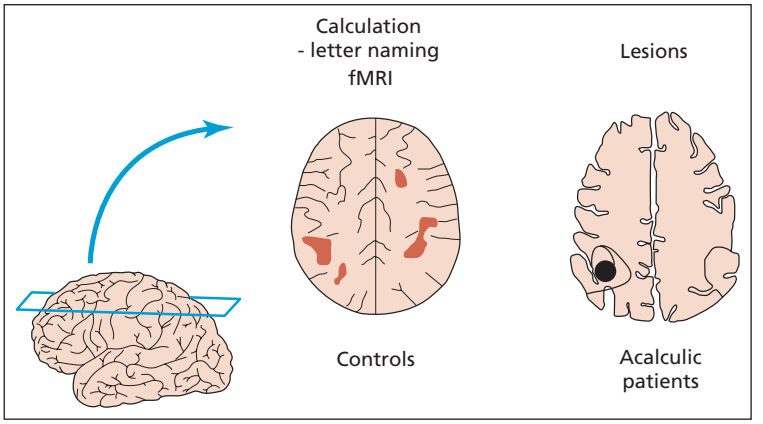

FIGURE 13.20: There is converging evidence from neuropsychology and functional imaging for the role of the parietal lobes in number meaning (particularly the left parietal lobe).

Left figure from F. Chochon, L. Cohen, P. F. van de Moortele, and S. Dehaene, "Differential Contributions of the Left and Right Inferior Parietal Lobules to Number Processing," Journal of Cognitive Neuroscience, 11:6 (Nov 1999), pp. 617–630. © 1999 by the Massachusetts Institute of Technology. Right figure reprinted from Dehaene et al., 1998a. © 1998, with permission from Elsevier.

ONLINE RESOURCES

Dig deeper with an online lecture by Stanislas Dehaene on "A Close Look at the Mathematician's Brain" by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

Acquired dyscalculic patients with left-hemispheric lesions may still have some numerical abilities that are presumably supported by the intact right hemisphere: for instance, they may be able to give approximate answers (e.g., 5 + 7 = "13 roughly"; Warrington, 1982) or detect the falsehood of 2 + 2 = 9, but not 2 + 2 = 5 (and with the precision decreasing with increasing number size; Dehaene & Cohen, 1991). Thus, although both hemispheres appear to be important for numbers, it may be the case that the number representations in the left hemisphere are more exact, and this is assumed to reflect interactions with the language system (Nieder & Dehaene, 2009). There is a strong correlation between the lateralization of the left superior temporal sulcus response to language and the left intraparietal sulcus response to arithmetic (Pinel & Dehaene, 2010). However, this study was in right-handers, and it would be important to extend the research to left-handers for whom language lateralization is more variable.

THE MAKING OF MATHEMATICAL GENIUS

> Genius is ninety-nine percent perspiration and one percent inspiration.
>
> (Albert Einstein)

Although many would be happy to label Einstein (Figure 13.21) a genius, the extent to which this reflects hard work or innate skill could be debated endlessly. "Genius" is a notoriously difficult word to define, but some scientific progress has been made in understanding the neural basis of unusual mathematical ability. The mathematical prodigy Gamm took part in a functional imaging study by Pesenti and colleagues (2001) while performing incredible calculations. For example, Gamm was able to divide prime numbers up to 60 decimal places (e.g., 31/61) and calculate the fifth root of numbers

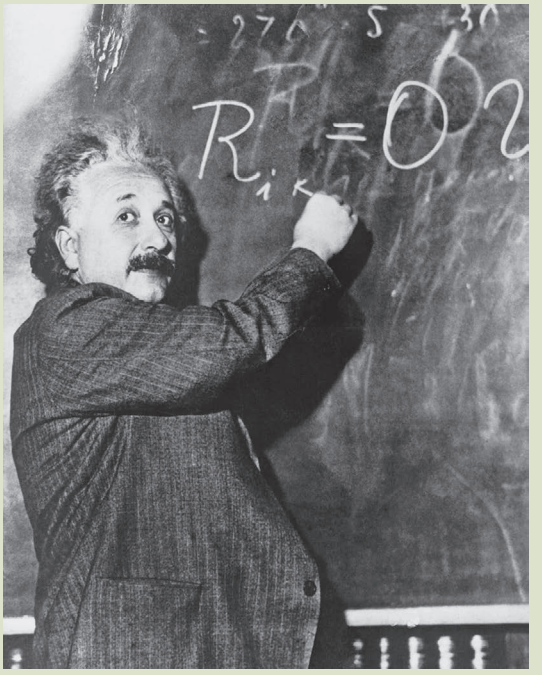

FIGURE 13.21: Albert Einstein, 1879–1955.

(e.g., $\sqrt[5]{8547799037}$). The regions of his brain that were activated included those involved in calculation and those involved in memory retrieval (control participants, given easier tasks, activated only the former). Gamm appears to have committed many number "facts" into long-term memory (he trained himself for six years for up to four hours per day) and uses these to reduce the high demands placed upon working memory during calculation. Observations of other prodigious calculators support this conclusion. Wim Klein can extract the 13th root of a 100-digit number in two minutes. To help him, he has learned the logarithm of all the integers up to 150 (Smith, 1983). Another prodigy, Aitken, solved the problem 777^2 by decomposing it to a simpler multiplication and a square: $[(777 + 23) \times (777 - 23)] + 23^2$. He had memorized all the squares from 1 to 100 (Gardner, 1990). In the case of Gamm and associates, it appears that their skills reflect perspiration more than inspiration. It is interesting to note that Einstein was almost certainly unable to perform these calculations, and conversely, it is a moot point as to whether Gamm is a "genius." Perhaps other factors are needed to explain the kind of ability possessed by Einstein (Witelson et al., 1999).

It would be premature to state that there is no genetic contribution to numerical ability at all. Genetic factors may certainly contribute to numerical disability (Bruandet et al., 2003). The interaction between genes, environment, and brain is likely to be complex. For example, autistic children may develop an unusual zeal for numbers that reflects a difficulty in socialization rather than a "gift" for numbers (Hermelin & O'Connor, 1986). Differences in motivation (as opposed to differences in some innate ability) can themselves be a product of genes and can result in a change in the environment that one creates for oneself.

The Triple-Code model

The Triple-Code model of numerical cognition is shown in Figure 13.22, and the triple codes refer to (1) a semantic magnitude representation, (2) a verbal store of arithmetical facts, and (3) a visual representation for recognizing numerals and that acts as a "workbench" for performing certain calculations (Dehaene, 1997; Dehaene & Cohen, 1995; Dehaene et al., 1998a). The semantic magnitude representation is assumed to lie (bilaterally) in the intraparietal sulcus and was discussed in the last subsection. The verbal store is used to comprehend and produce spoken number names and is also a repository for learned arithmetical facts and tables (e.g., "two and two is four"). This is assumed to be based in the left angular gyrus (Dehaene et al., 2003), which is in a separate region of the parietal lobe to number meaning. The visual code is used for recognizing and producing Arabic numerals and was assumed to lie bilaterally in the fusiform gyrus, which has been subsequently confirmed (Shum et al., 2013). It also consists of a visuo-spatial workspace for conducting multi-digit operations (e.g., 256 + 142).

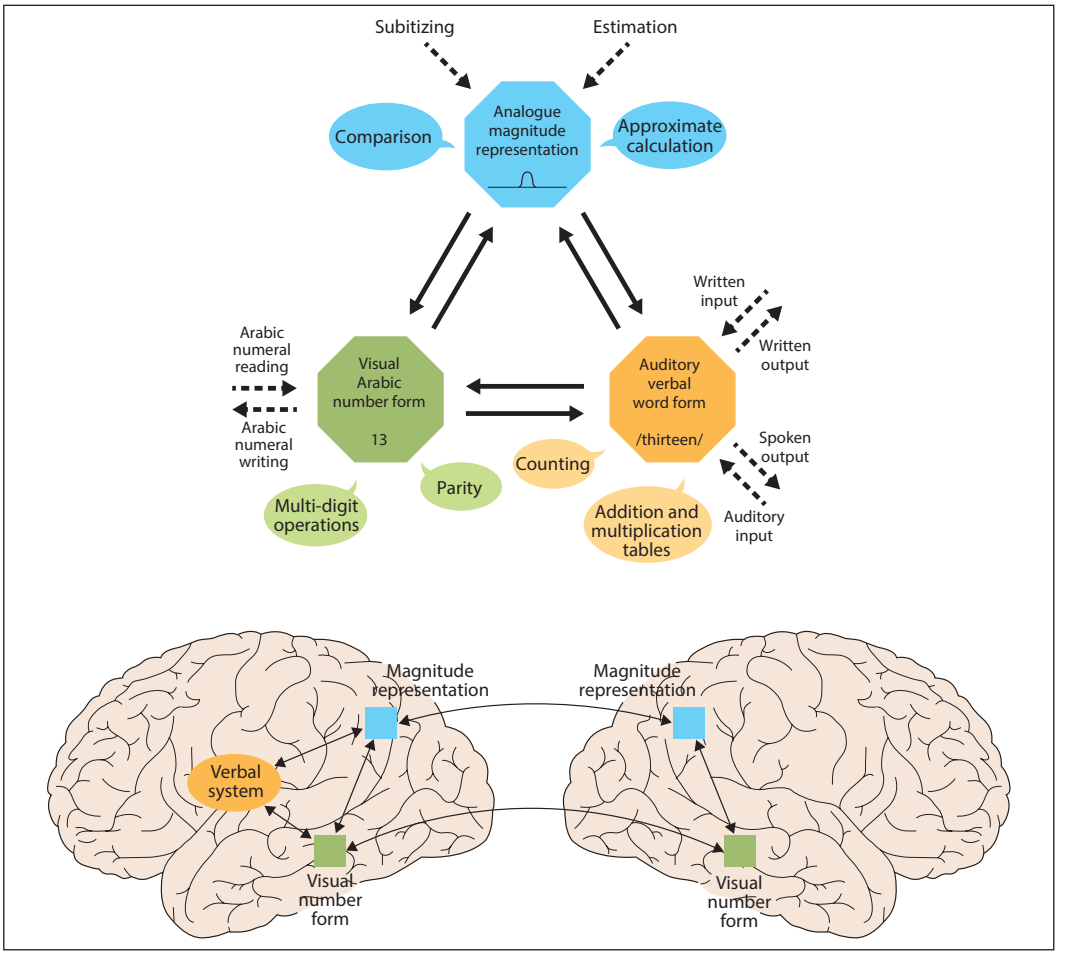

FIGURE 13.22: The three components of Dehaene's Triple-Code model are: (a) a semantic magnitude representation; (b) a verbal store of arithmetical facts; and (c) a visual representation for recognizing numerals and a "workbench" for performing certain calculations. Top: functional components; and bottom: their approximate anatomical locations.

From: top, Dehaene (1992); bottom, Dehaene and Cohen (1995) copyright © Taylor & Francis Ltd, reprinted by permission of Taylor & Francis Ltd, www.tandfonline.com.

One prediction of the Triple-Code model is that not all calculations are carried out semantically (via the IPS) but may be partially supported by the two code systems (verbal and written). In particular, simple multiplications as "facts" from the verbal code. Subtraction tends not to be learned in this rote fashion and may make more demands on the number semantic representation. Addition can be performed in both ways – simple additions are likely to have been verbally learned by rote but can also be easily computed using the number semantic representation. More complicated sums (e.g., multi-digit addition) may be accomplished visually or using visual images.

There is some positive evidence for these assumptions from both patient-based neuropsychology and neuroimaging. Delazer and Benke (1997) report a patient with a left parietal tumor who could recite and produce multiplication facts but had severely impaired knowledge of numbers (e.g., unable to add 13 + 9; unable to get 103 using poker chips with values of 100, 50, 10, 5, 1). By contrast, the severely aphasic patient, HAB, could still perform many calculations, but his multiplication (part of the verbal store in the Triple-Code model) was performed atypically (Rosser et al., 1995). For example, 9 × 5 was done by converting it into an addition problem 18 + 18 + 9 = 45 [i.e., 9 × (2 + 2 + 1)]. These studies support the conclusion that multiplication facts are stored in verbal form.

Difficulties in multiplication and subtraction form a double dissociation. Patients have been reported with greater difficulties in multiplication relative to subtraction and vice versa (e.g., Dehaene & Cohen, 1997; Van Harskamp & Cipolotti, 2001). In healthy participants, Lee and Kang (2002) found that simultaneous phonological rehearsal delayed multiplication more than subtraction, and that holding a visuo-spatial image in mind delayed subtraction, but not multiplication. In functional imaging experiments, the left angular gyrus (the putative "verbal code") shows more activity in multiplication than subtraction (Cochon et al., 1999) and is more involved in simple addition (below 10) than complex addition (above 10) (Stanescu-Cosson et al., 2000). Whereas *learning* a new multiplication fact activates the inferior prefrontal cortex and bilateral intraparietal sulcus, *retrieving* that fact involves the left angular gyrus in the parietal lobes (Ischebeck et al., 2006); see Figure 13.23. Subtraction, on the other hand, did not show the shift to the angular gyrus.

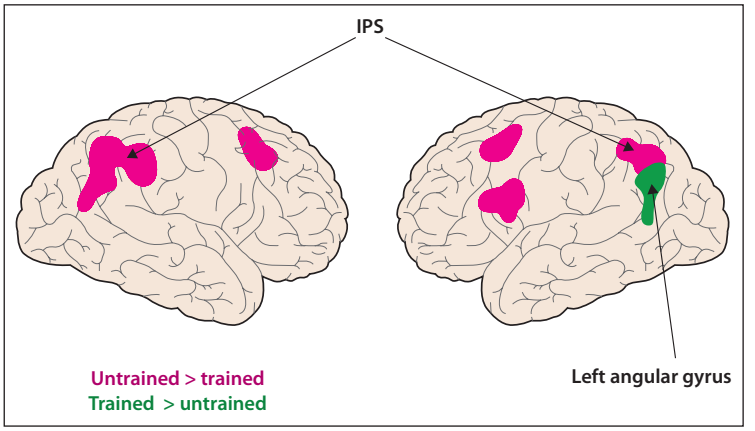

FIGURE 13.23: Learning new multiplication problems (red) versus retrieving previously learned problems (green) involves different brain regions.
Adapted from Ischebeck et al. (2006).

Evaluation

Different kinds of number tend to be processed in similar ways. Nonsymbolic processing of numbers (e.g., dot arrays) show striking similarities across species (distance and size effects), and in humans, processing of number symbols (e.g., digits) show comparable effects. Nonsymbolic numbers can only be processed approximately (e.g., "about 14") except for small numbers (< 4), whereas symbolic numbers (words, digits) enable an exact processing of number. Single-cell recordings from the parietal and frontal lobes of macaques suggest a likely neural substrate for this effect: namely, neurons that respond to some numbers more than others, but with a general tendency for larger numbers to be linked to less specificity in terms of the neural response. The Triple-Code model argues that skilled numeracy depends on both the core number system but also a verbal store (e.g., for number facts) and a visuo-spatial code (e.g., for multi-digit arithmetic).

SUMMARY AND KEY POINTS OF THE CHAPTER

- The recognition of letters within words occurs automatically and in parallel, supported by knowledge of the structure of the language (i.e., which letters tend to go together).
- A region in the left fusiform gyrus responds to familiar letter strings more than false letters or consonant string (the visual word form area, VWFA), and it may occupy this region because of its connectivity to the language system
- Evidence from acquired dyslexia suggests that there are two routes used in reading words aloud: a sub-lexical route that translates graphemes into phonemes (impaired in phonological dyslexia) and a lexical–semantic route (impaired in surface dyslexia).
- Brain imaging across different reading systems around the world suggest a common system with some variation (depending on the properties of the written system)
- Numbers can be processed either nonsymbolically (e.g., dot arrays) or symbolically (e.g., written digits). These culturally acquired symbols tap into the same brain regions (intraparietal sulcus) and mechanisms (e.g., size and distance effects) as more evolutionary conserved nonsymbolic mechanisms.
- The fact that numbers can be represented in multiple systems also leads to some division of labor in skilled numeracy (e.g., arithmetic can be done via fact retrieval or calculation); this is captured by the Triple-Code model of numeracy.

EXAMPLE ESSAY QUESTIONS

- What does the VWFA (visual word form area) do? Is it visual? Does it store word forms?
- Is the dual-route model of reading cross-culturally applicable? Include evidence from dyslexia (acquired and developmental) and neuroimaging.
- Which aspects of numerical cognition depend on learning and culture and which aspects do not?
- What is the evidence for neurons or brain regions that are specialized for number?

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- Test library for lexical decision, number judgments, and so on
- Video lectures and interviews on key topics with several leading experts and author Jamie Ward
- Multiple-choice questions and interactive flashcards to test your knowledge

CHAPTER 14

The executive brain

CONTENTS

The **executive functions** of the brain can be defined as the complex processes by which an individual optimizes his or her performance in a situation that requires the operation of a number of cognitive processes (Baddeley, 1996). A rather more poetic metaphor is that the executive functions are the brain's conductor, which instructs other regions to perform, or be silenced, and generally coordinates their synchronized activity (Goldberg, 2001). As such, executive functions are not tied to one particular domain (memory, language, perception, and so on) but take on a role that is meta-cognitive, supervisory, or controlling. Executive functions have traditionally been equated with the frontal lobes, and difficulties with executive functioning have been termed as "frontal lobe syndrome." More accurately, executive functions are associated with the *prefrontal cortex* (PFC) of the frontal lobes, and it is an open question as to whether all aspects of executive function can be localized to this region. Primates, relative to other mammals, have disproportionately more gray matter in their frontal lobes (Bush & Allman, 2004), and humans, relative to other primates, have further disproportionately enlarged this region of their brain (Donahue et al., 2018). This is shown in Figure 14.1.

DOI: 10.4324/9781003429975-14

KEY TERM

Executive functions
Control processes that enable an individual to optimize performance in situations requiring the operation and coordination of several more basic cognitive processes.

The concept of executive functions is closely related to another distinction with a long history in cognitive science – namely, that between automatic and controlled behavior (e.g., Schneider & Shiffrin, 1977). This distinction has already been encountered in another context, namely, the production of actions. When driving a car, one may accelerate, change gear, and so on, in an apparently "autopilot" mode. But if the traffic is diverted through an unfamiliar route, then one would need to override the automatic behavior and exert online control. This is often assumed to require the use of executive functions (Norman & Shallice, 1986). The same logic may also apply in situations that lack motor output, that is, in the online control of thoughts and ideas. This provides humans (and possibly other species) with a remarkable opportunity; namely, to mentally simulate scenarios and think through problems "in the mind" without necessarily acting them out. It is hardly surprising, therefore, that some theories of executive function are effectively synonymous with aspects of *working memory* (Baddeley, 1996; Goldman-Rakic, 1996).

Two other general points are in need of mention in this preamble. First, the extent to which behavior is "automatic" (i.e., not requiring executive function) versus "controlled" (i.e., requiring executive function) may be a matter of degree rather than all or nothing. Even when generating words in fluent conversation, some degree of executive control may be exerted. For example, one may need to select whether to say the word "dog," "doggy," "Fido," or "Labrador" depending on pragmatic context, rather than relying on, say, the most frequent word to be selected. Second, one must be cautious about falling into the trap of thinking that controlled behavior requires an autonomous controller. This is the homunculus problem: think of a little man inside your head making

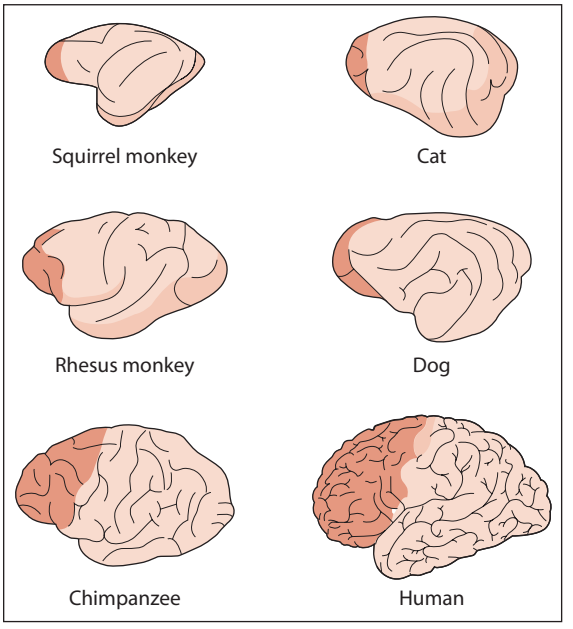


FIGURE 14.1: Enlargement of frontal cortex shows an evolutionary progression (the brains are not drawn to scale). In humans, this region occupies almost a third of the cortical volume.

Adapted from Fuster (1989).

your decisions, and then imagine another little man in his head making his decisions, and so on. Control may be an outcome of multiple competing biases rather than the presence of a controller. Decisions may arise out of an interaction of environmental influences (bottom-up processes) and influences related to the motivation and goals of the person (top-down processes). The sight of a cream cake may trigger an "eat me" response, but whether one does eat it may depend on whether one is hungry or dieting. This basic idea has already been introduced from the perspective of attention (Chapter 9) and action (Chapter 10) and will be explored here from the perspective of performing tasks with novel or complex configurations.

This chapter first considers the major anatomical divisions within the prefrontal cortex. The subsequent section outlines the main types of cognitive tests that are believed to depend critically on the functioning of the prefrontal cortex. The chapter then considers different possible functional organizations of the prefrontal cortex: for instance, different functional roles for the lateral versus orbital surfaces, different functional roles for posterior versus anterior portions of the lateral surface, and hemispheric differences. Before discussing executive functions, it is worthwhile to review the anatomy of the prefrontal cortex.

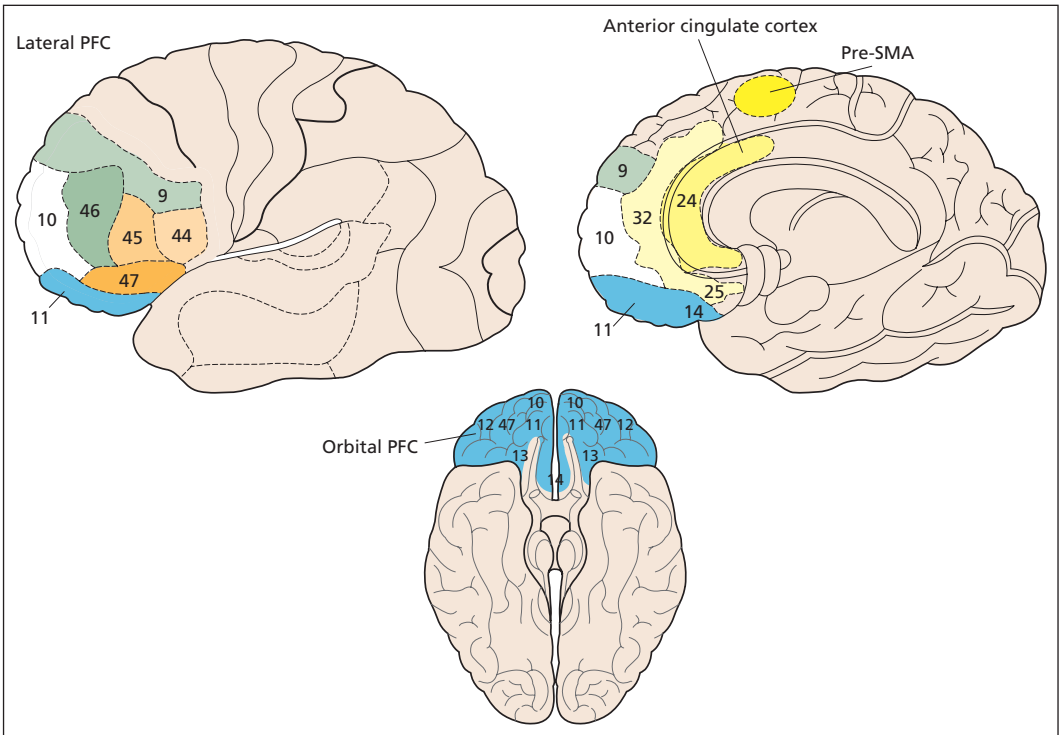
ONLINE RESOURCES

Watch the TEDx talk "How your brain's executive function works – and how to improve it" by Sabine Doebel by scanning the QR code or visiting routledgelearning.com/wardcognitiveneuroscience.

ANATOMICAL AND FUNCTIONAL DIVISIONS OF THE PREFRONTAL CORTEX

The most basic anatomical division within the prefrontal cortex is that between the three different cortical surfaces (Figure 14.2). The *lateral* surface of the prefrontal cortex lies anterior to the premotor areas (Brodmann's area 6) and the frontal eye fields (in Brodmann's area 8). This surface lies closest to the skull. The *medial* surface of the prefrontal cortex lies between the two hemispheres and to the front of the corpus callosum and the anterior cingulate cortex. In terms of anatomy, the anterior cingulate is not strictly part of the prefrontal cortex, but it does have an important role to play in executive functions and, as such, will be considered in this chapter. The *orbital* surface of the prefrontal cortex lies above the orbits of the eyes and the nasal cavity. The orbitofrontal cortex is functionally, as well as anatomically, related to the lower (ventral) part of the medial surface (termed ventromedial prefrontal cortex) (Öngür & Price, 2000). The terms orbito- and ventromedial PFC are sometimes used interchangeably when finer anatomical divisions are not necessary.

The prefrontal cortex has extensive connections with virtually all sensory systems, the cortical and subcortical motor system and structures involved in affect and memory (Yeterian et al., 2012). There are also extensive connections between different regions of the prefrontal cortex. These extensive connections enable the coordination of a wide variety of brain processes. The lateral prefrontal cortex is more closely associated with sensory inputs



Brodmann's areas	Other names	Possible functions (left hemisphere)	Possible functions (right hemisphere)
44, 45, 47	Ventro-lateral prefrontal cortex (VLPFC)	Retrieval and maintenance of semantic and/or linguistic information (Areas 44 + 45 on left also called Broca's area)	Retrieval and maintenance of visual and/or spatial information
9, 46	Dorso-lateral prefrontal cortex (DLPFC)	Selecting a possible range of responses, and suppressing inappropriate ones; manipulating the contents of working memory	Monitoring and checking of information held in mind, particularly in conditions of uncertainty; vigilance and sustained attention
10	Anterior prefrontal cortex; frontal pole; rostral prefrontal cortex	Multi-tasking; maintaining future intentions / goals whilst currently performing other tasks or sub-goals. (The medial portion has been implicated in "theory of mind" – see Chapter 16)	
24 (dorsal) 32 (dorsal	Anterior cingulate cortex (dorsal) Pre-SMA	Monitoring in situations of response conflict and error detection	
11, 12, 13, 14	Orbito-frontal cortex	Executive processing of emotional stimuli (e.g. evaluating rewards and risks)	

FIGURE 14.2: The prefrontal cortex has three different surfaces: the lateral surface (top left), the medial surface (top right), and the orbitofrontal surface (bottom). The numbers refer to Brodmann areas that are discussed in the text.

than the orbitofrontal cortex. It receives visual, somatosensory, and auditory information, as well as receiving inputs from multimodal regions that integrate across senses. In contrast, the medial and orbital prefrontal cortex is more closely connected with

medial temporal lobe structures critical for long-term memory and processing of emotion.

These anatomical distinctions are also captured by resting state fMRI approaches which divide the brain into a number of discrete networks such that regions *within* a network correlate strongly but regions *between* networks correlate weakly (Damoiseaux et al., 2006). Evidence from resting state analyses support a division between networks involving the medial PFC (including default mode network) versus lateral PFC (including frontoparietal control network), as well as divisions between ventrolateral and dorsolateral PFC areas (termed ventral and dorsal attention networks). Note that none of these networks are limited to the PFC and incorporate the regions that they tend to communicate with (e.g., parietal, temporal). Figure 14.2 provides a summary of the main PFC regions, also labelling by Brodmann's areas.

In addition to connections between different cortical regions, the prefrontal cortex is the starting and ending point of various circuits that pass through the basal ganglia and thalamus (Alexander & Crutcher, 1990). These circuits modify activity in prefrontal cortex (both upwards and downwards) such that it ultimately affects the probability of behavior. In motor behavior, these circuits might influence the likelihood of an action and how vigorous it is (see Chapter 10). In executive functions, it is proposed that the corresponding prefrontal loop through the basal ganglia acts as a gatekeeper by, for instance, making the information stored in working memory less stable so that it can be updated (O'Reilly & Frank, 2006). The basal ganglia loop to prefrontal cortex is believed to be crucial for learning of novel tasks and, hence, important for making the transition from controlled behavior to automatic behavior (O'Reilly & Frank, 2006). This is important for procedural learning as exemplified by complex tasks such as driving a car that, eventually, appear effortless. However, note that the basal ganglia are not normally considered to be responsible for directly determining the *content* of ongoing tasks. This depends on interactions between prefrontal cortex and posterior regions involved in, say, language, perception or emotion. Instead, the basal ganglia circuits are primarily concerned with task efficiency and task learning.

EXECUTIVE FUNCTIONS IN PRACTICE

This section considers some concrete situations in which executive functions are needed. Evidence will be presented that the prefrontal cortex (or subregions within it) are important for implementing this kind of behavior.

Working memory

The prefrontal cortex within the frontal lobes is widely recognized as playing a crucial role in working memory. Most models tend to

THE EXTRAORDINARY CASE OF PHINEAS GAGE

One of the most famous cases in the neuropsychological literature is that of Phineas Gage (Harlow, 1993; Macmillan, 1986; Figure 14.3). On 13 September 1848, Gage was working on the Rutland and Burlington railroad. He was using a large metal rod (a tamping iron) to pack explosive charges into the ground when the charge accidentally exploded, pushing the tamping iron up through the top of his skull; it landed about 30 m behind him. The contemporary account noted that Gage was momentarily knocked over but that he then walked over to an ox-cart, made an entry in his time book, and went back to his hotel to wait for a doctor. He sat and waited half an hour for the doctor and greeted him with, "Doctor, here is business enough for you!" (Macmillan, 1986).

Not only was Gage conscious after the accident, he was able to walk and talk. Although this is striking in its own right, it is the cognitive consequences of the injury that have led to Gage's notoriety. Before the injury, Gage held a position of responsibility as a foreman and was described as shrewd and smart. After the injury, he was considered unemployable by his previous company; he was "no longer Gage" (Harlow, 1993). Gage was described as

> irreverent, indulging at times in grossest profanity . . . manifesting but little deference for his fellows, impatient of restraint or advice when it conflicts with his desires . . . devising many plans of future operation, which are no sooner arranged than they are abandoned in turn for others.
>
> (Harlow, 1993)

After various temporary jobs, including a stint in Barnum's Museum, he died of epilepsy (a secondary consequence of his injury) in San Francisco, some 12 years after his accident.

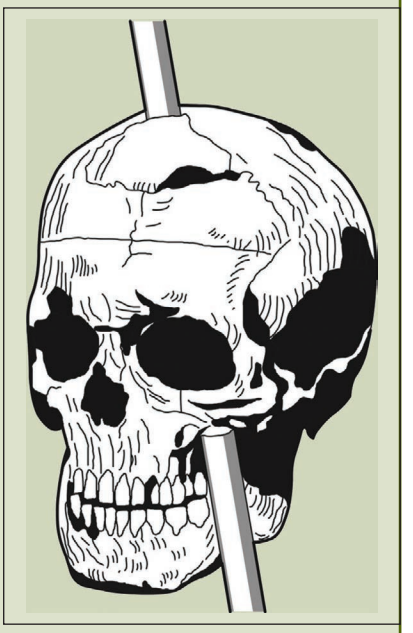


FIGURE 14.3: The skull of Phineas Gage, with tamping iron *in situ* and a recently discovered photograph of Gage. Modern reconstructions suggest that his brain lesion may have been specific to the medial and orbital surfaces of the prefrontal cortex, sparing the lateral surfaces.

Damasio et al. (1994). From the collection of Jack and Beverly Wilgus.

Where was Phineas Gage's brain lesion? This question was answered by an MRI reconstruction of Gage's skull, which found damage restricted to the frontal lobes, particularly the left orbitofrontal/ventromedial region and the left anterior region (Damasio et al., 1994). Research suggests that this region is crucial for certain aspects of decision-making, planning, and social regulation of behavior, all of which appeared to have been disrupted in Gage. Other areas of the lateral prefrontal cortex are likely to have been spared.

assume that the main storage site of information is not within the frontal lobes themselves but in the posterior cortex and that the function of the prefrontal cortex is to keep this information active (by forming loops between prefrontal and other regions) and/or manipulate the active information according to current goals.

In Baddeley's (1996) model, for instance, the notion of the central executive is effectively synonymous with models of prefrontal functioning. Goldman-Rakic's (1996) account also regards the prefrontal cortex as implementing a working memory system and draws primarily on animal lesion studies and single-cell recordings. Lesions to the lateral prefrontal cortex can impair the ability to hold a stimulus/response in mind over a short delay (Butters & Pandya, 1969). In one delayed response task, monkeys were presented with a box in a particular location on the screen. The box then disappeared and the monkey was required to hold the location "in mind." After a delay, they were then required to look at where the target was previously displayed (Figure 14.4). Single-cell recordings from monkeys show that some dorsolateral prefrontal neurons respond selectively during the delay period, suggesting that this is the neural mechanism for holding locations in mind (Funahashi et al., 1989).

Goldman-Rakic (1996) argued that there is a division between the content of information processed in dorsolateral and ventrolateral regions, but that the same types of process are used for both. Specifically, she suggests that ventral regions support working memory for objects and dorsal regions support spatial

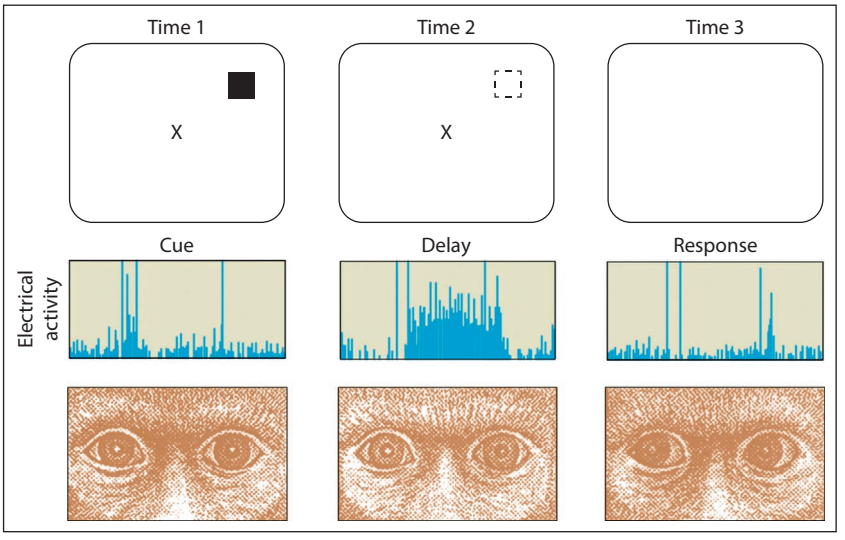


FIGURE 14.4: Single-cell recordings in the dorsolateral prefrontal cortex show that different neurons respond to (a) studying in a target location, (b) holding it "in mind" during a delay, and (c) responding to the removal of a cue by moving the eyes to that location.

From Goldman-Rakic (1992). Reprinted with permission of Patricia J. Wynne. www.patriciawynne.com.

working memory (that is, the dorsal and ventral visual stream is manifested at the level of executive functions). Other evidence is inconsistent with this view. Rao et al. (1997) report that individual neurons can change their responsiveness from being object based to being location based as the demands of the task change, irrespective of whether they are located in dorsolateral or ventrolateral regions.

Petrides (2000) offers an alternative account of working memory to that of Goldman-Rakic. He argues that the dorsolateral and ventrolateral prefrontal regions should be distinguished by the fact that they are engaged in different types of process and not that they are specialized for different types of material (e.g., spatial versus object based). This is a hierarchical model of working memory (Figure 14.5). In this model, the ventrolateral prefrontal cortex is responsible for activating, retrieving, and maintaining information held in the posterior cortex. The dorsolateral prefrontal region is responsible when the information held within this system requires active manipulation (e.g., ordering of information). Petrides and Milner (1982) found that patients with prefrontal lesions were impaired on a test of working memory termed the **self-ordered pointing task**. The patients were presented with an array of eight words or pictures and, on the first trial, required to pick anyone. On the second trial, they were asked to pick a different one from the first; on the third trial, they must pick a different one again and so on. As such, they must maintain and update an online record of chosen items. This is shown in Figure 14.6. Similar studies on monkeys suggest the critical region to be the dorsolateral prefrontal cortex (Petrides, 1995). In a human functional imaging study, Owen et al. (1996) found that maintaining and updating a record of which locations had been marked was linked to dorsolateral PFC activity whereas short-term retention of spatial locations was associated with ventrolateral activity.

KEY TERM

Self-ordered pointing task
A task in which participants must point to a new object on each trial and thus maintain a working memory for previously selected items.

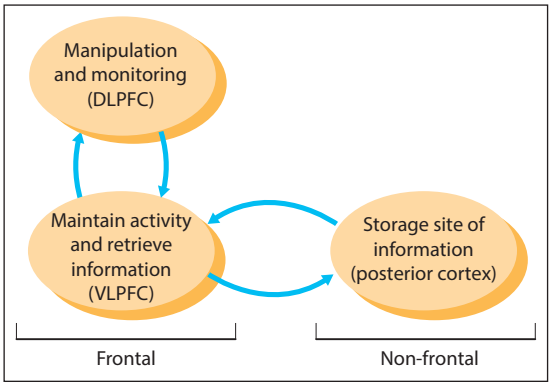


FIGURE 14.5: A hierarchical model of working memory in which ventrolateral prefrontal cortex (VLPFC) activates and maintains information, and the dorsolateral prefrontal cortex (DLPFC) manipulates that information.

Task-setting and problem-solving

Problem-solving is synonymous with many lay notions of what it is to exhibit intelligent behavior. So it is not surprising that executive functions, and the prefrontal cortex, have been linked to intelligence both within and across species. For instance, performance on tests of executive function tend to correlate with each other and correlate with certain standardized measures of intelligence (Duncan et al., 1997), as discussed in more detail later. In the lab, problem-solving is often tested by giving an endpoint (a goal) and, optionally, a starting point (a set of objects) and

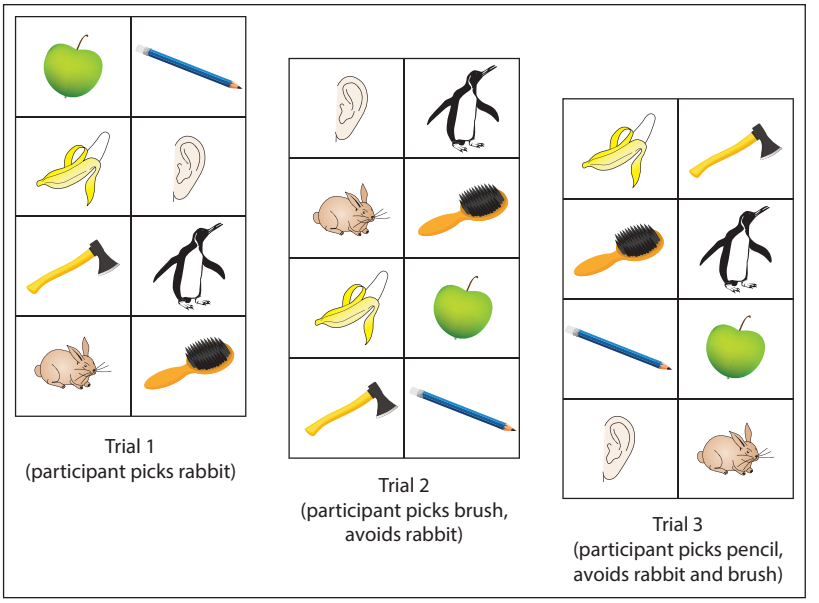


FIGURE 14.6: A self-ordered pointing task based on Petrides and Milner (1982). Participants are required to point to a new object on each trial and, as such, must keep an online record of previous selections.

participants must generate a solution of their own. This kind of open-ended solution is also referred to as task-setting.

Patients with lesions to the prefrontal cortex often show clinical symptoms of poor task-setting and problem-solving. To test this formally, a number of tests have been devised. Shallice (1982) reports a test called the "Tower of London," in which patients must move beads from one stake to another to reach a specified endpoint (Figure 14.7). Patients with damage to the left prefrontal cortex take significantly more moves. This implies that they perform by trial-and-error rather than planning their moves (see also Morris et al., 1997). Functional imaging studies of healthy participants suggest that activity within the dorsolateral prefrontal cortex increases with the number of moves needed to reach the endpoint (Rowe et al., 2001).

A number of verbal tests also involve finding solutions to problems in which there is no readily available answer. In the Cognitive Estimates Test (Shallice & Evans, 1978), patients

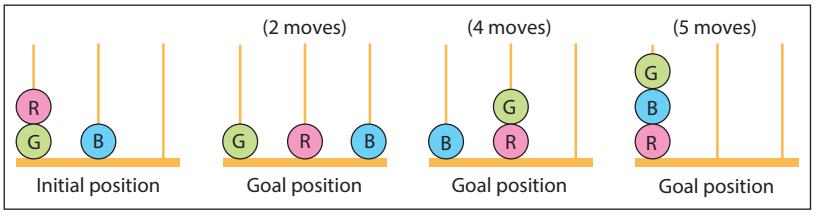


FIGURE 14.7: The "Tower of London" task requires beads to be moved from an initial position to a specified endpoint. Performance can be measured in terms of time to complete task or number of moves taken (relative to the optimal number of moves).

From Shallice (1982). Royal Society of London. Used with permission of The Royal Society. Permission conveyed through Copyright Clearance Center, Inc.

KEY TERMS

FAS test
A test of verbal fluency in which participants must generate words beginning with a letter (e.g., "F") in a limited amount of time.

Stroop test
Response interference from naming the ink color of a written color name (e.g., the word BLUE is printed in red ink and participants are asked to say the ink color, i.e., "red").

Go/No-Go Test
A test of response inhibition in which participants must respond to a frequent stimulus (go trials) but withhold a response to another stimulus (no-go trials).

Impulsivity
A behavioral tendency to make immediate responses or seek immediate rewards.

with damage to the prefrontal cortex are impaired at producing estimates for questions in which an exact answer is unlikely to be known ("How many camels are in Holland?") but can be inferred from other relevant knowledge (e.g., camels are only likely to reside in a small number of zoos). In the **FAS Test** (Miller, 1984), participants must generate a sequence of words (not proper names) beginning with a specified letter ("F," "A," or "S") in a one-minute period. This test is not as easy as it sounds (have a try) and involves generating novel strategies, selecting between alternatives and avoiding repeating previous responses. Patients with left lateral prefrontal lesions are particularly impaired (Stuss et al., 1998).

Overcoming potent or habitual responses

The classic example of overcoming a habitual response is provided by the **Stroop Test** (Stroop, 1935). In this task, participants must name the color of the ink and ignore reading the word (which also happens to be a color name), as shown in Figure 14.8. The standard explanation is that reading of words occurs automatically, and this generates a salient incorrect response that competes with the less-automatic task of naming colors (MacLeod & MacDonald, 2000). Performance on the Stroop Test has long been linked with the integrity of the prefrontal cortex (Perret, 1974).

Go/No-Go Tests involve the participant making a set of responses to some stimuli ("go" trials) but withholding responses to a subset of stimuli ("no-go" or "stop" trials). The no-go trials are often infrequent, so the participant gets into the habit of making a response. No-go rules can be defined in terms of simple rules (e.g., "respond to all stimuli except the letter B") or more complex rules (e.g., "respond to all stimuli except the letter B when it follows another letter B"). Brain activity during successful no-go trials is normally taken as indexing response inhibition, and the proportion of errors on no-go trials is taken as a behavioral marker of **impulsivity** (Perry & Carrol, 2008).

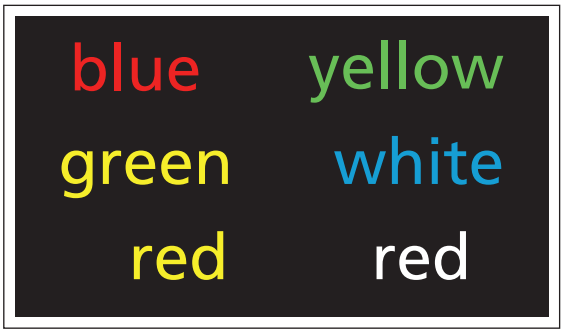


FIGURE 14.8: The Stroop Test involves naming the color of the ink and ignoring the written color name (i.e., "red, green, yellow, blue, yellow, white").

Both the Stroop Test and the Go/No-Go Test are related by virtue of the fact that they are typically explained with respect to the concept of inhibition. Inhibition, in terms of neural activity, has a very specific definition (reduced spiking rate) with a well-characterized mechanism at the synaptic level (more negative post-synaptic membrane potential). Behavioral or cognitive inhibition simply means reducing the likelihood of a particular thought/action and the mechanism behind it, at the neuronal level, is not clear. Some contemporary models of executive function do not rely on the

concept of inhibition at all and rely solely on biasing activation signals, also termed gain (Stuss & Alexander, 2007). Certainly, tasks such as the Stroop and Go/No-Go are likely to involve a variety of functions such as task-setting and monitoring ongoing performance, in addition to biasing of competing responses (either via gain or inhibition).

Contemporary research has suggested that performance on these tasks is related to particular brain regions rather than the prefrontal cortex in general. A meta-analysis of functional imaging studies of the Go/No-Go task suggests that a region of the medial prefrontal cortex (specifically the pre-SMA, pre-supplementary motor area) was common across tasks for No-Go stimuli with right lateral prefrontal cortex also implicated in more complex No-Go rules (Simmonds et al., 2008). Studies of patients with damage to the prefrontal cortex confirm that the pre-SMA region and the right lateral prefrontal cortex are important for this task (Picton et al., 2007). With regards to the Stroop Test, a similar picture emerges that highlights the importance of the anterior cingulate cortex and the nearby pre-SMA region (Alexander et al., 2007). The specific roles of the anterior cingulate and pre-SMA are returned to later.

Task-switching

In the **Wisconsin Card Sorting Test**, a series of cards must be matched against reference cards (Milner, 1963; Nelson, 1976). The cards can be matched according to one of three dimensions, namely color, number, and shape (see Figure 14.9). For example, in the color condition a blue card must be grouped with blue cards and red cards grouped with red cards (ignoring number and shape). After each trial, participants are told whether they are correct or not. Eventually, they are told that they are incorrect and they must then spontaneously switch task, that is, start sorting according to number or shape. Many patients with damage to the prefrontal cortex fail to make this shift and continue to incorrectly sort according to the previous rule, a behavior termed **perseveration**.

The Wisconsin Card Sorting Test has a number of features that make it demanding: the switches are unpredictable, and moreover, the relevant dimensions (color, shape, number) are not given but need to be inferred. This also makes it hard to know why, in cognitive terms, failure on the task happens. Other **task-switching** paradigms have been developed that enable more fine-grained analysis of the underlying mechanisms. These tend to be used in studies of non-brain-damaged participants using fMRI or TMS. To give an example of a task that involves switches that occur predictably, imagine that you are a participant looking at a square 2 × 2 grid such as that in Figure 14.10. A digit and/or number pair (e.g., L9) will appear in each part of the grid, moving clockwise, and you must make a response to each stimulus. When the stimulus is in the upper half of the grid, you must decide if the letter is a consonant or vowel using a left-right button press. When

KEY TERMS

Wisconsin card sorting test
A test of executive functions involving rule induction and rule use.

Perseveration
Failure to shift away from a previous response.

Task-switching
Discarding a previous schema and establishing a new one.

FREE
INSTRUCTOR & STUDENT RESOURCES

ONLINE RESOURCES

To test yourself on the Stroop Test and on task-switching, visit the demo test library (www.testable.org/ward).

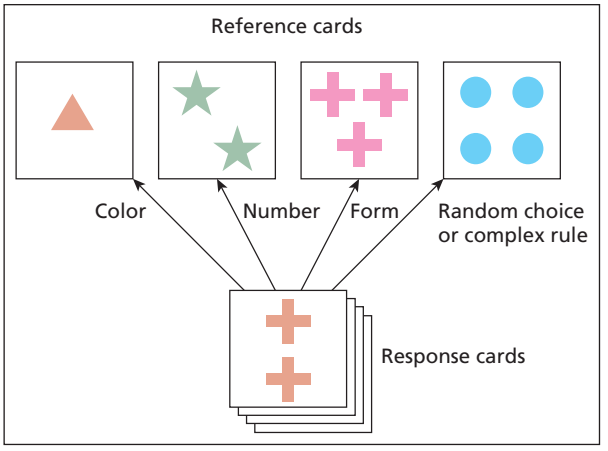


FIGURE 14.9: In the Wisconsin Card Sorting Test, patients are given a card that can be sorted by a number of rules (matching shape, number or color). Sometimes the rule unexpectedly changes and the patients must adjust their responses to the new rule.

KEY TERM

Switch cost
A slowing of response time due to discarding a previous schema and setting up a new one.

the stimulus is in the lower half, you must decide if the digit is odd or even (some participants would get the complementary set of instructions). This produces two types of trial – those in which the task switches and those in which it does not. The reaction times for the switch trials are significantly slower, and this difference remains even though the change is predictable and even if the subject is given over a second to prepare before each stimulus is presented (Rogers & Monsell, 1995). This difference in reaction time between switch and non-switch trials is called the **switch cost**.

The switch cost could either reflect suppressing the old task or reflect setting up the new task. This can be evaluated by considering switches between easy and hard tasks. A greater switch cost from easy to hard would imply a difficulty in setting up the new (harder) task, whereas a greater switch cost from hard to easy would imply a difficulty in inhibiting the old (harder) task. The evidence suggests it is the latter; that is, the switch cost has more to do with inhibiting the old task than setting up the new one. For example, bilinguals are slower at switching from their second to their first language than from their first to their second language in picture naming (Meuter & Allport, 1999). With Stroop stimuli, people are faster at

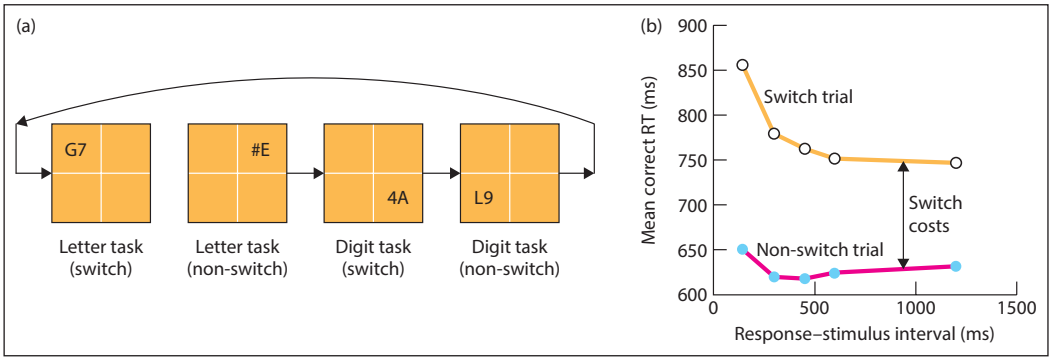


FIGURE 14.10: When the digit and/or letter pair is in the top half, the subject must decide whether the letter is a consonant or vowel. When it is in the bottom half, the digit must be classified as odd or even. This generates two types of trial – those in which the task switches and those in which it does not. Switch trials are significantly slower even though the switch is predictable and even if participants are given over one second to prepare before the stimulus is shown.

switching from word naming to color naming (easy to hard) than color naming to word naming (hard to easy) (Allport et al., 1994).

Functional imaging studies reveal a variety of prefrontal regions together with the anterior cingulate cortex/pre-SMA to be involved in task-switching, by comparing switch trials with no-switch trials (Ravizza & Carter, 2008) or contrasting the switch preparation time (before the stimulus) with switch execution after the stimulus (Brass & von Cramon, 2002). However, it is not always straightforward to link specific regions with specific cognitive processes because there are often different types of switching mechanism. Most task-switching experiments involve both a switching of response rules and a switching of the stimulus selected. In the study described previously, for example, the left hand switches from responding "consonant" to responding "odd," and the stimulus selected switches from letter to digit (i.e., multiple aspects of the task are switched). Rushworth et al. (2002) attempted to control for these differences in a combined fMRI and TMS study. They found that part of the medial frontal lobes (the pre-SMA region) are important for reassignment of stimulus–response pairings (e.g., which button to press), whereas lateral frontal regions may be involved in selection of the current rule (e.g., whether to respond to color or shape in their task).

Multitasking

Multitasking experiments can be regarded as having an element of maintaining future goals while current goals are being dealt with (Figure 14.12). This is related to, but an extension of, task-switching. In task-switching one goal is substituted for another. In multitasking several goals are maintained at the same time (but only one executed).

KEY TERM

Multitasking
Carrying out several tasks in succession requires both task-switching and maintaining future goals while current goals are being dealt with.

FIGURE 14.11: Bilingual speakers are faster at switching from their first to their second language, than from their second to their first language. How can this apparently paradoxical result be explained?

Akchamczuk/iStock

FIGURE 14.12: How do we perform multitasking? Could the anterior prefrontal region hold the key?

Patients with lesions to the prefrontal cortex may be particularly impaired at multitasking, even though each task in isolation may be successfully performed and even though they perform normally on other tests of executive function, including the Wisconsin Card Sorting Test and FAS Test (Burgess et al., 2000; Shallice & Burgess, 1991). This suggests a possible fractionation of executive functions (assuming it isn't simply related to task difficulty) – an idea returned to in the next section. In the Six Element Test the participant is given six open-ended tasks to perform within a 15-minute period (e.g., arithmetic, writing out names of pictures). Critically, they are instructed to attempt each task. However, they will be unable to complete all of them in the time allowed, and more points are awarded for earlier items. Constraints are placed on some of the ordering of tests. Patients with prefrontal lesions would often fail to switch tasks, spend too long planning (e.g., taking notes) but never execute the plans, and so on. The patients could easily perform the isolated tasks, but their difficulties were only apparent when they had to coordinate between them (Shallice & Burgess, 1991).

ONLINE RESOURCES

Is ADHD related to difficulties with executive functions? Dig deeper online by scanning the QR code or visiting routledgelearning.com/wardcognitiveneuroscience.

Evaluation

By the mid-1990s there was a generally agreed-upon definition of what the essential features of executive functions were, for eample, allowing flexible or "intelligent" behavior, exerting control via a biasing influence. There was also a general consensus that the prefrontal cortex had a critical role in implementing this, and there were also a set of frequently used tasks that were assumed to be a good indicator of prefrontal functioning (e.g., the Wisconsin Card Sort, the Stroop Test). There was also agreement on the kind of model that could account for this. One simple model of executive functions is the original version of the SAS (Supervisory Attentional System) model – introduced in Chapter 10. This consists of a set of tasks and behaviors (termed schemas) and a biasing mechanism that activated/suppressed these schemas according to the individual's current goals (Norman & Shallice, 1986). The activation of schemas was conceptualized as a balance between bottom-up processes (cues in the environment, habits, etc.) and top-down processes (task instructions, long-term plans, etc.). Disruption of this balance, for example, by a prefrontal lesion would tend to result in recent or habitual responses being inappropriately elicited (e.g., in the Stroop Test, or Wisconsin Card Sort), poor planning, and so on.

Although these core ideas and empirical results are as valid today as they were in the 1990s, the contemporary intellectual landscape relating to executive functions is far more detailed and complex. In the mid-1990s there was already some evidence that was hard to accommodate by existing theories. For instance, it was found that some patients with prefrontal lesions could pass the standard tests of executive functions, but yet show significant impairments in organizing their daily life and in their social interactions (Eslinger & Damasio, 1985; Shallice & Burgess, 1991). This revealed a potential flaw in the early accounts. However, these observations could still be explained away: for instance, by pointing out that lab tests may not be fully sensitive to deficits apparent in the "real world." Brain imaging has made a very significant contribution toward moving the debate forward.

This has enabled a more fine-grained analysis of the functions of different regions of the prefrontal cortex (and their connectivity) both in studying healthy participants (in fMRI) but also in identifying more precise lesion locations in patients. The next section considers various ways in which executive functions might be organized in the brain.

EGAS MONIZ AND THE PREFRONTAL LOBOTOMY

The career of Egas Moniz was an eventful one. In politics, he served as Portuguese ambassador to Spain and was president of the Portuguese Delegation at the Paris Peace Conference in 1918, following the First World War. However, it is his contribution to neurology and neurosurgery that gained him fame and infamy. In the 1920s he developed cerebral angiography, enabling blood vessels to be visualized with radioactive tracers. In 1935, he developed the prefrontal lobotomy/leucotomy for the treatment of psychiatric illness. Between then and 1954, more than 50,000 patients would have the procedure in the USA (Swayze, 1995) and over 10,000 in the UK (Tooth & Newton, 1961). This brought Moniz mixed fortunes. He was awarded the Nobel Prize for Medicine. However, he had to attend the ceremony in a wheelchair because, some years previously, he had been shot in the spine and partially paralyzed by one of his lobotomized patients.

Moniz's operation was designed to sever the connections between the prefrontal cortex and other areas, notably the limbic system (Moniz, 1937, 1954). This procedure was adapted by others in frighteningly simple ways, notably Dr. Walter Freeman in the USA. For instance, an ice pick–type implement was inserted through the thin bony plate above the eyes and waggled from side to side (Figure 14.13).

At that point, there were no pharmacological treatments for psychiatric complaints. Lobotomy was used for a variety of disorders, including obsessive-compulsive disorder, depression, and schizophrenia. The measurement of "improvement" in the patients was rather subjective, and the fact that the lobotomized patients tended to be duller and more apathetic than before was not sufficient to halt the appeal of the lobotomy. Formal assessments of cognitive function, if they had been carried out, would undoubtedly have revealed impairments in executive function.

Moniz died in 1955. By then, his surgical innovation had been phased out, and its success has been left to history to judge.

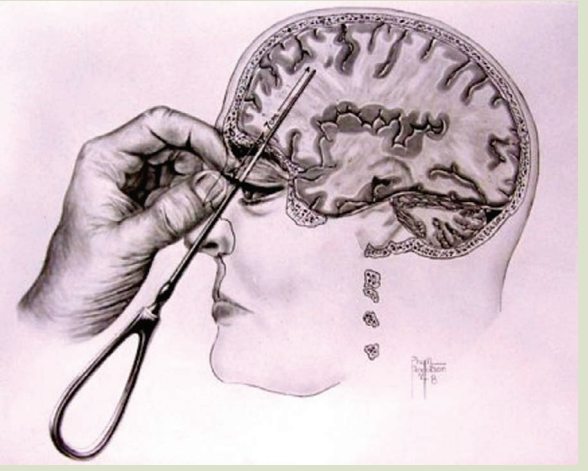


FIGURE 14.13: The surgical procedure of frontal lobotomy for psychiatric patients often done crudely using an implement inserted above the eyes and moved from side to side.

https://nihrecord.nih.gov/2019/11/01/when-faces-made-case-lobotomy

THE ORGANIZATION OF EXECUTIVE FUNCTIONS

Although there are many different approaches to explaining executive functions, it is important to emphasize that they typically agree on many of the core principles outlined so far. Namely, that they require flexible processing in order to override automatic behavior, switch flexibly between tasks, and carry out a current task while holding in mind other goals – and that this is achieved via a biasing influence (they make certain behaviors more or less likely) rather than dictating to the rest of the brain. As for differences between models, one of the key distinctions is the extent to which different models assume that executive functions can be decomposed into several modular-like processes versus executive functions construed as a more unitary idea. This section focusses on different models of organization of executive functions in particular reference to how they map onto different regions within prefrontal cortex.

"Hot" versus "cold" control processes

Perhaps the least controversial principle of organization of executive functions is the distinction between the control of affective or reward-related stimuli (i.e., "hot") versus purely cognitive (i.e., "cold") stimuli. Reward-related stimuli include money (in humans) and food (typically used in studies of nonhuman animals), whereas purely cognitive stimuli often involve sensory dimensions (such

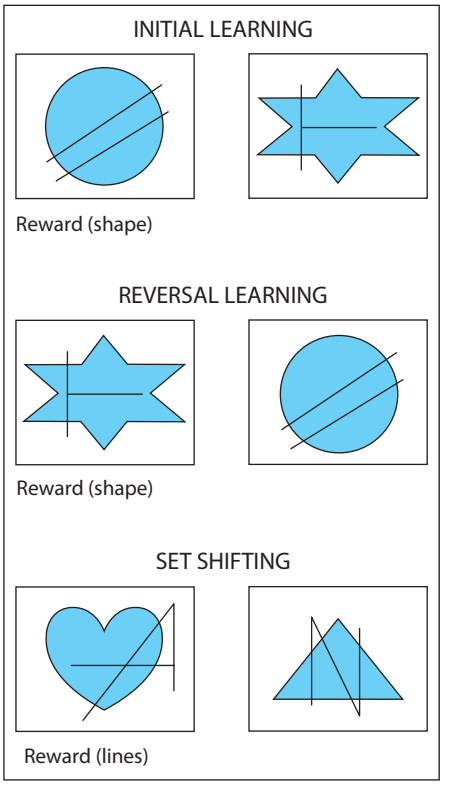


FIGURE 14.14: Marmosets were trained to respond using a touch screen to compound stimuli, presented in pairs, either to certain shapes or lines. After lesioning to the orbitofrontal cortex or lateral prefrontal cortex there were several kinds of task switches. In the reversal learning condition, the same stimuli were presented, but previously rewarded shapes/lines were no longer rewarded (lesions to orbitofrontal cortex impairs responding to this task-switch). In the dimensional-shift condition, different shapes and lines were presented, and the animals had to shift from responding to shapes and respond to lines or vice versa (lesions to the lateral prefrontal cortex impairs responding to this task-switch).

Adapted from Dias et al. (1996).

as color or shape). Most of the tests of executive function described thus far are of the latter kind (e.g., Stroop Test, Wisconsin Card Sort). Hot cognitive control involves primarily the orbitofrontal cortex (and associated ventromedial PFC), whereas cold cognitive control involves primarily the lateral PFC. This reflects the anatomical connectivity of these frontal regions to posterior regions involved in affective versus sensory/motor processes (Öngür & Price, 2000).

Dias et al. (1996) designed a test of task-switching that could be learned by marmosets (a species of primate). As noted before, the seemingly simple task-switching paradigm has several processes (establishing new tasks, inhibiting old tasks) that can be configured in different ways (switching stimuli, switching responses, switching rewards). The stimuli in their study consisted of compounds of black lines superimposed on blue shapes, similar to those in Figure 14.14. The animals were trained to respond to only one of these dimensions (shapes or lines) and had to remember which shapes or lines were correct. For instance, they may learn that a blue circle is rewarded (i.e., correct), but a blue star is not. They then received neurotoxic lesions, either to the lateral or orbital PFC, and subsequently undertook further training sessions that involved a task-switch. In the **reversal learning** condition, the same stimuli were presented, but such that the previously rewarded stimuli were no longer rewarded (in the previous example, the blue star is now rewarded, but the blue circle is not). In the dimensional-shift condition (which resembles the Wisconsin Card Sorting Task), new shapes and lines were presented and the animals had to relearn, for instance, that lines were now rewarded and not shapes. Lesions of the orbitofrontal cortex disrupted the ability to respond to the fact that the rewards had been switched (but not that the relevant cognitive dimension had switched), whereas lesions of the lateral PFC disrupted the ability to respond to the fact that the relevant cognitive dimension had switched from shapes to lines (but these animals were able to learn that previously rewarded shapes were

KEY TERM

Reversal learning
Learning that a previously rewarded stimulus or response is no longer rewarded.

no longer rewarded). They interpreted this double dissociation as evidence for two separate inhibitory control processes: one reward-related and another related to sensory stimulus dimensions.

The distinction between executive processing of affective versus nonaffective stimuli can account for one puzzle from the older literature. Namely, the fact that some brain-damaged patients with known pathology of the prefrontal cortex exhibit poor regulation of behavior in the "real world" (particularly with regards to financial management and social interactions) despite passing standard (i.e., "cold") tests of executive function (Eslinger & Damasio, 1985). Damasio and colleagues have developed the **somatic marker hypothesis** to account for this (Damasio, 1996). In this theory, somatic markers form the link between previous situations stored throughout the cortex and the "feeling" of those situations stored in regions of the brain dedicated to emotion (e.g., the amygdala) and the representation of body states (e.g., the insula). The somatic markers are assumed to be stored in the ventromedial frontal cortex (including parts of the orbital surface) and have a direct role in controlling ongoing behavior, notably in those situations in which feelings are critical (e.g., when taking risk, or interacting socially). To investigate this hypothesis, they devised the **Iowa Gambling Task** that has been shown to distinguish between different lesion sites and cognitive profiles (Bechara et al., 1994). Players are given four decks of cards (A to D) and a "loan" of $2,000 in fake bank notes and are instructed to play so that they win the most and lose the least as illustrated in Figure 14.15. On turning each card, the player receives either a monetary penalty or gain. Playing mostly from packs A and B leads to a net loss, whereas playing mostly from packs C and D will lead to a net gain. Control participants, without a brain lesion, learn to choose from C and D and to avoid A and B. Patients with lesions to the ventromedial frontal cortex do not (Bechara et al., 1994). Moreover, control participants generate an anticipatory skin conductance response (SCR) before making a selection from a risky pile (A and B), whereas these patients do not (suggesting the patients cannot use affective states to regulate behavior). Patients with lesions to the orbital/ventromedial PFC are impaired on the Iowa Gambling Task, but not on working memory tests (Bechara et al., 1998) and not impaired on tests such as the Stroop or Wisconsin Card Sorting (Glascher et al., 2012). Patients with lesions to the lateral PFC show the reverse profile.

When testing their patients with orbital and ventromedial prefrontal lobe lesions, Damasio and colleagues (1990) noted that many of their patients met a published American Psychiatric Association (APA) criterion for **sociopathy** (or Anti-Social Personality Disorder as it is now termed). The term *acquired* sociopathy is used to refer to those individuals who did not exhibit such symptoms prior to their brain injury. It is diagnosed by behavior such as: a failure to conform to social norms; irritability and aggressiveness; impulsivity or failure to plan ahead; and

KEY TERMS

Somatic marker hypothesis
A proposal that emotional and bodily states associated with previous behaviors are used to influence decision-making.

Iowa gambling task
A task in which participants must learn to avoid risky choices (generating a net loss) in favor of less risky (and more rewarding) choices.

Sociopathy
A personality disorder (now called Anti-Social Personality Disorder) associated with irresponsible and unreliable behavior that is not personally advantageous; an inability to form lasting commitments or relationships; egocentric thinking; and a marked degree of impulsivity.

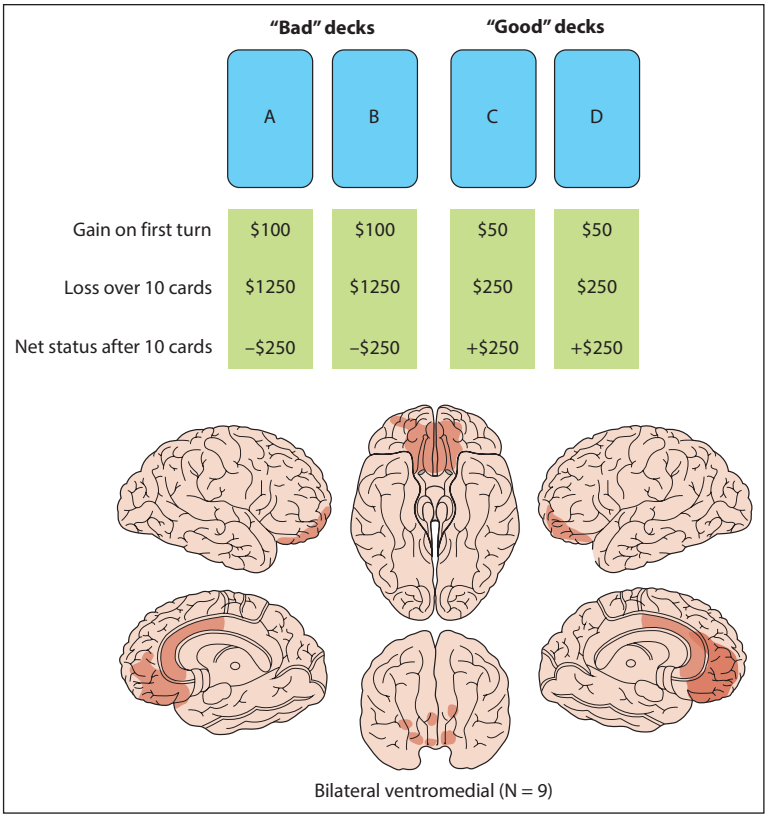


FIGURE 14.15: Players receive $2,000 and must choose hidden cards from one of four packs, A to D. Playing preferentially from packs A and B will result in loss, whereas playing preferentially from packs C and D will result in gain. Players are not informed of this contingency. Will they learn to avoid A and B? Patients with damage to ventromedial frontal lobes are impaired on this task.

From Bechara et al. (1998). Copyright 2007 Society for Neuroscience.

having shallow or seemingly nonexistent feelings. This is linked to poor executive control of social and emotional information, rather than lack of knowledge of conventional social rules (Saver & Damasio, 1991).

A somewhat different explanation of the results from the Iowa Gambling Task is that it reflects a failure of reversal learning (Maia & McClelland, 2004). This is because cards from bad decks A and B are rewarded with $100 on the first turn, and cards from the good decks C and D are rewarded with only $50. Thus, patients must learn to avoid the previously advantageous decks, A and B. If there is initially no larger reward on the first trial of the bad decks, then patients with ventromedial frontal lesions perform normally (Fellows & Farah, 2003). Other studies have shown a link between failure on reversal learning and poor regulation of social behavior (Hornak et al., 2004).

Finally, studies of **delay discounting (or temporal discounting)** also point to a clear difference between the lateral and orbital/ventromedial PFC. Delay discounting refers to the fact that future rewards are valued less than equivalent current rewards (e.g., $100 now has a higher subjective value than $100 next year). Tasks of delay discounting require decisions to be made whether to choose reward X at time 1 or reward Y at time 2. In the real world, one is faced with decisions such as whether to go on holiday this year or invest the money

KEY TERM

Delay discounting (or temporal discounting) The tendency for future rewards to have less subjective value than the same reward received now (or in the nearer future).

for a better holiday in the future or to spend money now or invest in a pension scheme. Recall that patients with orbitofrontal lesions fail to plan ahead and exhibit impulsive behavior by opting for immediate rewards. McClure et al. (2004a) argued, from the results of an fMRI study of healthy participants, that there are two different mechanisms for delay discounting, depending on whether an immediate reward was an option (i.e., a reward now compared with at some future time) or not (i.e., different rewards at two future points in time). The possibility of an immediate reward was associated with activation in the medial orbitofrontal cortex and reward circuitry (e.g., nucleus accumbens), but choosing between non-immediate rewards was more associated with lateral prefrontal and parietal regions (the nonaffective/cold executive system). The same pattern is found when the rewards are food-related and the time intervals are shorter (McClure et al., 2007).

The multiple-demand network

The previous evidence suggests that executive functions are organized into at least two broad divisions: those requiring control or evaluation of affectively loaded stimuli (requiring orbitofrontal and ventromedial cortex) and those requiring control or evaluation of nonaffective stimuli (requiring lateral PFC). However, are there further subdivisions of organization within the lateral PFC itself? In this section, one theory is considered (the multiple-demand network) that provides a generally negative answer to this question. In subsequent sections, alternative viewpoints are elaborated.

KEY TERM

Multiple-demand network
A set of brain regions in the lateral prefrontal and parietal lobes activated by a large range of tasks relative to baseline.

The **multiple-demand network** refers to a set of brain regions predominantly in the prefrontal cortex that are activated in fMRI studies by a wide set of tasks involving cognitive control and also by tasks in general relative to a resting baseline (Duncan, 2010). The network is identified by meta-analysis of large numbers of fMRI studies (Duncan & Owen, 2000). This network includes regions of the lateral PFC (left and right) and the anterior cingulate cortex (Figure 14.16). It also includes regions of the parietal lobes, notably around the intraparietal sulcus (IPS). However, it excludes the orbitofrontal cortex (and related ventromedial PFC) and generally excludes the anterior-most portion of the PFC (termed the frontal poles or BA10).

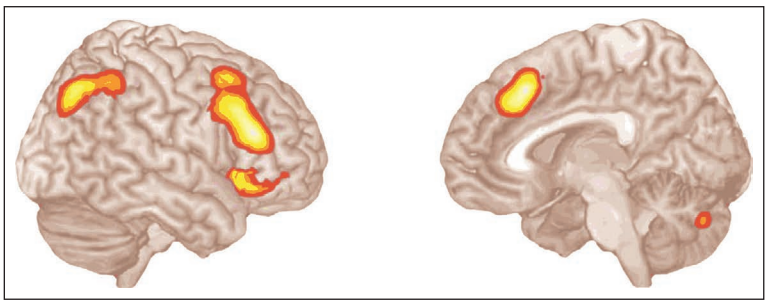


FIGURE 14.16: The multiple-demand network is identified, primarily, from meta-analyses of fMRI studies that show that common regions of the lateral prefrontal cortex (together with regions in the parietal lobe and anterior cingulate) are activated by a wide variety of tasks requiring some form of nonautomatic behavior.

From Duncan (2010).

NEUROECONOMICS

The relatively new field of **neuroeconomics** uses neuroscientific methods and theories to account for economic decision-making (for a review see, Loewenstein et al., 2008). The term "economic" can be construed in the broadest sense as referring not only to financial decisions (e.g., whether to spend, save or invest) but to other kinds of decisions that require allocation of a scarce resource (e.g., time) or an assignment of value. Whereas much of theoretical economics describes how people should make decisions to achieve maximum benefits, the psychology of economics (and neuroeconomics) is concerned with how people actually do make decisions. For example, most people do not purchase clothing for purely utilitarian reasons (i.e., to keep warm) but for other reasons, including the need to advertise one's social status or personality, or, in some cases, because one simply enjoys the act of shopping (retail therapy). That is, the concept of value may have more to do with the perceived rewards to a given individual than the actual functional reward that may ultimately be obtained.

There is also a strong social element as to how economic decisions are made. For example, consider the financial sharing game termed the **Ultimatum Game** (Guth et al., 1982). This involves two players: a proposer and a responder, as shown in Figure 14.17. The proposer is given a sum of money (e.g., $20) and must decide how much to give to the responder (between $1 and $20). The responder must then decide whether to accept the offer (and the offer is then split) or reject the offer (both players leave with nothing). From a purely financial point of view, in a one-trial game, the optimal decision of the proposer is to give the minimum ($1), and the optimal decision of the responder is to accept whatever is given (because something is always better than nothing). In reality, the responder typically rejects offers that are less than 20 percent of the pot, because they perceive the offer as unfair and wish to punish the proposer. Another way of thinking about it is that they are weighing up two values: a purely monetary value pitted against a social value of fairness.

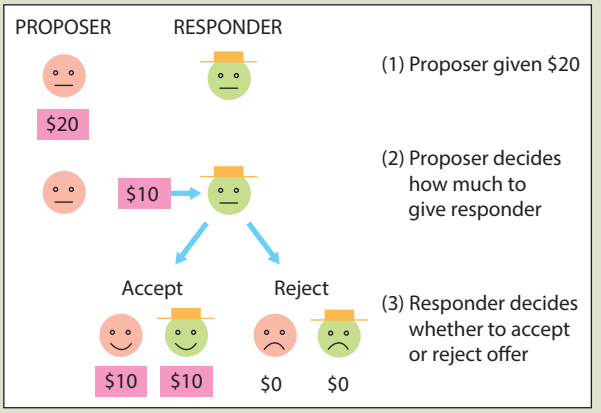


FIGURE 14.17: Sanfey et al. (2003) studied the Ultimatum Game using fMRI, in which participants acted as responders and received either fair or unfair offers. Activity in a part of the brain that is linked with emotional processes (the insula) reliably predicts whether a player will reject an unfair offer. However, applying TMS over the right lateral prefrontal cortex increases the probability of accepting unfair offers (Knoch et al., 2006). This is consistent with a biasing control signal (from the prefrontal cortex) and a bottom-up emotional response competing for selection.

Much of the emerging field of neuroeconomics is concerned with the interaction between one's gut reactions (intuition or emotion) and one's goals and beliefs. For example, one's brand loyalty (e.g., to Pepsi versus Coke) may sometimes be at odds with one's true taste preferences when they are assessed blind. Whereas the dorsolateral prefrontal cortex is associated with people's beliefs about which of two brands they are tasting (Pepsi or Coke), the orbitofrontal cortex is associated with their actual ratings of how nice each drink is (McClure et al., 2004b).

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ONLINE RESOURCES

Visit the online demo test library to try out the Ultimatum Game for yourself (www.testable.org/ward).

KEY TERMS

Neuroeconomics
The use of neuroscientific methods and theories to account for economic decision-making.

Ultimatum game
A two-player game in which one player proposes a split of money and a responder either accepts the money (and obtains the agreed split) or rejects it (and both players get nothing).

Fluid intelligence
Flexible thinking and problem-solving in novel situations, independent of acquired knowledge.

Crystallized intelligence
The ability to use prior expertise and knowledge.

According to Duncan (2010), cognitive control involves several elements: focusing on the relevant features of the sub-task; as sub-tasks are completed, the new elements must be focused upon and old ones discarded, and selected results must be passed from one sub-task to another. Evidence from single-cell recordings in the primate lateral PFC sheds some light as to how this is achieved. These neurons respond primarily to the rules of the task rather than the specific stimulus or response (Asaad et al., 1998, 2000). For example, they may respond to a conjunction of a stimulus and response (e.g., "look left when I see object A"), but not to the same stimulus out of context ("see object A") or the same response in a different context (e.g., "look left when I see object B"). Thus, the coding of the task-relevant features is highly flexible. During performance of the task itself, the coding is also highly focused. In tasks such as these, up to 50 percent of all cells recorded in lateral prefrontal cortex discriminated targets from non-targets but, by contrast, many fewer cells made the task-irrelevant discriminations between one non-target and another (Everling et al., 2002). However, when the task involves multiple then different sub-populations of neurons with the lateral PFC tend to separately code for different attributes of the sub-tasks (Sigala et al., 2008).

One claim is that the multiple-demand network is related specifically to **fluid intelligence** (Duncan, 2010; Woolgar et al., 2010). Fluid intelligence relates to problem-solving ability and is tested using measures such as Raven's matrices (Raven, 1960). This test involves attending to multiple-features of a problem: in the example printed in Figure 14.18, the solution involves processing orientation, size, and shape as three different sub-tasks. This can be contrasted with **crystallized intelligence** (Cattell, 1971), which relies heavily on prior expertise and knowledge and is assessed by measures of IQ such as the WAIS (Wechsler Adult Intelligence Scale; Wechsler, 1981). The latter measures mental arithmetic, factual knowledge, speed of processing, and so on. Meta-analyses of functional imaging tests of fluid intelligence produce a very similar pattern to that of the multiple-demand network (Jung & Haier, 2007).

Patients with lesions of prefrontal cortex perform no worse on tests such as the WAIS relative to other brain-damaged controls (Warrington et al., 1986). By contrast, patients with lesions to the prefrontal cortex who score well on the WAIS IQ (scores between 125 and 130 with a scale average of 100) score 22–38 points lower on measures of fluid intelligence (Duncan et al., 1995). Moreover,

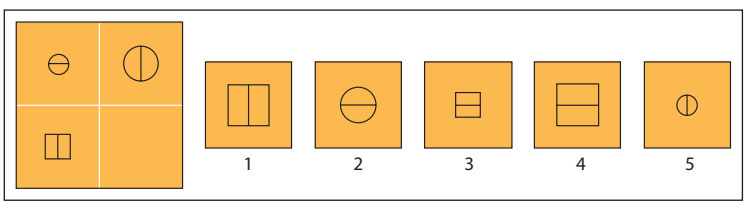

FIGURE 14.18: Patients with frontal lobe damage are impaired on tests of "fluid intelligence" such as this.

Reprinted from Duncan et al. (1995). © 1995, with permission from Elsevier.

performance on standard tests of executive function by patients with PFC lesions correlates strongly with fluid intelligence measures and with each other (Roca et al., 2010).

Claims such as these (i.e., that all tests of executive function tap the same network) have led some researchers to characterize the multiple-demand network as an undifferentiated entity. However, some relative degree of specialization of function within the network is tentatively acknowledged (Hampshire et al., 2011) but without recourse to any modularization of different executive components. Moreover, regions normally regarded as outside of the network (e.g., the frontal poles) are acknowledged to have a qualitatively different functional role (Roca et al., 2010).

A posterior-to-anterior organization?

Until relatively recently, little was known about the function of the anterior-most part of the frontal lobes, also called the rostral prefrontal cortex or the frontal pole. However, a number of studies and reviews have suggested that the region is specifically involved when multiple tasks need to be coordinated (e.g., Burgess, 2000; Koechlin et al., 1999a). Koechlin et al. (1999a) performed an fMRI experiment in which participants were required to hold in mind a main goal while concurrently performing sub-goals. Neither holding in mind a goal by itself (working memory) nor switching between alternate goals was associated with activity in this frontal pole region. Only when these two elements were combined was activity found in this region. The fact that some patients with frontal lesions are specifically impaired on multitasking, but not the component tasks and not other measures of executive function (e.g., the Wisconsin Card Sort, which involves task-switching but not multitasking) supports the view that there is a separate neuroanatomical substrate for this (Burgess et al., 2000). This has led to the proposal that there is a hierarchical organization of executive functions such that posterior parts of the prefrontal cortex (including what Duncan, 2010, refers to as the multiple-demand network) implements tasks with a single goal (including those requiring switching to different sub-tasks), but that the anterior-most PFC implements multiple tasks simultaneously.

Koechlin and Summerfield (2007) propose a specific model along these lines consisting of a hierarchy that runs from the premotor cortex (posteriorly) to the frontal poles (anteriorly), as shown in Figure 14.19. The premotor cortex is not anatomically part of the PFC but is known to implement simple stimulus-response mappings such as "press the left button when you see red, and right for green" (Passingham, 1988). However, adding contextual information (e.g., "perform consonant/vowel discrimination for red letters and UPPER-/lower-case discrimination for green letters") cannot be performed automatically, at least not without training, and does require cognitive control. Moreover, switching the instructions on a block-by-block basis (e.g., so that red becomes

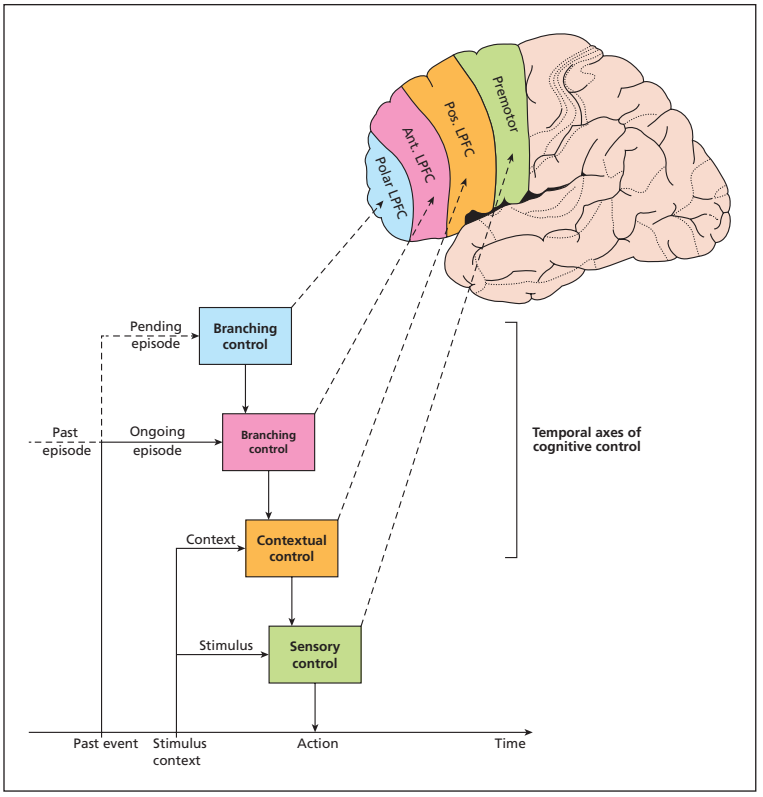

FIGURE 14.19: Koechlin and Summerfield (2007) argue for a posterior-anterior hierarchy of executive functions with more posterior regions involved in implementing simple stimulus-response mappings (e.g., "red stimulus → left button press"), and more anterior regions involved in more complex mappings (e.g., "red stimulus → left button press," but only if the stimulus is also a vowel).

From Koechlin and Summerfield (2007).

the UPPER/low task and green the consonant/vowel task) requires what Koechlin and Summerfield (2007) term episodic control, that is, knowing which context to apply at a given moment in time. The highest level in their model, termed "branching control," involves holding in mind pending tasks while carrying out an ongoing task (i.e., multitasking). In an fMRI study, Koechlin et al. (2003) compared the first three types of situation (sensorimotor rules, contextual rules, episodic rules) using the letter and color stimuli described previously. Implementing the sensorimotor rules (common to all tasks) invoked the premotor cortex, whereas the presence of contextual rules invoked more anterior activity, and the presence of episodic rules was more anterior still.

Badre and D'Esposito (2009) present a related view of the organization of the lateral PFC to Koechlin and Summerfield (2007). One of the key differences in their formulation is that they propose two different posterior-to-anterior gradients in the lateral

PFC: one that is ventrally based and one that is dorsally based. This is consistent with several other prominent views that allocate different functions to dorsal and ventral regions of the lateral PFC (e.g., Fletcher & Henson, 2001; Petrides, 2000). In their model, the dorsal posterior-anterior gradient is linked specifically to action planning (perhaps by virtue of connectivity to the parietal lobes), whereas the ventral posterior-anterior gradient is linked to, among others, language and objects (perhaps by virtue of connectivity to the temporal lobes). To give a concrete example from the literature, one study found a posterior-anterior gradient in the ventral part of the lateral PFC when participants were asked to make semantic decisions about objects such as "Is the object bigger than a 13-inch box?" or "Is the object made of an organic substance?" (Race et al., 2009). The clever aspect of the study design is that they measured priming of the BOLD response when different elements of the task were repeated: either by repeating the same semantic item (irrespective of task or response), the same task (e.g., size judgment), or the same manual response. This led to a gradient of activity (anterior-most for semantic repetition, posterior-most for manual repetition) running along the ventral portion of the lateral PFC.

Finally, Burgess et al. (2007) have proposed a theory concerning the functions of the frontal pole region (BA10) but without an assumption of a gradient/hierarchy across the lateral PFC. They suggest that its specific role is to act as a "gateway" between stimulus-driven cognition (e.g., maintaining focus on a task involving sensorimotor demands) versus internal thoughts (thinking "in one's head"). Multitasking involves maintaining internal cognitions (i.e., future intentions) while engaging with an external task. This connects their theory to a much wider literature showing that the medial anterior PFC region forms part of a default mode network – discussed in more detail in Chapter 15 – concerned with inner thoughts and implicated in social cognition. Patients with lesions limited to the frontal poles are impaired on tasks of multitasking and on tasks of social cognition (theory-of-mind, understanding *Faux pas*) but perform well on many other tests of executive function (Roca et al., 2010; Roca et al., 2011).

Hemispheric differences

Functional differences between the left and right lateral PFC are more controversial than the other principles of organization discussed thus far. For instance, they tend not to be found in single-cell recordings from the monkey PFC (Miller & Cohen, 2001), but this may not be surprising since humans are known to possess far more lateralization of higher cognitive functions than other primates. It is also less apparent in the functional imaging data of humans (Duncan & Owen, 2000). Perhaps the most convincing evidence comes from neuropsychological investigations of lesions to the PFC which has revealed reliable functional differences (Stuss & Alexander, 2007). Even here, it is to be noted, that the

dissociations tend to be relative rather than absolute: that is, patients with left and right PFC lesions differ with respect to each other, but both groups are impaired relative to controls. That is, "classical" dissociations that affect only one function tend not to be observed (to use the terminology of Shallice, 1988). This may also explain why the functional imaging data are not so clear-cut in this regard; that is, both hemispheres appear active, and the statistical difference in activation between hemispheres is rarely directly contrasted. Nor is it clear whether hemispheric differences in activation relate to actual differences in behavior from fMRI studies (e.g., does activity reflect trying harder or contributing more?).

One of the main models regarding hemispheric specializations of executive function originates from Stuss et al. (1995). In their model, the *left* lateral PFC is considered relatively specialized for task-setting, whereas the *right* lateral PFC is relatively specialized for task-**monitoring**. Task-setting will tend to be maximized when the task itself is open-ended (e.g., problem-solving) as opposed to situations in which explicit instructions are given as to how the task is to be performed. As noted previously, these problem-solving tasks tend to be more impaired after damage to the left frontal lobe irrespective of whether the stimuli are verbal (e.g., the FAS Test; Stuss et al., 1998) or visuo-spatial (e.g., the Tower of London; Shallice, 1982). Task-monitoring is linked to the notion of **sustained attention** and involves keeping "on task" and maintaining the currently relevant rules. They associate a rather different functional role ("energization") to medial regions of the frontal lobes, including both the anterior cingulate and pre-SMA region.

KEY TERMS

Monitoring
The process of relating information currently held in mind back to the task requirements.

Sustained attention
Maintaining focus on the task requirements over a period of time.

The Wisconsin Card Sorting Test is impaired after lesions of both the left and right lateral PFC relative to controls (Stuss et al., 2000). However, a left-right hemispheric dissociation is found for different versions of administering it. In the standard version, the participant is given no information about the three rules or when they will change. Patients with left lateral PFC damage perform worse than right PFC damage on this version. In a modified version, the patient is told of the rules, is given a starting rule (sort by color), and is told when the rules will change (after every ten trials). In this version, patients with right lateral PFC lesions fare worse than their left hemispheric counterparts. In the standard/open-ended version, the performance limitations may stem primarily from task-setting (taxing the left hemisphere more), whereas in the more constrained version performance, limitations may come from monitoring the current rule (taxing the right hemisphere more).

Patients with both left and right prefrontal lesions are impaired at task-switching but for different reasons (Aron et al., 2004; Mayr et al., 2006). In the study of Aron et al. (2004) patients with left lateral PFC damage tended to show much longer switch costs (consistent with a general impairment in task-setting), but patients with right lateral PFC damage tended to be particularly error-prone, specifically in the tendency to perseverate to the previous task-set

(interpreted by the authors as a failure of response inhibition but potentially explicable in terms of failed monitoring).

In a review of the literature, Frith (2000) argues that the role of the left dorsolateral PFC is in "sculpting the response space." He suggests that the region is responsible for highlighting the range of possible responses and for suppressing inappropriate responses. This is related to the concept of task-setting. It suggests that this region will be recruited more when the task parameters are not strongly constrained (e.g., when there is a large range of stimulus-response mappings to choose from). For instance, this region is activated more when participants have to choose which finger to move relative to when they are told which finger to move, and also when they are asked to generate a word from a letter cue (e.g., "F") relative to simple repetition of a word (Frith et al., 1991). The region is also active when participants are free to select *when* to make a response (Jahanshahi et al., 1995). Generating random sequences (e.g., of digits) is a cognitively demanding task that involves setting up and selecting "freely" from a pool of potential responses. There is a tendency, particularly under time pressure, for randomness to break down and participants to start generating familiar sequences from memory, such as consecutive runs (4, 5, 6; X, Y, Z) or stored knowledge (e.g., acronyms, "B, B, C"; telephone numbers), as shown in Figure 14.20. Repetitive TMS over the left, but not right, DLPFC results in less random and more familiar sequences (Jahanshahi et al., 1998). Another study found that repetitive TMS over left DLPFC impairs "free choice" even in tasks with no working memory demands (Hadland et al., 2001). The previous responses were displayed on a monitor so they need not be held in mind.

Monitoring is the process of relating information currently held in mind back to the task requirements. It is also a checking mechanism to ascertain whether retrieved or perceived information is valid. The region may be important both for monitoring the content of internally held information, such as monitoring the content of episodic or working memory (Habib et al., 2003), as well as for monitoring the content of externally presented information, as in tasks of sustained attention (Kanwisher & Wojciulik, 2000). Cabeza et al. (2003) directly compared fMRI activity in a memory retrieval task (word recognition) with a non-memory task of sustained

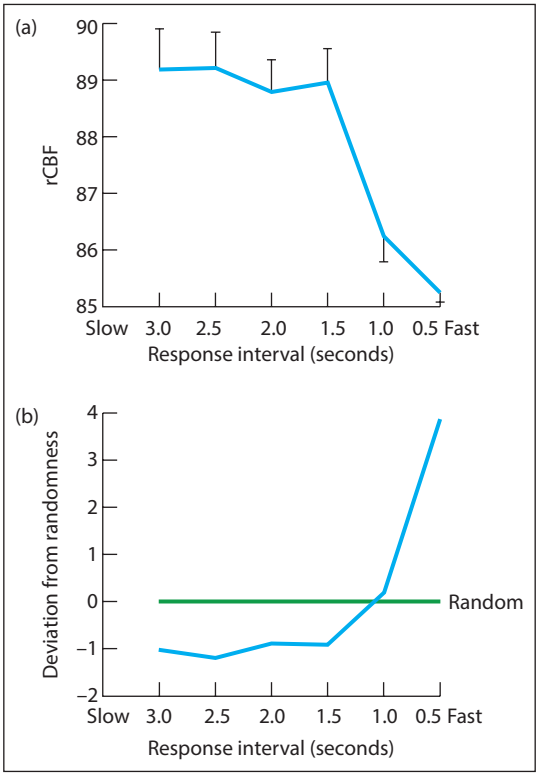

FIGURE 14.20: Activity in the left dorsolateral prefrontal cortex (a) is associated with ability to generate random sequences (b). When responses are required at a fast rate, the activity decreases, and the responses start to deviate substantially from randomness.

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attention (did the stimulus blip once, twice, or never during a 12-sec presentation?). The study found common regions of right DLPFC activity between the two tasks. As such, it appears as if the region is related more to monitoring and attending than to memory or perception per se.

An alternative view of the function of the right (inferior) lateral prefrontal cortex is that it is functionally specialized for response inhibition (Aron et al., 2004). This view emerges from studies on paradigms such as Go/No-Go, which are shown to activate the right more than left in healthy participants (on No-Go trials) and be particularly disrupted by lesions to the right lateral PFC (Aron et al., 2003). The inhibition explanation is not straightforward to separate from the monitoring account as a failure to monitor adequately would tend to lead to the automatic "go" response in No-Go trials. One fMRI study investigated the functional connectivity of brain regions during the processing of No-Go signals and found that the right lateral PFC was involved in the *detection* of the No-Go signal (i.e., consistent with the monitoring account), which then influenced the pre-SMA area (Duann et al., 2009). The pre-SMA area is, according to Duann et al. (2009), directly implicated in response inhibition of the motor program via the basal ganglia circuitry.

Evaluation

Although contemporary models of executive function retain their earlier character (i.e., flexibly implement task rules, controlling nonautomatic responses), far more is now known about how (and where) they are implemented in the prefrontal cortex. The notion of a general workspace that is essentially undifferentiated in character is not supported by the weight of evidence. Models along these lines would be the earlier versions of the SAS model (Norman & Shallice, 1986) and the models of Miller and Cohen (2001) and Goldman-Rakic (1996). The multiple-demand network (Duncan, 2010) is also largely an undifferentiated workspace, but it is certainly not to be considered synonymous with the entire prefrontal cortex (but focuses instead on the mid-lateral regions and certain parietal regions). Although we could conceptualize, from first principles, that a diverse range of tasks such as the Stroop, multitasking and reversal learning all require the same kind of control mechanism (e.g., flexibly associating stimuli and responses), the evidence suggests that the brain treats tasks such as these rather differently. Needless to say, the most extreme alternative viewpoint – that is, that each task has its own dedicated mechanisms – is untenable, because this is incompatible with the behavioral flexibility that needs to be explained in the first place.

In the previous sections several different levels of organization are considered. The distinction between cognitive versus affective control is well supported empirically and suggests a

division according to the type of information processed. There is some evidence of a posterior–anterior difference in prefrontal functioning that depends on whether single or multiple tasks are being simultaneously performed (and possibly finer gradients within that). The evidence for hemispheric differences in the lateral PFC is rather different in character from the other principles of organization in that claims have been made about the type of operation performed (left = task-setting; right = task-monitoring) rather than the type of information processed. The next section will consider in more detail another region, not strictly part of the prefrontal cortex, but strongly connected to it and implicated in other aspects of executive function: namely, the anterior cingulate cortex.

THE ROLE OF THE ANTERIOR CINGULATE IN EXECUTIVE FUNCTIONS

The anterior cingulate is shown in Figure 14.21, together with the related pre-SMA region. Historically, the anterior cingulate cortex has been classified as belonging to the limbic lobe rather than the frontal lobes. However, a more detailed understanding of its neural connectivity has suggested that it may function as

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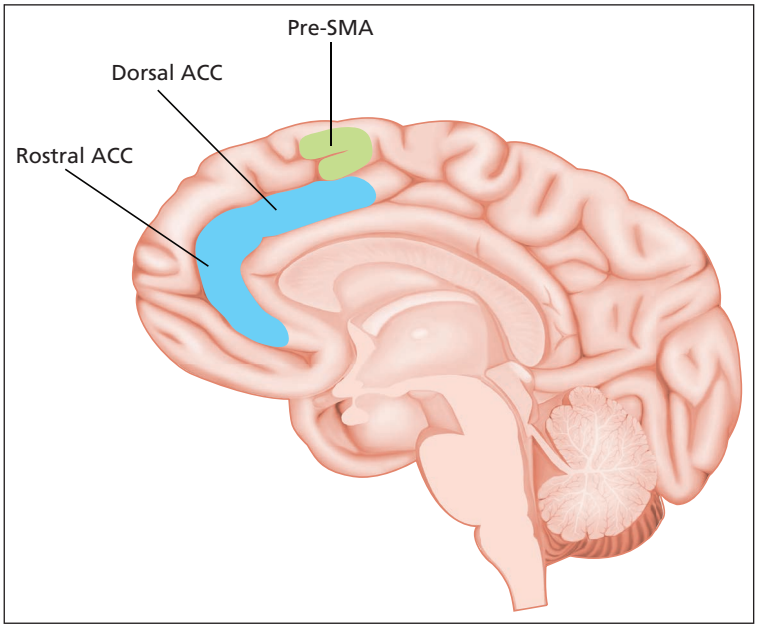

FIGURE 14.21: The anterior cingulate cortex (ACC) lies above the corpus callosum on the medial surface of each hemisphere. The dorsal region of the anterior cingulate, together with the neighboring pre-SMA region, are implicated in executive functions. A more rostral region is connected with limbic and orbitofrontal regions and may have different characteristics.

an interface between limbic and frontal regions. With regards to executive functions, research has tended to focus on a dorsal region of the anterior cingulate that has strong interconnections with the DLPFC (Bush et al., 2000). This may explain why these regions tend to be activated together in functional imaging studies. It also has connections with parietal, premotor, and supplementary motor areas. The remainder of this section will focus on the dorsal region of the anterior cingulate, and further use of the term "anterior cingulate" in this chapter will be used to refer to this region unless stated otherwise. The anterior cingulate and pre-SMA are assumed to have similar functions but with the pre-SMA being more strongly linked to control of motor responses (recall that SMA refers to Supplementary Motor Area) and the cingulate involved in task-level control.

One postulated role of the anterior cingulate in executive functions is in the detection of errors (Carter et al., 1998). In human reaction time experiments, the trial immediately after an error (error + 1) tends to be slower and more accurate than after a correct trial (correct + 1) (Rabbitt, 1966). This implies the existence of some cognitive mechanism that monitors for errors and recalibrates task performance accordingly (e.g., slowing down to ensure greater accuracy). In macaque monkeys with anterior cingulate lesions, errors are more likely on "error + 1" trials than "correct + 1" trials (Rushworth et al., 2003). This suggests that no such adjustment is made following errorful behavior, and errors are more likely to follow errors. Moreover, when monkeys (Gemba et al., 1986) and humans (Dehaene et al., 1994) make errors, an error potential can be detected at the scalp that appears to have its origins in the anterior cingulate. This response is called an **error-related negativity**, and its onset is simultaneous with the error being made and peaks around 100 ms after the response (Gehring et al., 1993), as shown in Figure 14.22. The studies cited previously are ambiguous as to whether the anterior cingulate is important just for the detection of the error, or also for the subsequent compensatory behavior. Event-related fMRI shows anterior cingulate activity on the error trial, in contrast to greater activity on the error + 1 trial in the lateral prefrontal cortex (Kerns et al., 2004). This suggests that the anterior cingulate's role is limited to error detection and not compensation, and the lateral prefrontal cortex is responsible for adjusting ongoing behavior.

KEY TERM

Error-related negativity
An event-related potential component in EEG that can be detected at the scalp when an error is made.

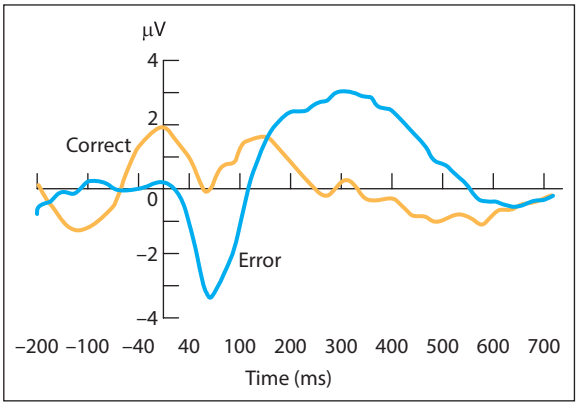

FIGURE 14.22: Error-related negativity is found at EEG scalp recordings following production of an incorrect response.

A related role for the anterior cingulate may be in evaluating response conflict. The classic example of response conflict is provided by the Stroop Test. Patients with lesions in this region perform poorly on the task (Alexander

et al., 2007). In fMRI of healthy participants, a comparison of incongruent trials (with high response conflict) relative to congruent trials is linked to activity in the anterior cingulate (Carter et al., 2000). This occurs in the absence of errors. As such, one more general account of anterior cingulate functioning is that it generates a conflict signal both in situations of likely error as well as after an actual error (e.g., van Veen & Carter, 2002).

These earlier accounts that centered on monitoring for conflict and errors were based, at least in part, on the assumption that this region was "cognitive" (or "cold" in the earlier terminology) as opposed to also responding to emotional stimuli such as rewards and punishers (following Bush et al., 2000). However, this is not the case. For instance, the dorsal anterior cingulate region responds to stimuli such as pain (Singer et al., 2006) and monetary incentives (Blair et al., 2006). As such, more recent accounts emphasize a broader role in cognitive control that encompasses both "hot" stimuli as well as "cold" ones. For instance, the model of Shenhav et al. (2013) suggests that that anterior cingulate cortex computes a cost-benefit analysis in terms of deciding how much control to allocate. The benefits of allocating control are obvious: it improves performance (fewer errors) and, hence, leads to better outcomes (including more rewards, less punishment). However, the cost of control is that it is effortful. Relatedly to this, others have conceptualized the role of the anterior cingulate in terms of motivation (Kouneiher et al., 2009) or energization (Stuss & Alexander, 2007).

There is evidence for these newer ways of conceptualizing this region. Rewards are less rewarding if we have to make an effort to obtain them. fMRI studies in humans show that this effort-based devaluation may depend on top-down interactions between the anterior cingulate and reward-related regions in the striatum (Botvinick et al., 2009). In another fMRI study, participants performed a task-switching study involving different monetary incentives: some blocks had a high incentive (more money for being correct), and others a lower incentive (Kouneiher et al., 2009). Within these blocks, there were either regular trials or "bonus trials" in which an even higher payoff could be obtained. High-incentive blocks were linked to greater sustained activity of the anterior cingulate. By contrast, performance on bonus trials was linked to pre-SMA activity. They suggested that motivational control also has a posterior-anterior axis along the medial prefrontal cortex (comparable to claims about lateral prefrontal cortex, such as Koechlin & Summerfield, 2007) with posterior being more trial-based motivation (pre-SMA) and anterior being more task-based motivation (anterior cingulate).

In animal models, rats with lesions to the anterior cingulate show a "lazy" profile of choosing low-effort rewards over bigger rewards that require more physical effort (Walton et al., 2003). In contrast, rats with orbitofrontal lesions show an "impulsive" profile of favoring immediate rewards over larger rewards that they have to wait for (Rudebeck et al., 2006).

In summary, the anterior cingulate appears to have a more modulatory role in executive functions. This may be achieved by monitoring for response conflict (older accounts) or by assigning motivational salience based on the costs and benefits of exerting effortful control (more recent accounts).

SUMMARY AND KEY POINTS OF THE CHAPTER

- Executive functions are needed to optimize performance when several cognitive processes need to be coordinated; a situation is novel or difficult; a situation does not require an automatic response (troubleshooting, problem-solving). The role of executive functions is typically described as "supervisory" or "controlling."
- Functional imaging studies and studies of brain-damaged patients point to a key role of the prefrontal cortex in executive functions. Patients with lesions here may have difficulties in problem-solving, overcoming habitual responses, multitasking and so on.
- The orbitofrontal and ventromedial prefrontal cortex has strong connections with regions involved in processing emotions; whereas the lateral (and dorsal medial) surfaces have strong connections to sensory and motor regions. Damaging these regions affects the ability to behave flexibly in response to changes in emotional value (orbital PFC) or changes in the task-relevant stimulus features (lateral PFC).
- There is evidence of a posterior-to-anterior organization of executive functions with the anterior-most region (frontal pole) implicated in multitasking.
- In humans, there is a degree of relative specialization of function between the left and right lateral prefrontal cortex: with the left more implicated in task-setting, and the right more implicated in task-monitoring.
- The dorsal anterior cingulate appears to be important for initiating cognitive control (balancing the need to perform well against cognitive effort), although lateral prefrontal regions may be needed to implement control and modify behavior.

EXAMPLE ESSAY QUESTIONS

- Can executive functions be fractionated?
- What are the problems faced by clinical tests aimed at detecting deficits in executive function?
- Is there an executive component to working memory? What is the evidence for it?
- Do the functions of the left prefrontal lobe differ from the right prefrontal lobe?
- How do we switch from one task to another?

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CHAPTER 15

The conscious brain

CONTENTS

We know that consciousness exists only because we experience it first-hand. To the philosopher, Descartes (1596–1650), this was considered a fundamental truth, which he stated as "I think, therefore I am." It can be considered a fundamental truth insofar as we know that we have thoughts, feelings, and sensations even in the extreme case scenario that they don't correspond to anything at all in external reality. We may be in a giant simulation, a brain in a vat, like in *The Matrix* movie. The process of reflecting on and reporting our own consciousness is termed **introspection**. Although we may be certain of our own consciousness – and this gives us reasonable grounds to attribute it to other humans – things become muddier when it comes to animals and machines (see the Box at the end of this chapter for discussion). There is no reason to assume that consciousness evolved in the human lineage, but without a reliable marker of consciousness, beyond introspection, even that would be up for debate. If animals were conscious, then we still have the challenge of what it would be like to be, for example, a bat (Nagel, 1974). Nor is it clear that a detailed account of the bat's neural activity, contrasting conscious and unconscious states, would tell us what it is like to be a bat.

DOI: 10.4324/9781003429975-15

KEY TERMS

Introspection
An active process in which a person becomes conscious of their inner states.

Hard problem
Explaining why and how consciousness emerges from a physical system.

Easy problem
Observing the detailed neural mechanisms and behaviors associated with consciousness.

Zombie
In philosophy, a hypothetical person who has the same cognitive capacities as everyone else but lacks consciousness.

This explanatory gap – between neuroscience and subjective states – is referred to as the **Hard Problem** of consciousness by the philosopher Chalmers (1995). He states,

> It is widely agreed that experience arises from a physical basis, but we have no good explanation of why and how it arises. Why should physical processing give rise to a rich inner life at all? It seems objectively unreasonable that it should, and yet it does.

These philosophical conundrums offer a pessimistic view of what a neuroscience of consciousness might achieve. But it is possible that by solving Chalmer's (1995) so-called **Easy Problem** (i.e., observing the detailed neural mechanisms and behaviors associated with consciousness) that the relationship between neural activity and consciousness will become as transparent as the relationship between water's chemical structure and its everyday properties (Searle, 1992). In effect, the explanatory gap may be narrowed if not completely bridged.

In previous chapters there was no real need to explain the function of vision, memory, or language because it was self-evident. But not so for consciousness. What function does it serve? Again, philosophers have a way of putting a fly in the ointment, and this time it is via the philosophical concept of a **zombie** (e.g., Kirk, 2005). A zombie is a hypothetical person who has the same cognitive capacities as everyone else but lacks consciousness. Neuroscientists largely sidestep this issue by thinking about cognitive functions that are associated with consciousness, so they don't need to worry about why it is this way and not some other way. The most common candidate for a function associated with consciousness stems from global workspace theories (Baars, 2002; Mashour et al., 2020). These state that consciousness is linked to information that is accessible to many systems of the brain so that it permits flexible behavior (e.g., creativity) and sustained coordination of the organism (e.g., planning for events in the distant future). A more recent extension of this approach is to argue that the function of consciousness is not merely to broadcast information to different systems *within* the same brain, but to broadcast information *between* different brains (e.g., Frith, 2023). That is, the function of consciousness may be inherently social. For example, if one gives several participants, of similar ability, a difficult perceptual

FIGURE 15.1: The philosopher Rene Descartes (1596–1650) argued that the conscious mind is not part of the physical world. This position, whilst at odds with neuroscience, resonates with contemporary debates (e.g., the Hard Problem) about how the brain can generate subjective experiences. Descartes also created an early version of the "brain in a vat" thought experiment: arguing that all our experiences may be a simulation (created by a demon), but even in this scenario, our experiences still exist.

Gwengoat/iStock

judgment and allow them to communicate (e.g., by sharing their subjective confidence in their judgment), then the group answer tends to be more accurate than any individual answer (Bahrami et al., 2010). This is not quite the same as saying that the function of consciousness is language (although that's part of it), but rather it is about being able to transform different kinds of basic information (e.g., from memory, perception, emotion) into communicable metrics like confidence or vividness (referred to as **metacognition**).

The structure of this chapter is broadly divided into levels of consciousness and contents of consciousness. **Levels of consciousness** are concerned with the degree to which an individual is conscious, such as coma, anesthetic, sleep, and wakefulness. The term state of consciousness is also often applied here as there is controversy as to whether all of these things fall on to a single dimension. **Contents of consciousness**, on the other hand, assume some degree of consciousness to be present but different kinds of information (vision, language, memory, imagination, etc.) are brought into focus. The contents of consciousness will be presented as a division between awareness of the external world (with most research coming from visual awareness) versus awareness of our internal world (mind wandering, self-awareness, agency). Different neuroscientific accounts of consciousness will be considered, but philosophical arguments are not developed further (links to online material for philosophical "head spinners" are given for students who want to delve deeper).

LEVELS OF CONSCIOUSNESS

Ranking consciousness levels from high to low makes intuitive sense because it is something we experience every day through our sleep and wake cycle. But there are other important examples of high and low levels of consciousness that come from a medical context. This includes general anesthesia and disorders of consciousness arising from brain damage such as **coma** and **vegetative state**. Figure 15.2 shows an influential attempt to map out these different normative and clinical states of consciousness by Laureys (2005) using two different dimensions. One of these dimensions, wakefulness, corresponds to the level of consciousness: a global measure of how conscious someone is. The other dimension, awareness, corresponds to the contents of consciousness: the degree to which one is aware of one's environment and self. These two dimensions tend to correlate together such that most of our experiences fall along the diagonal line: high/low levels of wakefulness correspond to high/low levels of awareness. However, there are some important exceptions to this. **REM (rapid-eye movement) sleep**, linked to dreaming, is considered to be an increase in awareness without an increase in wakefulness (although noting that the contents of awareness are internally generated as fragments of memory and imagination). **Lucid dreaming** is a rarer phenomenon where some people have a degree of control over the content of their dreams and can be distinguished from REM sleep by a wider network of brain activity including frontoparietal regions (Dresler et al.,

KEY TERMS

Metacognition
Second-order awareness of thoughts (e.g., perceiving red is a first-order state, and our confidence in perceiving red is a second-order state).

Levels of consciousness
The relative degree to which an individual is conscious.

Contents of consciousness
The information that one is presently aware of.

Coma
Loss of consciousness (low wakefulness, low awareness) due to brain damage.

Vegetative state
Disorder of consciousness associated with wakefulness but no awareness of self or environment.

REM sleep
A stage of sleep with high signs of wakeful brain activity and often linked to reports of dreaming.

Lucid dreaming
A state where some people report a degree of control over the content of their dreams.

2012). Vegetative state, on the other hand, is considered an off-diagonal example in the other direction: high wakefulness but low awareness. Patients with vegetative state emerge from a coma and appear outwardly awake but, by definition, are diagnosed to be unaware of themselves or their surroundings. They can have their eyes open, and they may move their heads or bodies, or smile, but in a way that is not contingent on specific external stimuli and seems unmotivated by any personal goals. Minimally conscious state is hard to diagnose as a distinct entity as these patients, like vegetative state, are non-communicative, but produce some purposeful responses to external stimuli. Patients with **locked-in syndrome** are also non-communicative but for entirely different reasons. Namely, due to complete paralysis arising from brainstem damage but retaining an ability for voluntary blinking. The book (adapted into a film) *The Diving Bell and the Butterfly* (Bauby, 1998) was written using 200,000 blinks, with an average of approximately two minutes per word. As implied by the term "locked in," these patients are assumed to have normal levels of consciousness.

To what extent does evidence from neuroscience offer support for this kind of taxonomy, and if so, what exactly is the neural basis for levels of consciousness? Let's first consider what is known about sleep. Sleep is broadly divided into two phases (**NREM** and REM) which occur in cycles around four to six times per night. NREM itself can be broken into early phases, a transition between wakefulness and sleep, and later deep sleep or slow-wave sleep, so-called due to its characteristic EEG signature (1-4 Hz oscillations). These characteristic wave patterns are caused by rhythmic cycles of activity between thalamus and cortex. Waking people up in REM sleep is far more likely to result in reports of dreaming than in NREM sleep (Dement & Kleitman, 1957). However, other forms of mental activity are reported when woken in NREM sleep, such as thoughts and impressions that lack the vivid narrative quality of a

KEY TERMS

Locked-in syndrome
Complete paralysis (except for vertical eye movements) arising from brainstem damage, but preserved cognitive ability and normal levels of consciousness.

NREM sleep
A stage of sleep (consisting of several sub-stages) and generally low signs of wakeful brain activity.

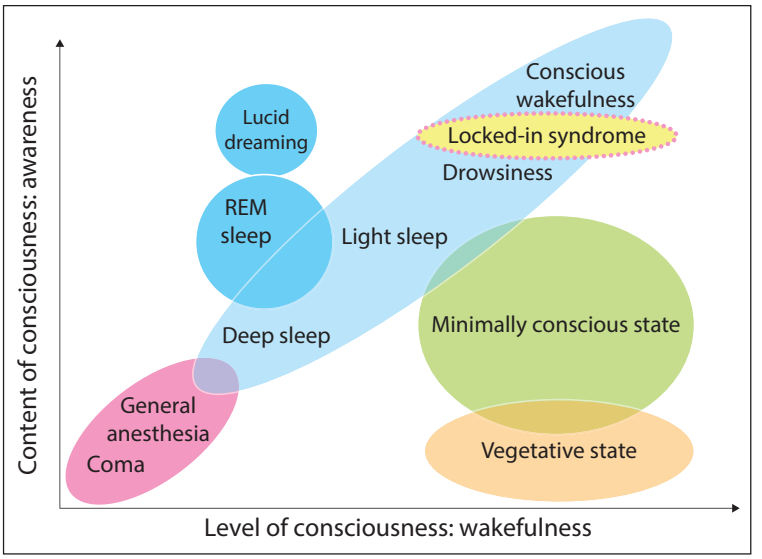

FIGURE 15.2: States of consciousness could be mapped on to two dimensions: wakefulness (a global measure of how conscious someone is) and awareness (the degree to which one is aware of one's environment and self).
Adapted from Laureys (2005).

TABLE 15.1 EFFECTS OF BRAIN INJURY ON CONSCIOUSNESS. ADAPTED FROM GOSSERIES ET AL. (2014).

Clinical entity	Disorder of consciousness?	Characteristic behavioral features
Coma	YES	No wakefulness No awareness of self or environment
Vegetative State (VS)	YES	Wakefulness No awareness of self or environment No sustained, reproducible, purposeful behavioral responses to external stimuli No language comprehension or expression
Minimally Conscious State (MCS)	YES	Wakefulness Fluctuating awareness with reproducible, purposeful behavioral responses to external stimuli
Emergence from Minimally Conscious State (EMCS)	NO	Functional communication Functional object use
Locked-in Syndrome (LIS)	NO	Wakefulness Awareness Quadriplegia or quadriparesis Presence of communication through the eyes Preserved cognitive abilities

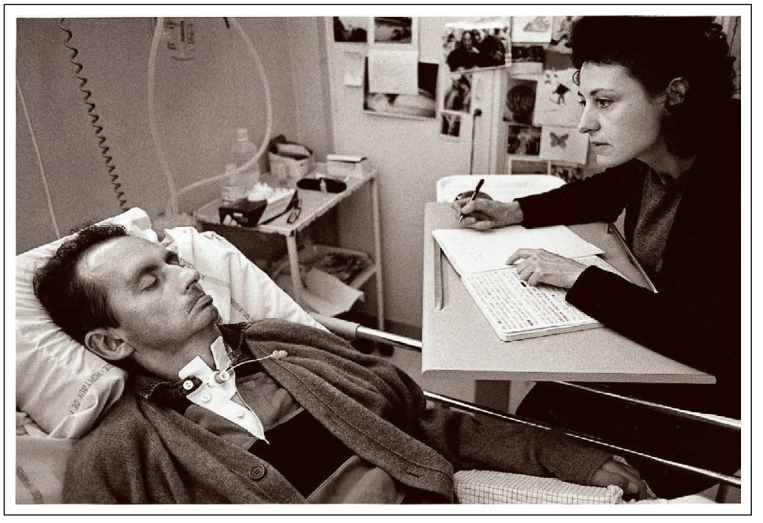

FIGURE 15.3: Jean-Dominique Bauby, the editor-in-chief of French *Elle* magazine, suffered a stroke in 1997 and fell into a coma. When he came around he was completely paralyzed with what is known as locked-in syndrome. However, he was fully conscious and able to write a book, *The Diving Bell and the Butterfly*, with his left eyelid whilst a transcriber repeatedly recited a French language frequency-ordered alphabet (E, S, A, R, I, N, T, U, L, etc.) until Bauby blinked.

dream (Nielsen, 2000). Hence, it is a questionable point as to whether people are truly unconscious during NREM sleep. EEG signatures of both wakefulness and REM sleep appear superficially similar (less wave like, more complex), but in other key respects they differ. The increased brain activity in REM sleep is driven by one particular neurotransmitter (acetylcholine), which activates some regions (e.g.,

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Watch related videos, such as Science on Screen: The Story of *Jean-Dominique Bauby* and the Miramax movie *The Diving Bell and the Butterfly* (2007) by scanning the QR code or visiting routledgelearning.com/wardcognitiveneuroscience.

hippocampus, amygdala) but not others (e.g., dorsolateral prefrontal cortex) (Nir & Tononi, 2010). This may explain why dreams have certain features, such as lack of volitional control and unawareness of the environment. Visual cortex is activated in REM sleep by the lateral geniculate nucleus originating from midbrain cholinergic inputs rather than signals from the eyes (Gott et al., 2017). Visual cortex may also be activated top-down by other cortical regions such as the hippocampus: damage to the hippocampus disrupts dream reporting on being awoken (Spano et al., 2020).

An important set of studies have used TMS-induced EEG activity to show that the different EEG characteristics are linked to different levels of consciousness, including sleep (Casali et al., 2013). A brief TMS pulse triggers localized activation of neurons beneath the stimulation site, and this can be measured by EEG or fMRI. But in addition to this direct activity, there can be a propagation of activity to more distant regions. That is, the stimulation site behaves like a node in a network. The extent to which this propagation occurs is related to levels of consciousness, and it can be captured mathematically by a measure called the Perturbation Complexity Index, or PCI. It is important to note that this is not just a measure of the amount of brain activity but is a measure of the *complexity* of brain activity. Complex brain activity is not completely rhythmic, regular, or otherwise predictable. Massimini et al. (2005) found this discriminated wakefulness from NREM sleep such that more complex spreading perturbation waves followed TMS when awake. Moreover, PCI measures are high during REM sleep (Massimini et al., 2010) but low following anesthesia (Casali et al., 2013). This measure also ranks patient groups according to the postulated level of consciousness: from vegetative state (low PCI), minimal conscious state (mid PCI), and locked-in state (high PCI) (Casali et al., 2013). These results are summarized in Figure 15.4.

ONLINE RESOURCES

Philosophical head-spinners: panpsychicism and the China Brain

There are neuroscientific attempts to describe consciousness mathematically based on the flow of information between neurons and/or brain regions (Tononi et al., 2016). But if we then find that other natural or artificial systems have this mathematical property, then would we be forced to conclude that this system is also conscious? This kind of logic is favored by adherents of panpsychicism, a view that consciousness can potentially be found in all things.

A philosophical thought experiment related to this is called the China Brain (e.g., Block, 1978). (China is chosen because of its very large population, although it is still a far way off the 80 billion neurons in the human brain.) Imagine 80 billion people each with a phone that can connect simultaneously with up to 1,000 other people. You can see where this is going, right? (neurons = people, synapses = phone connections). We've identified the neural correlates of consciousness, and we now apply that to our very large network of people. Is there now a collective consciousness across the population of China?

Watch the related videos by scanning the QR code or visit routledgelearning.com/wardcognitiveneuroscience.

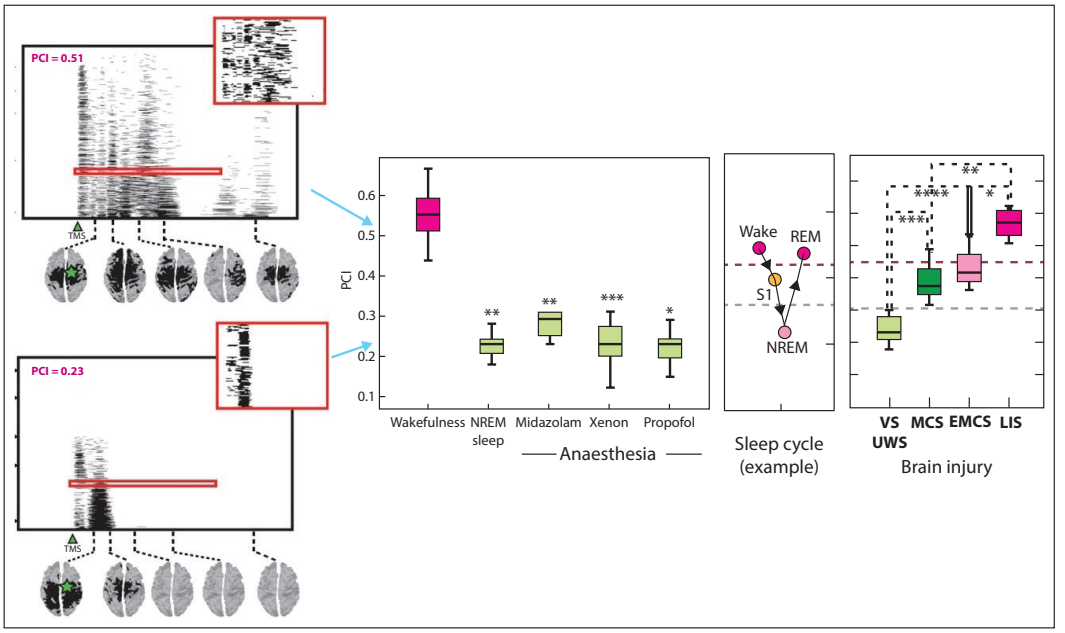

FIGURE 15.4: A single TMS pulse (here over the premotor cortex) activates the brain, and this can be detected with EEG. This pattern of activity is not constant but depends on the level of consciousness which is mathematically described by a measure called Perturbation Complexity Index (PCI), essentially a measure of the complexity of propagation of connectivity from the stimulation site. Boxplots show the PCI when awake, when under different forms of anesthetic, in different cycles of sleep (here an illustrative example from one person, S1 is the drowsy stage of NREM sleep), and following brain damage (VS = vegetative state, MCS = Minimal Conscious State, EMCS = Emergence from Minimal Conscious State, LIS = Locked-in Syndrome).

Adapted from Casali et al. (2013).

Equivalent measures of the complexity of spontaneous EEG/MEG signals (rather than TMS-induced signals) yield a similar picture. Of note, a study of the psychedelic drugs (psilocybin, LSD, ketamine) found that they were associated with a *higher* measure of signal complexity than normal waking (Schartner et al., 2017). In neural terms one could, with some justification, refer to the psychedelic state as a "higher state of consciousness." But it is important to note that these states are generally linked to worse, rather than better, cognitive performance (Bayne & Carter, 2018). It is possible that there exists a "sweet spot," not too high and not too low, for conscious cognition.

Task-based neuroimaging has also been used to assess levels of consciousness in patients who are non-communicative. Asking a participant in an fMRI study to "imagine navigating around your house" or "imagine playing tennis" elicits distinct patterns of neural activity related to spatial and motor imagery (Figure 15.5) but, crucially, does not require a behavioral response. Some patients, initially diagnosed with vegetative state, have been shown to be able to perform these tasks when instructed (Monti et al., 2010; Owen et al., 2006), thus requiring a revision of their diagnostic status (to **minimal conscious state**). These different neural signatures can be used to answer questions such as "Is your father's name Alexander?

KEY TERM

Minimal conscious state
A disorder of consciousness associated with wakefulness and fluctuating awareness.

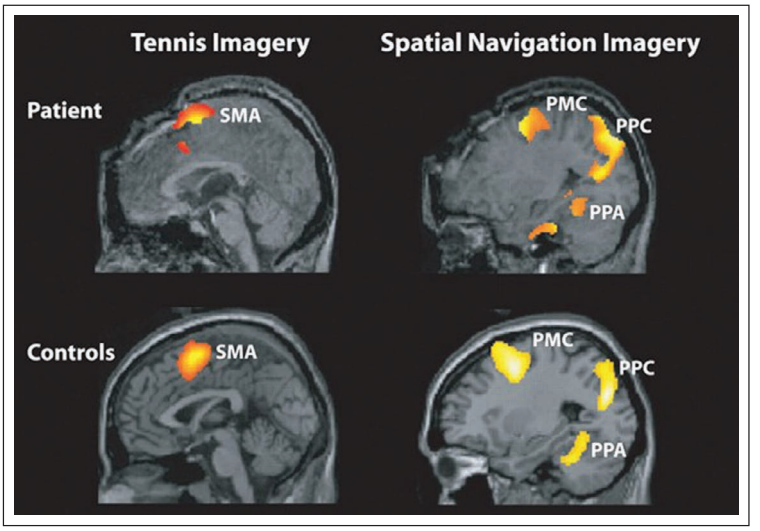

FIGURE 15.5: Imagining playing tennis (left) and imagining navigating around your house (right) has different patterns of brain activity. But around 20 percent of non-communicative patients in a vegetative state can follow these instructions. Are these patients conscious? SMA = supplementary motor area, PPC = posterior parietal cortex; PPA = parahippocampal place area, PMC = premotor cortex. Reprinted from Owen et al. (2006).

Owen, A. M., Coleman, M. R., Boly, M., Davis, M. H., Laureys, S., & Pickard, J. D. (2006). Detecting awareness in the vegetative state. *Science*, *313*(5792), 1402–1402.

(yes = imagine playing tennis, no = imagine navigating your house)." (Monti et al., 2010). Appropriate control conditions are needed to ensure that this isn't a reflexive brain response. Listening to the instructions, without performing the task, does not yield the same response, and participants are instructed to maintain each task for 30 seconds to ensure an active, rather than reflexive, response. Comparable studies using EEG have been conducted that compare the same stimuli in active and passive conditions: listening to their name in a stream of words or counting their name (Schnakers et al., 2008). Of course, the patient can't communicate the answer, but the EEG response to active counting is taken as evidence of voluntary (i.e., conscious) behavior.

Evaluation

There is now an impressive body of evidence that creates a largely coherent picture of levels of consciousness ranging from sleep, anesthesia, and disorders of consciousness following brain injury. It is not simply the case that the brain is more active when consciousness is high, although there is some general truth in that statement. Instead, levels of consciousness are related to connectedness (the flow of activity between brain regions) and complexity (not just a simple wave-like pattern). These basic principles of connectedness and complexity may also apply to theories of the contents of consciousness; for example, when comparing conscious versus subliminal perception. This is considered later. What is unclear from the evidence presented so far is whether particular brain regions or networks have a privileged status in determining the level of consciousness or whether any brain network can support consciousness if it has those particular properties (complex spatiotemporal signals).

It is also important to note that the idea of "levels" of consciousness is not universally endorsed (Bayne et al., 2016).

Bayne et al. (2016) accept that states of consciousness can be ordered in a "rough and ready manner" but argue that the underlying mechanisms may not be one that can be reduced to a single dimension (e.g., such as implied by measures such as PCI). Instead, they suggest that there might be multiple dimensions. For example, dreaming and wakefulness may both be high on some dimensions (e.g., perceptual experiences) but high versus low on others (e.g., low volitional control in dreams). One resting state fMRI study suggested the presence of multiple networks that support different aspects of levels of consciousness such as overall arousal, communication with external environment, and awareness of self and surroundings (Amico et al., 2017). In summary, whilst the notion of levels of consciousness has some

PSYCHEDELICS AND CONSCIOUSNESS

The two psychedelic drugs most commonly used/studied are LSD, or "acid" (lysergic acid diethylamide), and psilocybin (from "magic" mushrooms); these are also referred to as hallucinogens. Although there are differences between the effects of these drugs, from a neurobiological standpoint their effects are similar insofar as they target a specific serotoninergic receptor called 5-HT2A. Resting state neuroimaging shows that they increase the complexity of interactions between brain regions (Schartner et al., 2017).

FIGURE 15.6: Psychedelic art emerged from the counterculture movement of the late 1960s and is characterized by highly distorted or surreal visuals and bright colors to convey or enhance psychedelic experiences from drugs such as LSD and psilocybin (magic mushrooms). svekloid/Shutterstock

Bayne and Carter (2018) summarize three broad domains of consciousness that are affected by these drugs.

1) Sensory and perceptual experience

Visual experiences, both seen and imagined (e.g., with eyes closed) are experienced as brighter, more colorful, and more intense (Studerus et al., 2010). However, they are not necessarily more "real" insofar as they are accompanied by anomalous experiences such as hallucinations (e.g., faces morphing) and synesthesia (e.g., sounds triggering vision), and performance is not improved on objective tests such as color discrimination (e.g.,

Hartman & Hollister, 1963). One candidate neural mechanism is that these drugs lead to increased spontaneous neural activity in sensory regions which disrupts externally elicited responses (Kometer & Vollenweider, 2018).

2) Cognitive capacities

Attentional abilities are disrupted in the psychedelic state when measured objectively (Carter et al., 2005) or with questionnaire responses to statements such as "I had difficulty making even the smallest decision" and "Everything around me was happening so fast that I no longer could follow what was going on" (Studerus et al., 2010). Although there is no evidence that people are more creative during the psychedelic state, they report higher levels of the creativity-related personality trait "openness to experience" in the period afterwards (Carhart-Harris et al., 2016).

3) Experiences relating to time, self, and space

One key feature of the psychedelic state is a distorted experience of time, with subjects typically reporting that time has stopped or slowed (Ludwig, 1966) and objective measures of time perception show impairment (Wittmann et al., 2007), although this could reflect a more generic cognitive problem. Aspects of self can be disrupted in terms of out-of-body experiences or agreeing with statements such as "The boundaries between myself and my surroundings seemed to blur" (Studerus et al., 2010).

face validity, many researchers predict that it is likely to be replaced by a multidimensional approach as further evidence accumulates.

CONTENTS OF CONSCIOUSNESS: THE EXTERNAL WORLD

The previous section discussed how consciousness can be globally disrupted by brain-damage (disorders of consciousness), anesthesia, and sleep. However, many of the previous chapters in this book have presented examples of disorders of consciousness of a fundamentally different kind. Consider cerebral achromatopsia where damage to area V4 leads the perceiver to experience the world in shades of black and white (Zeki, 1990). It would be odd to say that their level of consciousness is disrupted (i.e., that they are less conscious than other people) but it makes more sense to say that a particular content of consciousness (color) is absent. (Of course, one could entertain the view that level of consciousness is just the summed total of the contents of consciousness, but this chapter will stick to the more standard thinking that contents and levels are separate.) We don't need to rely solely on evidence from brain damage to study the contents of consciousness. There are experimental manipulations that can contrast conscious versus unconscious processes by varying the length of time a stimulus is presented, whether a stimulus is presented in or outside the focus of attention, and so on. This general approach, when accompanied with neuroimaging, is termed the **neural correlates of consciousness** (Chalmers, 1998; Frith et al., 1999).

KEY TERM

Neural correlates of consciousness (NCC)
The minimal set of neuronal events and mechanisms sufficient for a specific conscious percept (e.g., comparing conscious and unconscious processes to the same stimulus).

ONLINE RESOURCES

Philosophical head-spinners relating to color

Mary the Colorblind Scientist (Jackson, 1982). She knows every scientific fact about color but can't see in color, so does she really know everything? This thought experiment is an illustration of the Hard Problem.

The Inverted Color Spectrum. Maybe my experience of red is your experience of blue, and vice versa. How could we know? This thought experiment is suggesting that the contents of consciousness don't really have a function (they might be an epiphenomenon) and is also a push back on the limits of introspection.

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Sticking with the example of color, a parsimonious explanation of cerebral achromatopsia would be to say that area V4 is both necessary and sufficient for these conscious experiences. This theoretical position is termed micro-consciousness (Zeki & Bartels, 1999). More generally, this theory argues that the contents of consciousness are highly localized to the particular brain regions that support that aspect of cognition, and this information does not need to be passed between some other system that makes them conscious. However, most current theories argue for something different (Seth & Bayne, 2022). Namely, that specialized regions (e.g., V4) are necessary for the contents of consciousness but they are not sufficient. Here is a brief overview of some of these accounts that will be expanded on in the chapter (see also Figure 15.7):

- In higher-order thought (HOT) theories, it is a secondary representation elsewhere in the brain (e.g., prefrontal cortex) that determines whether information is conscious (e.g., Brown et al., 2019).
- In global workspace theories, content is considered conscious if it is globally available to other cognitive operations (e.g., language, action), and this may be supported by a lateral frontoparietal network of regions (e.g., Mashour et al., 2020). In this view, consciousness is linked to flexibility in behavior.
- In integrated information theory, conscious content is related to a mathematical measure of connection complexity (Koch et al., 2016), similar to the PCI measure discussed previously. More importance is placed on a posterior cortical hub zone than the prefrontal cortex.
- In predictive processing (e.g., Clark, 2013) and re-entry theories (e.g., Lamme, 2010), conscious contents are linked to top-down processing; for example, perceptual illusions occur because they are based on our expectations about the world.

In all these theories, consciousness is something that emerges through an interaction between multiple brain systems, although

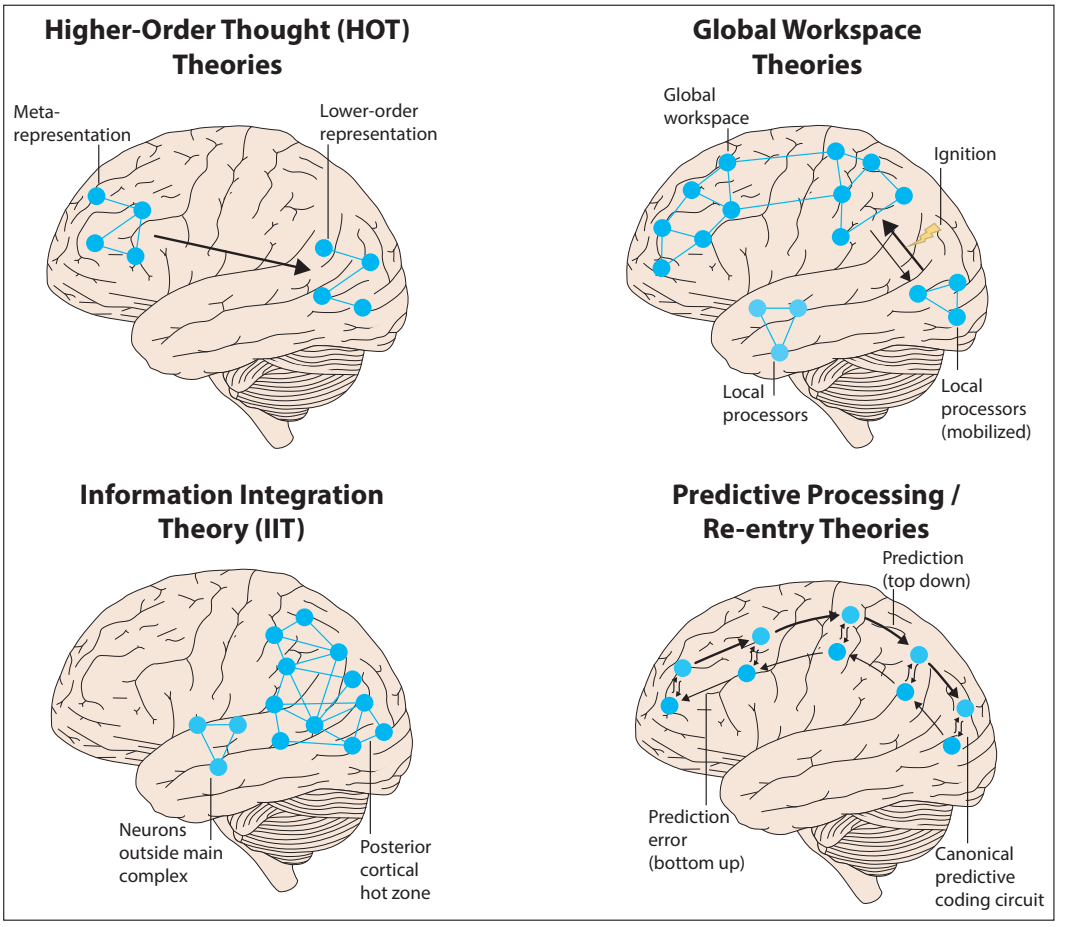

FIGURE 15.7: Four different theoretical approaches for explaining consciousness. In all these theories, consciousness is something that emerges through an interaction between multiple brain systems, although the nature of the interaction and the relevant brain systems differ from theory to theory.

Adapted from Seth and Bayne (2022)

the nature of the interaction and the relevant brain systems differ from theory to theory.

The global workspace and the role of frontal-parietal network in awareness

There are many ways in which one could study conscious versus unconscious processes but not all methods would constitute a fair comparison. For example, comparing stimuli presented for very short (likely unconscious) and long (likely conscious) durations would confound exposure duration with consciousness. However, many studies within the neural correlates of consciousness framework have tackled this issue by presenting participants with physically identical stimuli but where consciousness itself is inherently variable. In that way, one can use the participants own

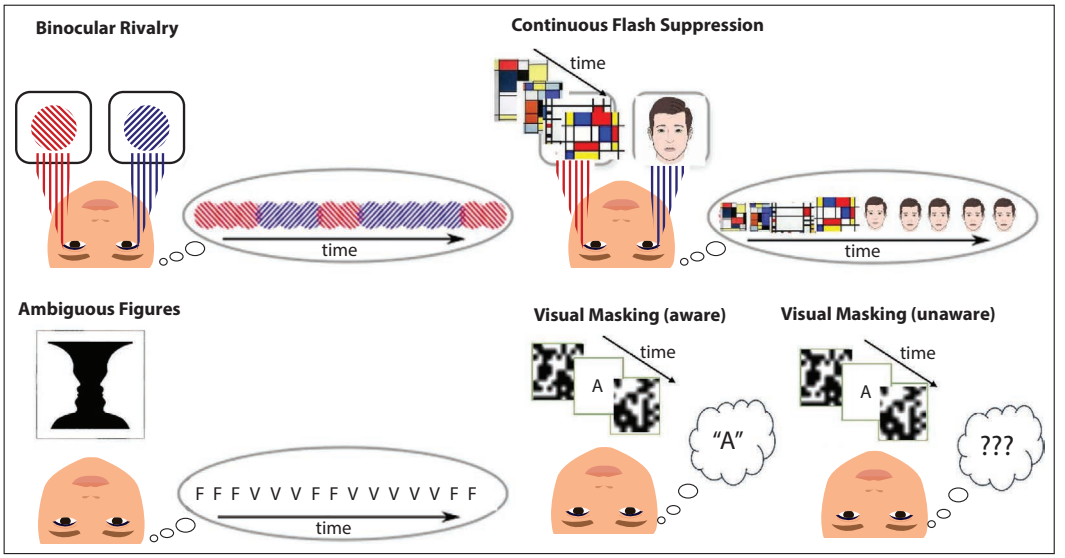

FIGURE 15.8: Many classic studies for exploring the neural correlates of consciousness have presented a constant visual stimulus (so physical conditions are perfectly matched) that is capable of generating two different contents of consciousness (measured via self-report). The neural activity (fMRI, EEG, etc.) associated with these two contents, or the transition between them, can then be contrasted in the analysis. Binocular rivalry: two images presented to different eyes and participant perceives a single images which alternates. Continuous flash suppression: two images presented to different eyes, but a rapidly changing image stream dominates initially and is then suppressed. Ambiguous figures: perception alternates between face (F) and vase (V). Visual masking: a briefly presented stimulus may be aware on some trials and unaware on others.

self-reported experiences in order to group trials together (e.g., as conscious versus unconscious) with no external confounds. Examples of this approach are shown in Figure 15.8.

In masking studies, visual stimuli are presented briefly but near a threshold of detection so that some trials they are consciously perceived and others they are not (Dehaene et al., 2001). To return to the previous point, both conscious and unconscious trials have the same duration. In such studies, conducted with fMRI, a typical pattern of brain activity has two main features: firstly, there is greater activity in regions involved in perception (e.g., ventral visual stream) when participants are aware of a stimulus rather than unaware, and secondly, there is a spread of activity to distant brain regions, in the frontoparietal network, in the aware state (see Dehaene et al., 2006). Similar findings are found when stimulus detection is variable due to attention demands. In the attentional blink paradigm activity in frontal and parietal regions discriminates between awareness versus unawareness of the second target (Kranczioch et al., 2005). Recall from Chapter 9 that this paradigm involves detecting a target (e.g., digit) from a rapid series of visual stimuli, and participants tend to be unaware when a second target follows soon after a first. The results of these kinds of studies are summarized in Figure 15.9.

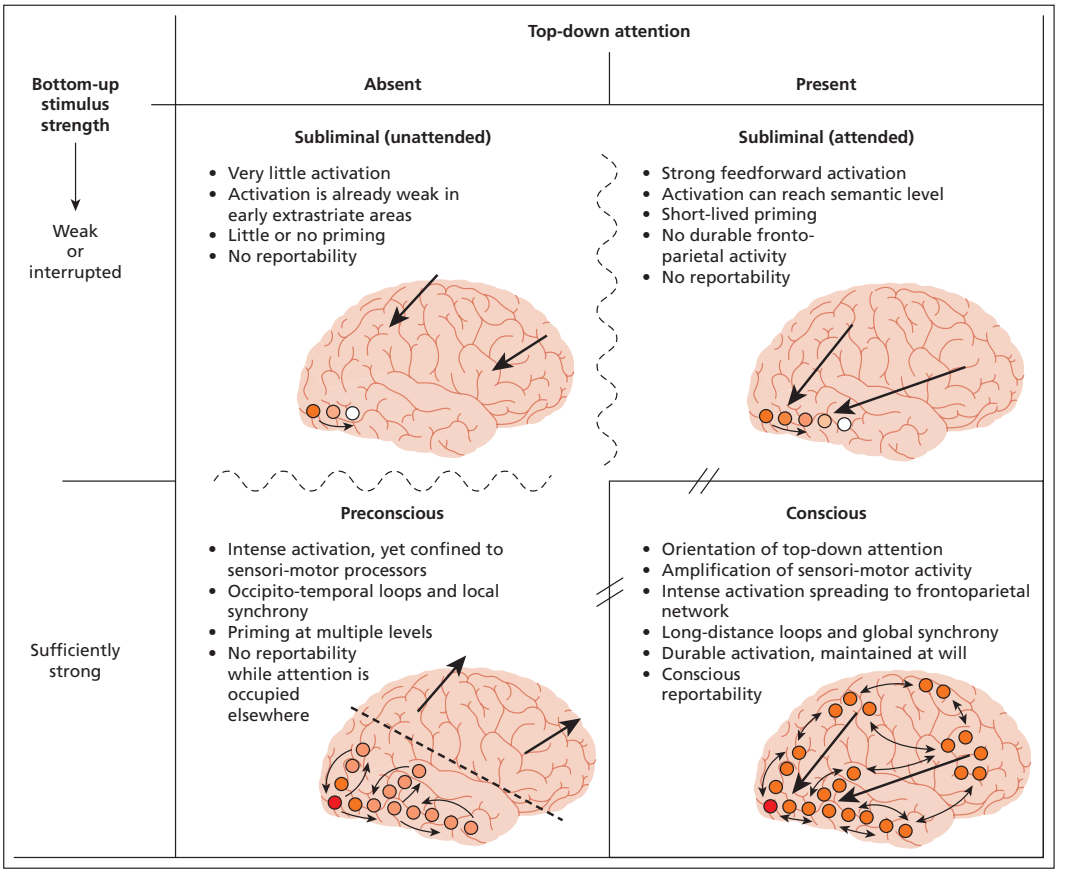

FIGURE 15.9: In the Global Neuronal Network Model of Dehaene et al. (2006), awareness is linked to top-down attention to a sufficiently strong sensory stimulus. This is associated with activity spreading to a frontoparietal network. In contrast, non-aware conditions (e.g., attending to a very weak sensory signal, inattention to a strong sensory signal) are linked to varying levels of activity in the sensory cortex alone.

Adapted from Dehaene et al. (2006).

KEY TERM

Binocular rivalry
Presentation of two different images, one to each eye, which typically results in a single image being perceived which alternates over time.

A comparable set of studies varies the content of consciousness itself (rather than presence or absence of consciousness), keeping the physical stimuli constant. Imagine that your right eye is shown a face and your left eye is shown a house, what would you see? This experimental setup is called **binocular rivalry**, and participants typically report seeing one stimulus at a time, reversing after several seconds (e.g., face-house-face-house- etc.). Activity in the frontoparietal network ramps up at the transition points (Lumer & Rees, 1999). There are other kinds of perceptually ambiguous stimuli that show a similar pattern of changes in the content of consciousness (e.g., the face-vase illusion, or rotating patterns of dots that can appear to turn clockwise or counter-clockwise) (Kleinschmidt et al., 1998). TMS over the parietal lobes can speed up and slow down the rate of transitions (Kanai et al., 2011). After taking psilocybin people are more likely to report a blended percept during binocular rivalry rather than two clear alternating ones, and

they have slower transition times overall (Carter et al., 2007). This suggests reduced control over perception in the psychedelic state.

One of the key features of the Global Neuronal Network Model is that of ignition. This is a large and sudden engagement of the wider network that occurs 200–300 msec after stimulus onset that discriminates conscious and unconscious trials (Mashour et al., 2020). This mechanism is not only found for vision but also for audition and touch where, using EEG, it is possible to distinguish conscious versus unconscious trials from the presence/absence of ignition (Sanchez et al., 2020). One consequence of this, at least according to this framework, is that consciousness is essentially an all-or-nothing phenomenon that is present (and can be reported) or absent: in effect neural activity linked to consciousness transforms a continuous signal (varying in strength) to a binary one (Vul et al., 2009). This idea is returned to later, in terms of a distinction between different kinds of consciousness.

Brain-damaged patients with damage to the frontal-parietal network present with problems in executive functions and attention (see Chapter 14), but are they unconscious? Seemingly not. But it is important to note that the kinds of neurological patients who act as participants in these studies tend to have circumscribed lesions (not damage to the whole network), and they would also need sufficient residual cognitive ability to follow instructions to meet the inclusion criteria for testing. Widespread lesions in frontoparietal regions do indeed result in low levels of consciousness such as coma or vegetative state (Tshibanda et al., 2009). Moreover, even circumscribed lesions within this network may produce selective disruptions to the contents of consciousness, such as spatial neglect (Chapter 9). Bilateral damage to the parietal lobes can impair subjective aspects of memory (e.g., confidence, vividness) without impairing objective performance (Simons et al., 2010). Damage to the prefrontal cortex can impair subjective reports of visibility of brief stimuli (Del Cul et al., 2009).

The approach of global workspace theories has been criticized for implementing something along the lines of a Cartesian Theatre (Dennett, 1991): a space in which all our sensations are projected for us to view. (The term Cartesian refers again to Descartes, who was a proponent of the idea of mind and body being separate.) A Cartesian Theatre would be a useless exercise for the brain. Why would information need to be copied to a workspace, and why would that help us to see it? However, this criticism is a misrepresentation of the model (at least in its later forms). The information within the frontoparietal network isn't merely copied, but rather it is transformed (e.g., filtered to contain the most salient features of a visual scene; Bisley & Goldberg, 2010). Moreover, the purpose of passing sensory information to the frontoparietal network is not to "see" it but to act on it. Many of the clever paradigms for studying consciousness (e.g., binocular rivalry) don't involve action at all (beyond the act of self-report), so the function is not so obvious. Voluntary actions themselves also depend critically on the frontoparietal network as discussed later (and see also Chapter 10).

ONLINE RESOURCES

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Alternative models of the contents of consciousness

Perhaps the main criticism of global neuronal workspace theories is that they rely too heavily on explicit self-report (typically the participant needs to report on a trial-by-trial basis on the nature of their consciousness). In other words, it may be the act of reporting on consciousness rather than the "raw" experience of consciousness that depends on the frontoparietal network (Seth & Bayne, 2022). Block (2005) refers to these processes as **access consciousness** (reporting on the contents of consciousness) and **phenomenal consciousness** (the quality of the contents of consciousness). Global workspace is primarily a theory of access consciousness. Phenomenal consciousness is harder to study experimentally because it is not straightforward to infer consciousness in a third-person way (i.e., without using self-report). The function of phenomenal consciousness is also far from clear-cut, unlike access consciousness (where the function is global availability including for reporting).

KEY TERMS

Access consciousness
The ability to report the content of awareness.

Phenomenal conscious
The "raw" feeling of a sensation, the content of awareness.

There is some supportive neuroscientific evidence for the access/phenomenal distinction. Frässle et al. (2014) used a version of binocular rivalry in which the dominant percept was inferred from brain activity alone (using multivariate pattern analysis) so that participants did not have to directly report it themselves. In this "no-report" version, brain activity in fMRI was more posterior (occipito-parietal) whereas the standard self-report version was more anterior (frontoparietal). Other research shows that the visibility of unattended stimuli is related solely to activity in the occipital lobe (Tse et al., 2005). Newer versions of integrated information theory argue that it is a posterior "hot zone" that gives rise to the contents of visual consciousness rather than the frontoparietal networks (Koch et al., 2016). Predictive processing and re-entry accounts also do not argue for a key role of the frontoparietal cortex but instead argue that localized feedback from higher to lower regions give rise to consciousness (Clark, 2013; Lamme, 2010). Arguably, these are primarily theories of phenomenal consciousness.

Proponents of the idea of phenomenal conscious point to the apparent mismatch between our subjective impressions of a uniformly rich and colorful visual field and objective facts about vision (e.g., Campana & Tallon-Baudry, 2013). Our peripheral vision lacks detail (compared to the central fovea) and becomes increasingly achromatic. However, our subjective experience of the world does not reflect that. In experimental settings, when participants are briefly presented with numerous objects (e.g., an array of letters), they are only able to report a small number of them but nevertheless have some awareness of the gist of seeing a larger set of letters (Bronfman et al., 2014; Sperling, 1960). According to many theories, reporting a small number of letters would be access consciousness, whereas the sense of seeing a larger array of letters would be phenomenal consciousness. Global

workspace theories explain the former but not the latter. But other theories of consciousness suggest that phenomenal consciousness can be generated more locally (e.g., within visual cortices) including via a process of filling-in (e.g., filling in color in peripheral vision) (Seth & Bayne, 2022). A final possibility is that perceptual richness exists only as a higher-order thought, somewhat akin to a delusion (see Brown et al., 2019).

Almost all theories of consciousness involve top-down as well as bottom-up activity. The difference lies in the relative importance of it and the brain regions that participate in it. In global workspace theories, top-down activity (from the global workspace to specialized modules) is important for amplifying and sustaining the perceived stimulus as well as for broadcasting it to other systems. **Predictive processing** models, on the other hand, rely on the assumption that the whole brain is a hierarchically organized system in which higher levels are making predictions ("best guesses") about lower levels (Friston & Kiebel, 2009). Predictions flow downwards and evidence flows upwards, and mathematically, the system is trying to minimize the difference between predictions and evidence (termed the prediction error). Predictions are a loose term that can encompass long-term perceptual and non-perceptual knowledge (e.g., light tends to come from above) but also short-term manipulations (e.g., a cued expectation). Predictive processing accounts of perception state that our phenomenal consciousness is based on our best guess predictions of external reality (Clark, 2013). It is our best guesses that we consciously see and not our sensory signals (but our sensory signals are nevertheless helpful for selecting the best guess). In this way, perception has been referred to as a controlled hallucination (Seth, 2021).

Predictive processing explanations offer a natural account of perceptual illusions because illusions, whilst deviating from external reality, can be shown mathematically to reflect the best guess of the perceiver (Brown & Friston, 2012; Shams et al., 2005). For

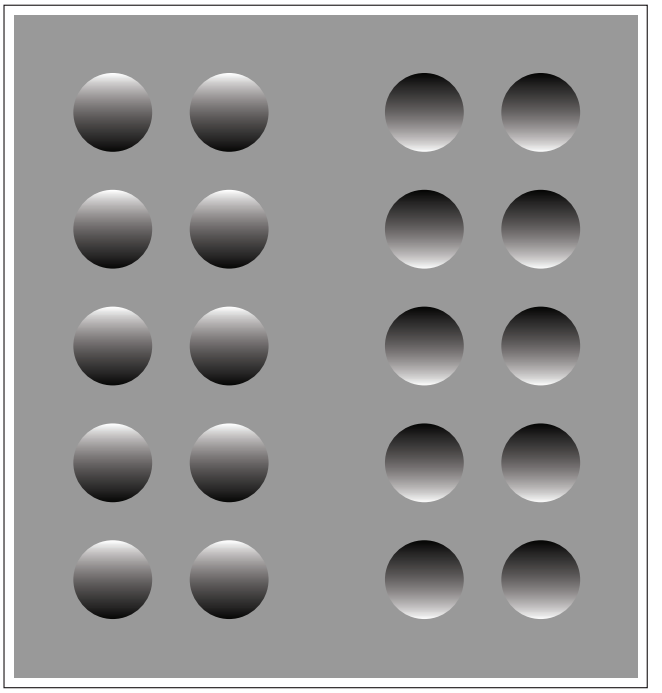

FIGURE 15.10: Do we see the world as we expect it to be? In this example, we have a strong expectation that light comes from above together with an ambiguous sensory input. The ambiguity is resolved in line with expectations: this makes the left circles appear as convex (sticking out as light hits the upper surface) and the right ones as concave (sticking in as light hits the lower surface). Predictive processing models of perception don't merely state that top-down processes are important for what we perceive but go one step further in saying the top-down processes *are* what we perceive (i.e., they fully determine our contents of consciousness). There is also top-down knowledge that we know the stimulus to be flat, but the brain attempts a "best guess" that weights our lifetime of 3D visual experiences more strongly than our knowledge that it is not 3D.

KEY TERM

Predictive processing
A model of the brain as a hierarchically organized system in which higher levels are making predictions ("best guesses") about lower levels with an aim of minimizing the discrepancy between the levels.

example, the McGurk illusion occurs because we have strong predictions, based on a lifetime of experience, about how lip movements and sound generation occur and (without video editing) people can't move their mouth to a "ga" position whilst saying "ba." To come back to the example of binocular rivalry, the predictive processing explanation is that the brain is receiving input from two possible interpretations but makes a best guess, at each point in time, as to which is more probable. Assuming both are equally probable, then the strongest signal will be selected, and as that signal fades, the other option overtakes it and becomes selected, and so on. Given that our phenomenal consciousness largely corresponds to our best guesses, not the sensory evidence, what we "see" are abrupt transitions between clear images rather than the underlying tug-of-war that is probably taking place. What happens if one image is, in some way, more probable than the other? In this scenario, we consciously see our expectations when presented with a sequence of biasing stimuli (Denison et al., 2011). This has also been extensively investigated with a variation of binocular rivalry called **continuous flash suppression** in which one eye is presented with continuously changing "junk" images, and the other is presented with a target stimulus (Tsuchiya & Koch, 2005). The junk images tend to dominate (because the changes are salient), but eventually, the target stimulus will breakthrough and be reported. Expectations based on associated geometric cues (Pinto et al., 2015) or words such as "chair" (Lupyan & Ward, 2013) speeds up the breakthrough time. This is interpreted as providing support to predictive processing models of perception.

If perception is a controlled hallucination, then a **hallucination** can be thought of as an uncontrolled perception (Seth, 2021). Surprisingly, perhaps, many theories of consciousness do not have much to say about hallucinations perhaps because they are hard to study experimentally. Within the global workspace theory, noisy spontaneous neural activity (not elicited by an external stimulus) might cross a threshold for ignition of the frontoparietal mechanism and be experienced as a hallucination. There are some hallucinations that could be explained in this way. When people go blind they often have vivid and detailed spontaneous visual experiences – this phenomenon is called Charles Bonnet Syndrome (ffytche et al., 1998), see Figure 5.11. However, the notion of hallucinations as above-threshold neural noise can't explain hallucinations that have structured content. Many hallucinations are not random. As examples, visual hallucinations in the blind can involve seeing faces during a conversation (i.e., they are contextually appropriate) and auditory-verbal hallucinations ("hearing voices") comprise meaningful sentences (Sacks, 2012). These can be easily explained within the predictive processing framework where the contents of consciousness are created from the top-down, and in some people, they may create their own "sensory evidence" (i.e., hallucinations) to match the predictions (Sterzer et al., 2018). People who are

KEY TERMS

Continuous flash suppression
Presentation of two different images, one to each eye, where one image initially dominates perception by continuously changing.

Hallucination
A perception of something that is not present such as hearing voices.

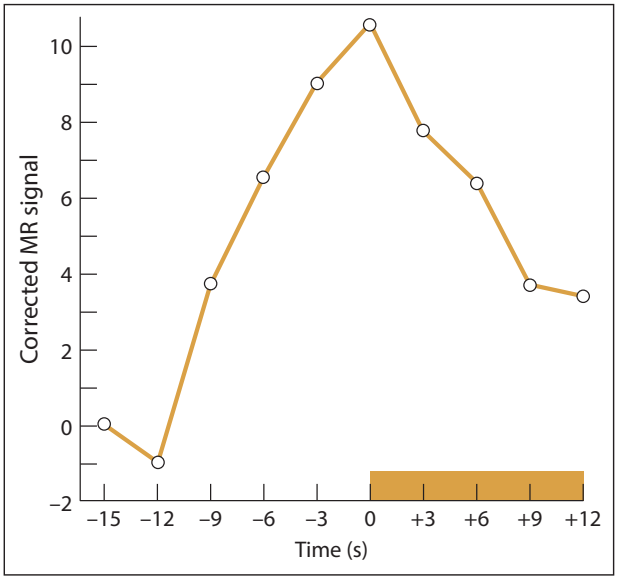

FIGURE 15.11:
A hemodynamic response function related to the onset of visual hallucinations (at 0 seconds, shown by orange bar). This is derived by averaging together a number of hallucinations involving visual regions of the brain. Note how the brain activity precedes the onset of the conscious experience by as much as 12 seconds. An example of a reported hallucination is as follows: "colored shiny shapes like futuristic cars or objects found in the pyramids. The shapes contained edges within them and did not look like real objects."

Adapted from Ffytch et al. (1998).

prone to auditory-verbal hallucinations show a greater tendency to weight their own predictions strongly in experimental tasks that produce false perceptions in the lab (Powers et al., 2017). In this task, visual checkerboards are paired with a tone but the tone is made gradually quieter (and sometimes completely absent). But hallucinators carry on hearing the tone and activity in auditory cortex offers corroborating evidence.

Within the predictive processing framework, delusions can emerge in the same way. A **delusion** is a false belief whereas a hallucination is a false percept (of course, all perceptual experiences could be described as false, but some are further from reality than others). There are several ways in which delusions can occur. For example, you may get taught them in school or acquire them via your social media bubble(!). However, a delusion can also be a best guess based on individual anomalous experiences as an attempt to rationalize them (Sterzer et al., 2018).

KEY TERM

Delusion
A false belief (not experienced by others).

Evaluation

The approach of finding the neural correlates of consciousness has used elegant experimental paradigms for comparing conscious and unconscious processes. Conscious (versus unconscious) perception is linked to high brain activity in regions that are specialized for that particular content (e.g., color, sounds), but the prevailing view is that this emerges via its interactions with other systems of the brain. Some theories argue that these "other systems" might themselves be relatively specialized or domain-specific systems. For example, higher-order visual regions sending predictions to lower order-visual

ONLINE RESOURCES

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regions. Whereas other theories, such as global workspace, suggest that these interacting "other systems" are domain-general in nature such as the frontoparietal network (which can flexibly respond to all/most kinds of information). There is positive evidence for both of these positions. A resolution of this apparent contradiction may come a consideration of access versus phenomenal consciousness; that is, being able to report on conscious experience (access) versus the subjective quality of the experience itself (phenomenal). Reportability may depend on the frontoparietal network, which is functionally important for selection (attention) and action. But the subjective contents of consciousness, as exemplified by visual illusions, aren't readily explained by these accounts but, instead, can be explained by "best guess" predictions made by other relatively specialized systems (e.g., depth inferences from statistical regularities in lighting) that are beyond our voluntary control.

KEY TERM

Split brain
A surgical procedure involving severing of the corpus callosum (and potentially other fibres) that connect the two hemispheres.

SPLIT BRAIN, SPLIT CONSCIOUSNESS?

In the 1960s a small group of patients underwent radical surgery in an attempt to control the spread of epileptic seizures in their brain (e.g., Gazzaniga, 2002). The main white matter bundle that connects the two hemispheres, the corpus callosum, was severed albeit without damaging the brain itself: a **split brain**. So neurocognitive "modules" are essentially intact but unable to communicate across the hemispheres. In daily life these patients have minimal impairment – perhaps being clumsy in unfamiliar bimanual tasks (Franz et al., 2000). But what is it like to be a split-brain patient? Whilst one could ask this question to the patients, the concern is that we'd only ever hear the viewpoint of the verbally communicative left hemisphere. Does the right hemisphere have a silent consciousness of its own?

One influential set of studies that offers support to a "split consciousness" viewpoint involves the generation of contradictory verbal and manual responses (e.g., Sperry, 1968). To give one example from the patient "Joe" – when the word TEXAS was presented to the left hemisphere, he could read it aloud, but when the same word was presented to the right hemisphere, he denied seeing it but, at the same time, drew a cowboy hat with his left hand (which is controlled by his right hemisphere). Typically, these patients would have no insight into why they drew the object or invent some story to justify their actions (i.e., the left hemisphere acts as an interpreter of the right hemispheres actions; Gazzaniga, 2000).

The interpretation of these findings remains controversial (de Haan et al., 2020). For example, split-brain patients can detect and localize simple visual stimuli presented to both visual fields either verbally or using both hands, and this is likely permitted by subcortical connections that bypass the corpus collosum (e.g., Pinto et al., 2017). That is, patients may be able to "see" the word (as a visual experience) even if it can't be

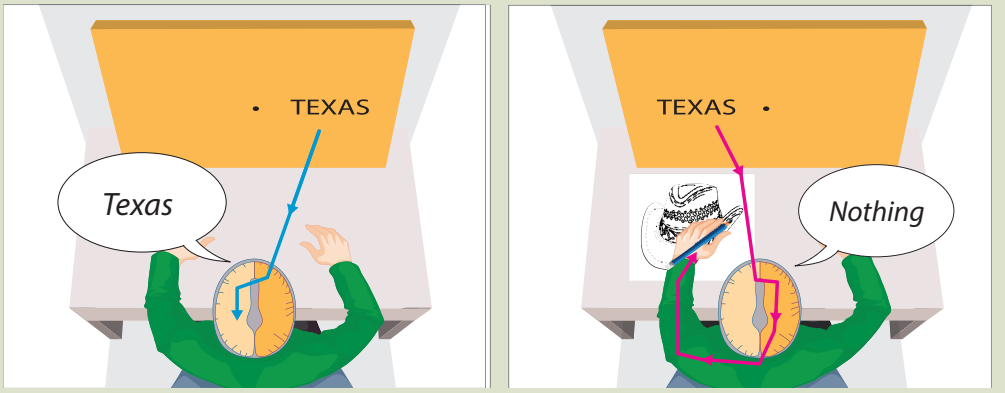

FIGURE 15.12: In split-brain patients, words presented to the left hemisphere can be read aloud, but words presented to the right hemisphere cannot. Nevertheless, the right hemisphere has some understanding of the stimulus that can, for example, be expressed by the left hand. (Recall that the left visual field is projected to the right hemisphere, and vice versa, providing central gaze is maintained). Does the right hemisphere have a different conscious experience to the left?

named, and this may also permit some level of understanding. Semantic memory (more so than speech production) is bilaterally represented as discussed in Chapter 12.

The basic idea that the contents of consciousness can be split is not so surprising: for example, there can be a selective loss of color or visual motion experiences after brain damage. But when it comes to split brain, the surprise occurs because the split appears in the same patient, and we introduce an inappropriate metaphor of imagining a "person" trapped in each hemisphere. In other real-world situations, our words and actions may not match (because we are fatigued and make mistakes), but we wouldn't imagine two separate people in our brain generating the mismatch (we'd just understand that these systems are semiautonomous).

ONLINE RESOURCES

Philosophical head-spinners: the Teletransportation Paradox

Our brain constructs a sense of self that provides continuity over time and also continuity against physical changes in the body (e.g., as you grow you replace cells and chemicals). A philosophical head-spinner that taps into this is called the Teletransportation Paradox (Parfit, 1984). The tele-transporter can "beam you up" to another planet, like in *Star Trek*, by reading off all the atoms in your body and then reforming you with the same kinds of atoms in a distant place whilst removing you from the original location. You presumably have little problem in believing that your sense of self is preserved in your replica. But what if the original "you" was not deleted and, instead, multiple copies now exist?

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KEY TERMS

Free will
The feeling that "I" control my own actions and thoughts (a content of consciousness relating to self-control).

Agency
The subjective feeling that our voluntary actions are owned and controlled by us.

CONTENTS OF CONSCIOUSNESS: AWARENESS OF OUR INNER WORLD

The previous section considered how the brain constructs the contents of consciousness based on sensory signals from the external world (with most evidence coming from vision). However, our brain receives internal signals from within the body (e.g., interoceptive signals relating to emotion) and is also capable of self-generating an inner world of experience from thoughts, imagination, and memory (e.g., this occurs in mind-wandering). It is also able to generate voluntary actions, which is itself linked to a controversial content of consciousness called **free will** or **agency**, that is, the sense in which you can choose how and when to act. But what is this "you" that makes this decision if not just the physical material of your brain? This section will consider these contents of consciousness, and in doing so, it will also have to deal with the notion of the self.

The self is not represented in the brain by some single module, and researchers have debated whether there are any self-specific neural mechanisms in the brain at all (Gillihan & Farah, 2005). Instead, it is perhaps more appropriate to think of the self as an attribution or inference that arises in certain circumstances. For example, if we perform an action, then we can accurately predict the consequences of it (e.g., what it will sound like, look like, whether it will make your heart race), and we can predict it accurately because it originates in our own brain. Self-recognition may – according to some predictive processing theories – be nothing more than the ability to accurately predict the consequences of our own thoughts and actions (or, at least, predict them more accurately than for other things outside our control) (Apps & Tsakiris, 2014). For others, the self is likely to be made up of several different mechanisms. Gallagher (2000) broadly divides the self into two levels.

(1) The *minimal self* consists of the feeling that we own our body and control our actions. This might be implemented by something like the predictive processing model of self by Apps and Tsakiris (2014).
(2) The *narrative self* consists of our social identity and autobiographical memory that extend through time. This aspect of self tends to be assessed using introspection (e.g., reflecting on your personality – "are you a worrier?") and is likely to tap different cognitive processes.

Mind wandering

People spend somewhere between 25 percent and 50 percent of their waking hours engaged in thoughts unrelated to the here and now (Kane et al., 2007; Killingsworth & Gilbert, 2010). This can be referred to as a "Stream of Consciousness" or an ebb and flow of self- or spontaneously generated ideas (Smallwood & Schooler,

2015). But what kind of consciousness is this? What are its contents? Is it supported by the same kinds of neural mechanisms that support conscious (versus unconscious) perception of the external world?

The lateral prefrontal and parietal cortices tend to be active when performing a task (versus no task). These have been ascribed some "executive" role in selecting information (i.e., attention) and, according to some theories, has a key role in consciousness (e.g., Mashour et al., 2020). However, there is another network, the **default mode network (DMN)**, that tends to be activated in fMRI studies by the reverse contrast, that is, for no-task minus task (Raichle et al., 2001). It is perhaps surprising that the brain would have a network of regions that are active when "doing nothing" because this is metabolically costly (Raichle, 2006). However, one key claim about the DMN is that it is actively involved in cognition and supports what is termed stimulus-independent thought or **mind wandering**. Mason et al. (2007) conducted one of the first studies to test this claim. They first identified the DMN in their participants through a standard fMRI contrast comparing rest against engagement in verbal and visuo-spatial working memory tests. They then showed that the DMN was more active in easy than harder blocks, where participants were more likely to mind wander, and found a correlation between individual differences in mind wandering tendencies (in daily life) and DMN activity during the tasks. In general, the DMN supports perceptual decoupling from the environment: for example, there is a negative correlation between DMN and visual cortices (Fox et al., 2005).

What are the contents of consciousness in mind wandering? One way to assess this is through **experience sampling**. The most common version of this is to unexpectedly probe people with either open-ended questions (what are you thinking about?) or closed questions (e.g., are you thinking of the past, present, or future?). People are more likely to think about the future than past, and this is true across cultures and across lab and real-world settings (Smallwood & Schooler, 2015). Analyses of these experiences suggest they fall on different

KEY TERMS

Default mode network (DMN)
A set of brain regions that are activated more during rest or baseline conditions than during an outward-facing task.

Mind-wandering
A stream of thoughts (intentional or spontaneous) that are disconnected from the external environment.

Experience sampling
A method for probing participants about ongoing thoughts (e.g., sending a text message and asking what they were just thinking about).

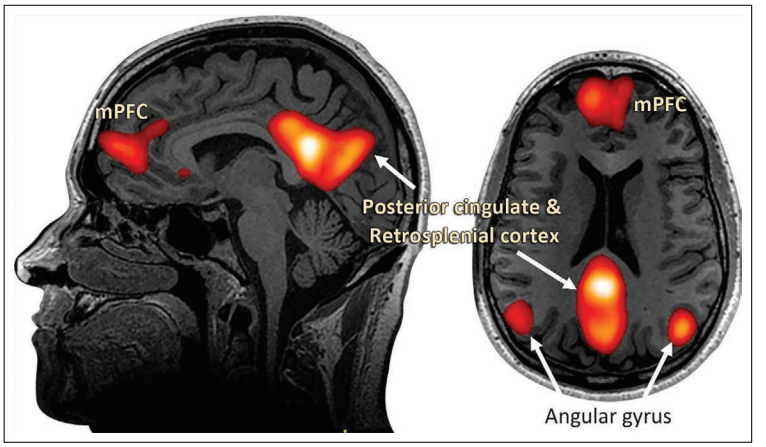

FIGURE 15.13: The default mode network (DMN) consists of several regions which are active more during "rest" or "baseline" conditions than externally oriented tasks. These are likely to support internally generated thoughts such as those involved in mind-wandering.

Adapted from Graner et al. (2013).

KEY TERMS

ADHD (attention deficit and hyperactivity disorder)
An ongoing pattern of inattention and/or hyperactivity-impulsivity that interferes with functioning or development.

Meditation
A technique to train attention and awareness to achieve a calm and stable state.

dimensions such as these: whether they are experienced as images or words, whether they involve emotion or not, whether they are thinking about the task or about themselves (e.g., Gorgolewski et al., 2014). Neuroimaging offers some corroborating evidence that there is this level of granularity linked to the content of mind wandering, rather than just a monolithic DMN network (Andrews-Hanna et al., 2014). For example, social thoughts engage the ventromedial prefrontal cortex (Konu et al., 2020), whereas autobiographical remembering may depend more on links between hippocampus and posterior medial parietal regions such as the precuneus (Hebscher et al., 2018). Golchert et al. (2017) considered the self-reported intentionality of mind wandering (i.e., whether a participant chose to engage in stimulus-independent thought or whether it occurred spontaneously). They looked at individual differences in this tendency and correlated it against functional connectivity and argued that those who engage in intentional mind-wandering have stronger coupling between frontoparietal network and the DMN.

More generally, the frontoparietal network may serve to regulate mind wandering so, similarly to its role in the selective attention of different streams of information in the external environment, it may also act like a switch in selecting between the external and internal world itself (Smallwood et al., 2021). Mind wandering need not be a bad thing if it happens in non-demanding circumstances. It is not something to be avoided entirely. But a high tendency to mind wander, for example during lectures, has negative consequences (Farley et al., 2013) and could be regarded as a failure of executive control to stay "on task." This kind of cognitive mechanism may also help to explain **ADHD, attention deficit hyperactivity disorder**, which is linked to increased spontaneous (but not intentional) mind wandering (Seli et al., 2015) and increased fidgeting during those periods (Seli et al., 2014).

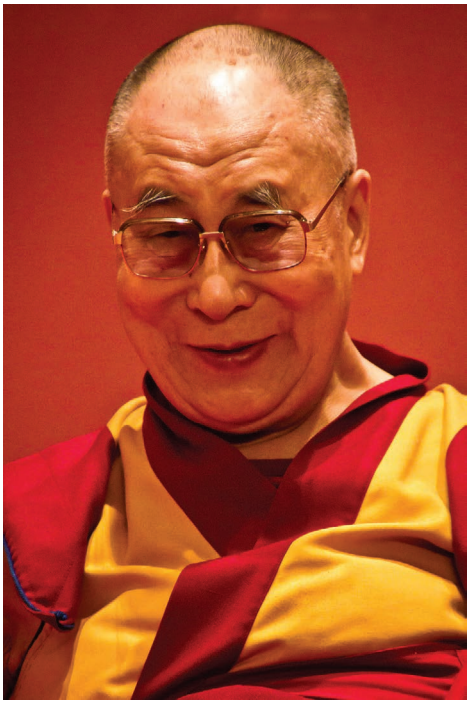

FIGURE 15.14: The Buddhist leader the Dalai Lama spoke at the 2005 Society for Neuroscience (SfN) meeting, prompted by some early findings in the cognitive neuroscience of meditation. The invitation for a religious leader to speak at a scientific meeting provoked some controversy (Cyranoski, 2005). Jules2013/iStock

Meditation, like mind wandering, involves some form of inward reflection accompanied by decoupling from the external environment. But in other regards meditation and mind wandering are very different. Meditation is an intentional act that is involved with *suppressing* the meandering "stream of consciousness" and replacing it with acceptance of the present moment without reflection (mindfulness), or the maintenance of a narrow focus of attention such as to ones breathing (mindful breathing), heartbeat, a visual image, or a mantra (repeated word or phrase). Brewer et al. (2011) found that experienced meditators deactivate the DMN during various types of meditation and exhibited

stronger coupling between the lateral prefrontal cortex and posterior regions of the DMN. Alongside other research (see Tang et al., 2015), this suggests that meditation is not an altered state of consciousness but, rather, a special example of the brain's capacity to intentionally regulate its attentional focus creating positive effects on relaxation and well-being.

Self-related thoughts

There is a particular region of the medial prefrontal cortex, also part of the DMN, that is strongly implicated in self-referential processing and, presumably, self-awareness. It is important to note that research in this field has tended not to contrast conscious versus unconscious processing of self (i.e., analogous to the literature on conscious and unconscious perception). Instead, the main manipulation has been to contrast self and non-self (i.e., other people). Broadly speaking, this would relate more strongly to Gallagher's (2000) notion of a narrative self than a minimal self (the latter is more related to the relationship between self and body).

Kelley et al. (2002) found that making trait personality judgments about oneself relative to a familiar other (George W. Bush) activates this mPFC region. However, making judgments of personality per se, relative to a control task (judging whether the word is in upper/lower case) activates a region implicated in semantic memory retrieval in the left lateral prefrontal cortex (Kelley et al., 2002). The response of the mPFC region does not depend on whether the personality traits are positive or negative but depends, instead, on thinking about these traits relative to the self (Moran et al., 2006). This region is not strictly specific to self in that it also responds, to some degree, to thinking about emotionally close others (Krienen et al., 2010) – although this could be reconceptualized by saying that certain others are part of your self-concept (Aron et al., 1992).

Traits judged relative to the self (versus other people) are better remembered when given a later memory test and this reflects activity in the mPFC (Macrae et al., 2004). It suggests that the memory benefit is due to self-relatedness rather than semantic depth of processing (as the latter relies on a different region). Other research shows that recalling that a photograph was taken by the participant, rather than another person in the same campus setting, activates the mPFC (Cabeza et al., 2004). Attending to one's own emotional response, relative to the response of someone depicted in a photograph, activates the mPFC (Ochsner et al., 2004). Hearing one's own first name also activates this region (Perrin et al., 2005). It is hard to control for various confounds that might make the self "special." For instance, self-related stimuli are acquired early in life and occur very frequently. One experimental approach for tackling this problem is to arbitrarily associate stimuli to self or other (e.g., triangle = self, circle = a friend, square = stranger). Attending to a geometric shape that has been associated to the self also taps a

network involving the mPFC that also boosts the ability to detect that shape (Sui et al., 2013). Within the framework of the Global Workspace Theory one could say that self-referential tagging of stimuli boosts the "ignition" process and leading to awareness.

If this region of the brain is damaged then do these patients become self-unaware? It's hard to draw that conclusion from available evidence, but certain aspects of relevant behavior can change. When asked to make preference judgments about pairs of people (Britney Spears versus Shaquille O'Neal) or colors (pink versus yellow), then patients with damage in this region show more unstable choices (Fellows & Farah, 2007). This region, together with more ventromedial prefrontal cortex, is also linked to the symptom of confabulation, and on objective tests, events are misplaced in time but not necessarily forgotten (Gilboa & Moscovitch, 2002). Thus, the region is important in maintaining a stable "self" over time, and it may achieve this by working alongside memory systems within medial temporal regions.

Sense of embodiment

There is a sense in which our self is located within the space occupied by our own bodies. Researchers such as Damasio (1999) argue that bodily awareness lies at the core of self-awareness. Bodily senses not only include the sense of touch but also the sense of where our limbs are located in space (proprioception), which is given by stretch receptors in the muscles and ligaments, and also internal senses (interoception) that convey the internal state of the body and may include pain, core temperature, hunger, heart rate, and breathlessness. According to Damasio (1999) the reinstatement of bodily sensations (in the brain, rather than in the body itself) is a key aspect of emotion representation and decision-making. As such, in his view, the **sense of embodiment** accounts for self-motivated behavior in addition to the feeling of the self being located within the body.

A disruption of the sense of embodiment can accompany various brain lesions. **Out-of-body experiences**, in which the participant reports being in a location different from their actual physical location, can arise following damage to the right temporo-parietal junction (Blanke et al., 2004). This region may be involved in shifting perspective or focusing attention between self and other, including the bodily self (e.g., Blanke et al., 2005). Certain illusions can also produce something akin to an out-of-body experience in neurologically normal participants as illustrated in Figure 15.15 (Lenggenhager et al., 2007). If participants see, using virtual reality, an image of someone placed in front of them and if the virtual person and the participants are stroked on the back in synchrony then the participant may report feelings such as "I felt as if the virtual character was my body." The participant also has difficulty in locating him or herself in space when displaced by the experimenter, and he or she gravitates towards the virtual

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KEY TERMS

Sense of embodiment
The feeling that the self is located within your body.

Out-of-body experience
Reports of being in a location different from the physical location of one's body.

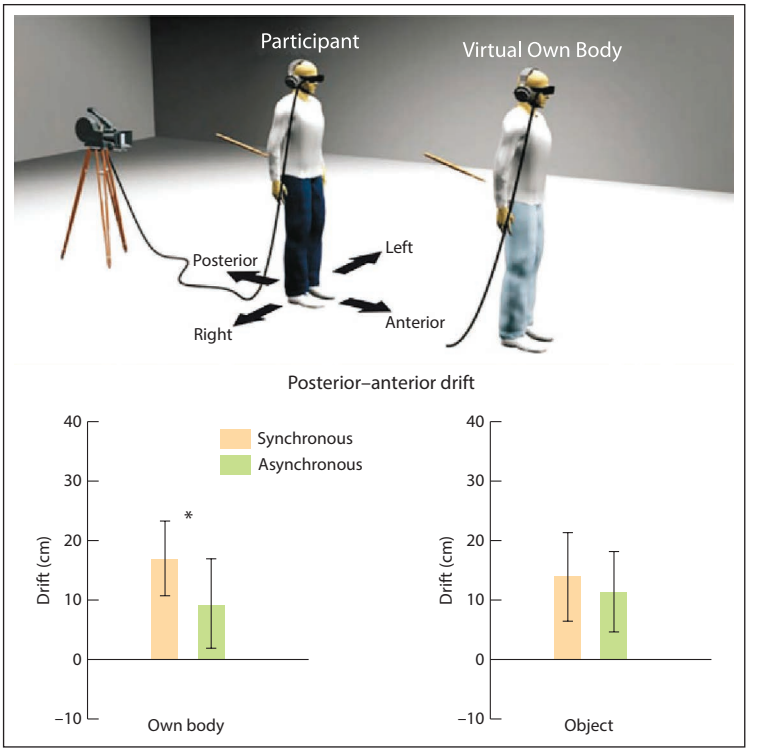

FIGURE 15.15: Is it possible to create an experience similar to an out-of-body experience in an experimental setting? If you see an image of yourself or another person projected in front of you (using virtual reality), and if that person's back is seen to be stroked at the same time as your own back is stroked, then you tend to lose your sense of location in space and report feeling that the virtual character is your own body. The effect is not found if the stroking is out of synchrony, or if an object is seen instead of a body.

Adapted from Lenggenhager et al. (2007).

body. The same is not found when an object rather than a body is stroked. Using virtual reality to take on a friend's body, disrupts other aspects of self-processing including the memory advantage for self-relevant information and alters judgments about one's own personality (Tacikowski et al., 2020).

Sense of agency

Our voluntary actions appear, at least introspectively, to have at least two elements: an intention/decision to act and the execution of that action. Our subjective feeling of ownership over our intentions to act is referred to as a **sense of agency**. This also provides the foundation for the notion of having social responsibility for one's actions (Frith, 2014). However, the intention to act can be nothing more than the firing of some set of neurons which seems to suggest that our "free will" (i.e., the feeling that "I" decide my own actions) and our sense of agency is little more than an illusion.

KEY TERM

Sense of agency
The subjective feeling that voluntary actions are owned and controlled by the actor.

Libet et al. (1983) recorded EEG activity from the scalp above the primary motor cortex and the SMA when participants simply pressed a key "whenever they felt the urge to." The exact time at which the key was pressed could be recorded from an electrical signal from the wrist movement. In addition, participants reported the time at which they were first aware of wanting to move. This was achieved by noting the position of a hand on a gradually rotating clock face. Libet and colleagues found that the EEG activity (or readiness potential) started several hundred milliseconds before the participants reported an intention to act (see Figure 15.16). The results appeared to suggest that the brain had made an unconscious commitment to act before participants experienced a conscious intention to act, consistent with the interpretation that "free will" is something of an illusion.

Haggard and Eimer (1999) identified which particular cognitive mechanism is likely to be associated with the conscious intention. In their variation of the experiment, the participant could freely choose either a left or right response, resulting in

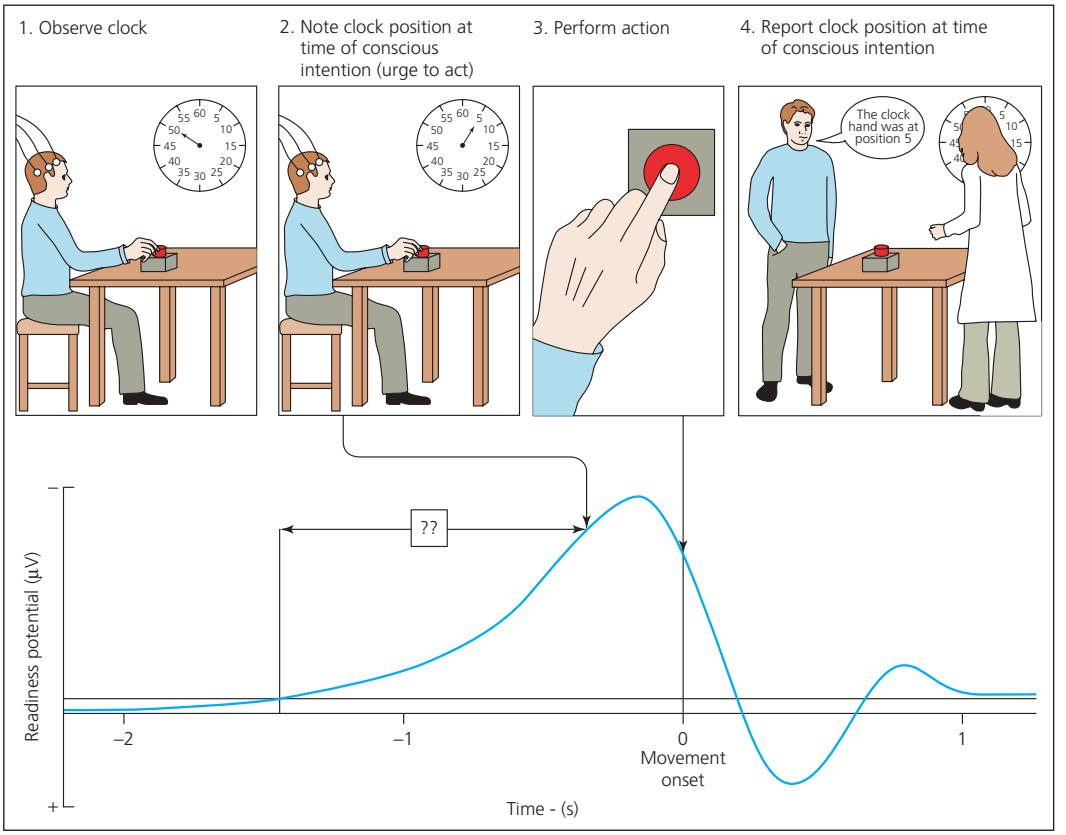

FIGURE 15.16: The motor cortex generates a readiness potential long before the participant declares an intention to act. This challenges the classical Cartesian view that the mind controls the brain.

Adapted from Haggard (2008). Reproduced with permission from Springer Nature.

a lateralized readiness potential over the opposite hemisphere. Their results suggested that awareness of intentions is related to the selection of a specific movement (left or right) rather than a generalized intention to act. Selecting which hand to move may involve the parietal lobes (Oliveira et al., 2010), as well as the prefrontal cortex, which is involved more generally in selecting amongst multiple responses (Frith et al., 1991; Jahanshahi & Frith, 1998). Electrical stimulation of the parietal cortex in neurosurgical patients generates a strong intention to move (Desmurget et al., 2009).

One way in which a sense of agency over actions could be generated is by predicting the sensory outcomes of our actions (Wolpert et al., 1995), which is a particular example of a predictive processing model. The main assumption is that a representation of the motor command (a so-called efference copy) is used to predict the sensory consequences of an action. For example, tickling oneself feels less ticklish than being tickled by another person, because we can use our own motor commands to predict what the sensation will feel like (Blakemore et al., 1998). The motor command when one tickles oneself can be used to predict what the sensation will feel like (and, hence, it is possible to compensate for it). Another example comes from eye movements. When we move our eyes, the visual world appears static rather than moving, even though the image on the retina changes considerably. In this instance the motor commands to move the eyes are used to predict (and compensate for) changes in visual input. These may arise via interactions between frontally based action systems and structures such as the cerebellum (Wolpert et al., 1998) and superior colliculus (for sensory consequences of eye movements, see Wurtz, 2008).

One potential consequence of these models, which has been studied experimentally, is that voluntary actions (e.g., a button press), and their sensory consequences (e.g., a beep or flash) appear to be closer together in time than they really are – called **intentional binding**. Haggard et al. (2002) had participants press a button as a voluntary action (they chose when to press it) or as an involuntary action (triggered by TMS of their motor cortex). Following the button press, a sound appeared soon after (250 msec) and participants made timing judgments about these events. The action and sound are judged as closer together in time following a voluntary action, but further apart in time following an involuntary action (see Figure 15.17). The degree of intentional binding is reduced by stimulation (with tES or TMS) of parietal regions (Khalighinejad & Haggard, 2015) and a region anterior to the SMA termed the pre-SMA (Moore et al., 2010). Note that TMS to these regions doesn't actually induce a movement in its own right (so the action is still technically voluntary). Instead it disrupts mechanisms that are important for matching planned actions with their sensory consequences.

KEY TERM

Intentional binding
The phenomenon that voluntary actions and their sensory consequences appear closer together in time than they really are.

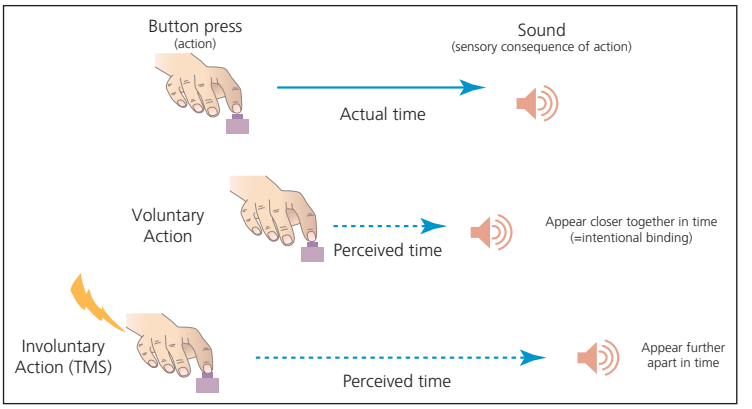

FIGURE 15.17: For voluntary actions, the action and the sensory consequences of the action appear to be closer together in time (intentional binding). This is assumed to reflect the ability of the brain to predict the occurrence of the sound when an action is "owned" relative to the control scenario of an involuntary action (in this case, caused by stimulating the primary motor cortex).

Evaluation

Internal thoughts, including thoughts about one's self, take up a significant proportion of our waking time but are less studied because they are harder to experimentally control. The default mode network is activated by various kinds of internal (stimulus-independent) thought and consists primarily of various midline frontal and parietal regions that tend to co-activate. However, there may also be some specializations within this network that can be construed as contributing to different contents of consciousness. The medial prefrontal cortex (mPFC) has been related to self-referential thinking (often in social contexts), and the medial parietal areas, such as precuneus, has been linked to recalling or imagining scenes. These regions are anatomically separate from the (lateral) frontoparietal network implicated in theories of consciousness such as Global Workspace, but interactions between these systems are important. For example, the frontoparietal network may have a role in selectively attending to internal thoughts (implemented by the DMN) just as it can be involved in allocating attention to vision or hearing.

In addition to self-related thoughts (which are related to the notion of the self as continuing in time), there are mechanisms involved in creating a sense of self that exists within the body and is under voluntary control (agency or free will). These also depend on brain mechanisms involved in the selection and control of action (again, including regions of the lateral frontoparietal network). Predictive processing models of consciousness have also been applied to explain the sense of embodiment and agency, just as they have been applied to visual illusions. Recall that the basic idea is twofold: the brain is generating a "best guess" to explain incoming evidence, and secondly, the best guess (not the underlying

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evidence) is the content of consciousness. In this account, a sense of self is our brain's best guess as to why we can predict our own actions (and body states) but can't accurately predict other events in the world. One could argue that the sense of self is illusory. But it is no more illusory than any of our other experiences.

CONSCIOUSNESS IN ANIMALS AND MACHINES

In the absence of a convincing way of asking "are you conscious?" our scientific efforts to attribute consciousness to (nonhuman) animals and machines are based on proxy measures. These fall into two basic types. Firstly, one can identify the kinds of computations linked to consciousness in the human brain and then determine their presence in other systems/organisms (Dehaene et al., 2017). Secondly, one can identify a set of behaviors that are linked to consciousness in humans (i.e., that can't be performed unconsciously) and determine the extent to which they are found elsewhere (Birch et al., 2020). Of course, both approaches fall into an entirely anthropocentric view of what consciousness is (but we have to start somewhere). Using behavioral proxies of consciousness in machines, such as playing chess, is highly problematic because they are programmed to do these tasks by humans. The situation is different in animals where such behaviors are evolved from a common ancestor who we might reasonably infer was also conscious.

Levels of consciousness, as indexed by sleep and the effects of anesthetics, are evolutionarily ancient. Sleep as defined behaviorally by periods of acquiescence and requiring more stimulation to rouse is found in most animal species, with increased electrophysiological activity (analogous to EEG) during wakefulness also observed in the fly, Drosophila Melanogaster (Keene & Duboue, 2018). Some animals (certain birds and dolphins) have evolved the ability to put one hemisphere to sleep at a time in order to avoid stopping during migration or avoid predation (Mascetti, 2016). Zalucki and van Swinderen (2016) found that the concentration of anesthetic required to produce immobility was remarkably conserved across the vertebrate species that they tested (including two non-mammal species; lizard and goldfish) with Drosophila also vulnerable to the drug. Psychoactive drugs, such as caffeine and LSD, also exert behavioral effects on other species: spider's webs become more regular on LSD and less regular with other drugs (Witt, 1971). In summary, if we take sleep or the action of drugs that effect consciousness as proxy markers of consciousness, then we have to go back to very ancient species indeed (invertebrates). Here we might feel more comfortable labeling these states as "arousal" rather than consciousness and take the view that high arousal states are a necessary, but not sufficient, condition for consciousness to occur (Parvizi & Damasio, 2001). For example, high arousal states may permit certain forms of complex functional connectivity (Koch et al., 2016). Whatever the function of sleep it is clearly a feature of biological entities because there is nothing like it in machines.

Dehaene et al. (2017) offer a perspective on the kinds of computations needed to think that a machine was conscious, although their logic applies to animals too. They

identified two principles. Firstly, the selection of information for global broadcasting, thus making it flexibly available for computation and report. Highly specialized brain modules don't meet that criterion, and neither do highly parallel architectures (e.g., those involved in deep learning). They give the example of an elephant finding water over long distances (which requires coordinating memory, sensory, and motor systems towards a goal that is sustained over time), and contrast this with the seemingly coordinated behavior of bacteria that operates in the here-and-now. The second principle they identified was the self-monitoring of those computations leading to a subjective sense of certainty or error. This corresponds roughly to metacognition. They argue that localized circuits may compute their own decision certainty but a conscious expression of confidence may supervene on this (based in prefrontal cortex in humans and similar animals; Fleming & Dolan, 2012). Computational methods called adversarial learning (Tzeng et al., 2017) in which a second network monitors, and corrects, its output are considered an approximation to this mechanism.

Finally, Birch et al. (2020) provide a dimensional approach to animal consciousness based on different patterns of behavior: namely, selfhood (e.g., mirror-self recognition), temporality (future planning), unity (coordination across multiple systems), perceptual richness (e.g., for vision, touch), and evaluative richness (e.g., inner states such as anxiety). Although the exact details of this approach are speculative, their basic aim is to move away from ranking animals from high to low in consciousness and instead consider them with respect to their ecological niches. The figure shows an example of what this might look like across three species.

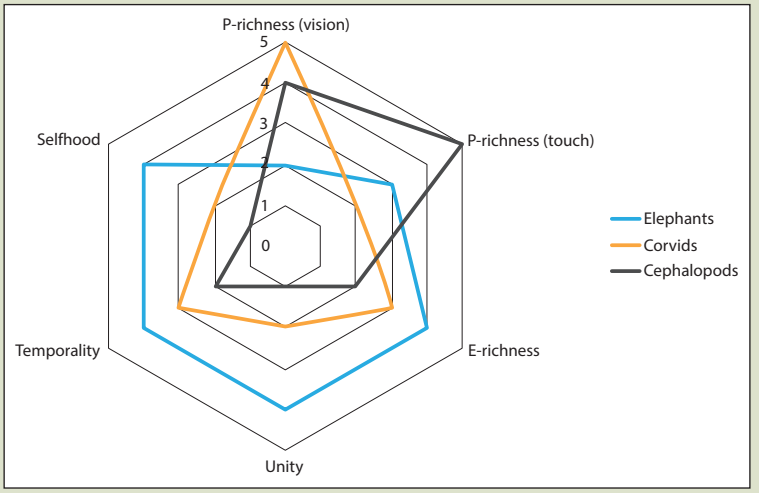

FIGURE 15.18: An example of how animal consciousness might be mapped on to dimensions rather than levels (although low on all dimensions would be equivalent to low consciousness) here considering elephants, corvids (the crow family), and cephalopods (e.g., octopus).

Adapted from Birch et al. (2020).

SUMMARY AND KEY POINTS OF THE CHAPTER

- The neuroscientific study of consciousness can be conveniently divided into levels (wake, sleep, coma, etc.) and contents (whether aware of sound, vision, memories), although these distinctions are not completely separate (one needs a certain level to have any content)
- Levels of consciousness are related to connectedness (the flow of activity between brain regions) and complexity (not just a simple wave-like pattern) as measured using EEG or fMRI
- Neuroimaging studies that require participants to introspect on the presence or nature of the content of consciousness suggest the importance of a frontoparietal network. This is consistent with global workspace models that suggest a close connection between consciousness and attention and its importance in broadcasting that information to other regions of the brain.
- Some researchers propose a distinction between access consciousness and phenomenal consciousness. Access consciousness may be linked to the frontoparietal network and phenomenal consciousness may be linked to more localized interactions between regions.
- The default mode network supports contents of consciousness that require a decoupling from the external environment, such as mind-wandering, recollecting, and imagining.
- The sense of self consists of several elements including persistence over time, attentional prioritization of self-relevant information, sense of embodiment, and agency. These different facets involve different brain regions and these regions are not strictly self-specific.
- Predictive coding models of consciousness are based on the assumption that the brain is hierarchically organized such that higher systems make best guesses about lower systems (minimizing the discrepancy between the guess and the evidence) and the claim that our contents of consciousness track the best guess.
- Predictive processing has been used to explain a variety of phenomena from visual illusions (we see our best guess rather than the world as it it) to free will (a best guess that "I" caused something to happen rather than it being a random event or caused by something/someone else).

EXAMPLE ESSAY QUESTIONS

- What, in the human brain, is linked to different levels of consciousness?
- Critically evaluate the global workspace theory of consciousness.
- What are predictive processing theories of the brain and how have they been linked to consciousness?
- What kind of neural mechanisms are implicated in mind-wandering?

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CHAPTER 16

The social and emotional brain

CONTENTS

Emotions act as internal signposts: they guide us on how to behave, what to avoid and what to seek out. Emotions are one way of tagging certain stimuli to ensure that they receive priority treatment and are responded to appropriately. Emotions are linked to stimuli and situations in which there is an inherent survival value: for instance, fear may be linked to threatening stimuli that require vigilance or withdrawal; disgust may be linked to stimuli relating to contamination; anger may be linked to situations that threaten territory and status; and so on. Although some stimuli may be naturally rewarding (e.g., food, sex) or punishing (e.g., pain), we can learn to assign emotional states to a wide range of novel stimuli such as pop music and fashions, giving rise to extremes from phobias to fetishes. There is an almost unlimited flexibility in the range of stimuli that can be linked to emotions even though they may ultimately tap into a narrower repertoire of emotional-related responses (fight, flight, avoidance, etc.) and states (fear, anger, etc.).

Emotions also play a crucial role for guiding social behavior in most social species, including humans and primates. Group living has obvious survival advantages. There is safety in numbers and cooperation enables the sharing of limited resources. As such, it not surprising that emotions guide social decision-making. This chapter gives many examples of how the emotional brain is recruited in social situations. For instance, social rejection may

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KEY TERMS

Emotion
A state associated with stimuli that are rewarding (i.e., that one works to obtain) or punishing (i.e., that one works to avoid). These stimuli often have an inherent survival value.

Mirroring
The process of sharing the emotions or mental states of others.

Mentalizing
The process of inferring or attributing mental states to others.

Mood
An emotional state that is extended over time (e.g., anxiety is a mood and fear is an emotion).

Interoception
The brain's ability to sense the current state of its internal organs (e.g., heart rate).

share neural circuitry with physical pain, and moral disgust may have something in common with contamination-related disgust. Similarly, the reward circuitry of the brain is activated more if $10 is won by cooperating with another player than if the same amount is obtained without cooperation (Rilling et al., 2002). It is as if the act of cooperating is a reward in its own right. However, we are not a slave to our emotions. We do not always act on our "gut instincts" and can engage in nonaffective cognitive control to guide behavior.

The chapter begins by considering various theories of emotion, both historical and contemporary, and then places these theories into the context of the known neuroscientific basis of emotional processing. The chapter then considers how social information is extracted from faces. This provides an important introduction to how *perceiving* emotions (in other people) may result in a simulation of that emotional state in the perceiver (i.e., a sharing of emotion). This idea is taken further in relation to the neural mechanisms of empathy. Several kinds of mechanisms enable us to connect with and understand other people which can be broadly divided into **mirroring** (a process of simulation of emotional, motor or bodily states) and **mentalizing** (inferring mental states such as beliefs, also called theory of mind).

THEORIES OF EMOTION

Emotions are multifaceted in nature, and the list below captures the key characteristics. Different theories of emotion have tended to concentrate on some aspects more than others based on the assumption that some features are more core than others. It also means that there are many different ways of measuring emotion depending on whether one concentrates on their subjective nature (e.g., using questionnaires), their bodily responses (e.g., using skin

SOME CHARACTERISTICS OF EMOTIONS

- An emotion is a state associated with stimuli that are rewarding (i.e., that one works to obtain) or punishing (i.e., that one works to avoid).
- Emotions are transient in nature (unlike a **mood**, which is where an emotional state becomes extended over time), although the emotional status of stimuli is stored in long-term memory.
- An emotional stimulus directs attention to itself, to enable more detailed evaluation or to prompt a response.
- Emotions have a hedonic value; that is, they are subjectively liked or disliked.
- Emotions have a particular "feeling state" in terms of an internal bodily response (e.g., sweating, heart rate, hormone secretion). The brains ability to sense changes in the body is termed **interoception**.
- Emotions elicit particular external motor outcomes in the face and body, which include emotional expressions. These may prepare the organism (e.g., for fighting) and send signals to others (e.g., that one intends to fight).

conductance, or recordings of facial expression), or their behavioral consequences (e.g., pressing a lever for a reward).

Darwin and Freud

Two early views of emotion came from some well-known figures in science: Charles Darwin (1809–1882) and Sigmund Freud (1856–1939). Although their approaches are very different from each other, they share the fundamental assumption that human emotions possess continuity with their animal counterparts.

In 1872, Charles Darwin published *The Expression of the Emotions in Man and Animals* (Darwin, 1872/1965). For much of this work, Darwin was concerned with documenting the outward manifestations of emotions – **expressions** – in which animals produce facial and bodily gestures that characterize a particular emotion such as fear, anger, or happiness. Darwin noted how many expressions are conserved across species; anger involves a direct gaze with mouth opened and teeth visible and so on (see Figure 16.1). He claimed that such expressions are innate; "that is, have not been learnt by the individual." Moreover, such expressions enable one animal to interpret the emotional state of another animal; for example, whether an animal is likely to attack or is likely to welcome a sexual advance. Darwin's contribution was to provide preliminary evidence as to how emotions may be conserved across species. His reliance on expressions resonates with some contemporary approaches, such as Ekman's attempts to define "basic" emotions from cross-cultural comparisons of facial expressions (Ekman et al., 1972). More recent research has elucidated the functional origins of some of these expressions. For instance, a posed fear expression increases the visual field and nasal volume and leads to faster eye movements (adaptive for detecting danger), whereas a disgust expression has an opposite effect (adaptive for avoiding contaminants) (Susskind et al., 2008).

For Freud, our minds could be divided into three different kinds of mechanisms: the id, the ego, and the super-ego (e.g., Freud, 1920/2010). The id was concerned with representing our "primitive" urges that connect us to nonhuman ancestry including our basic emotional needs for sex, food, warmth, and so on. The id was concerned with unconscious motivations, but these ideas would

KEY TERM

Expression
External motor outcomes in the face and body associated with emotional states.

FIGURE 16.1: Darwin argued that many emotional expressions have been conserved by evolution.

sometimes be accessible via the ego (the conscious mind), and perhaps conflict with our super-ego (our cultural norms and our aspirations). Freud's basic idea that emotions are an unconscious bias on our behavior is very much relevant to current thinking (Tamietto & De Gelder, 2010). Freud's other enduring influence is the notion that mental health problems (such as anxiety) can be understood as emotional disturbances (Le Doux, 1996). Although some of the general approach is recognizable today, the specific details of Freud's theory no longer have contemporary currency (e.g., ideas relating to childhood sexual fantasies).

James–Lange and Cannon–Bard

KEY TERM

James–Lange theory
The self-perception of bodily changes produces emotional experience (e.g., one is sad because one cries).

According to the **James–Lange theory** of emotion, it is the self-perception of bodily changes that produces emotional experience (James, 1884). Thus, changes in bodily state occur *before* the emotional experience rather than the other way around (Figure 16.2). We feel sad because we cry, rather than we cry because we feel sad. This perspective seems somewhat radical compared with the contemporary point of view. For instance, it raises the question of what type of processing leads to the change in bodily states and whether this early process could itself be construed as a part of the emotion.

Changes in the body are mediated by the autonomic nervous system (ANS), a set of nerves located in the body that controls activity of the internal organs (the soma). There is good empirical evidence to suggest that changes in bodily states, in themselves, are not sufficient to produce an emotion. Schacter and Singer (1962) injected participants with epinephrine (also termed adrenaline), a drug that induces autonomic changes such as to heart rate. They found that the presence of the drug by itself did not lead to self-reported experiences of emotion, contrary to the James–Lange theory. However, in the presence of an appropriate cognitive setting (e.g., an angry or happy man enters the room), the participants did self-report an emotion. A cognitive setting, without epinephrine, produced less intense emotional ratings. This study suggests that

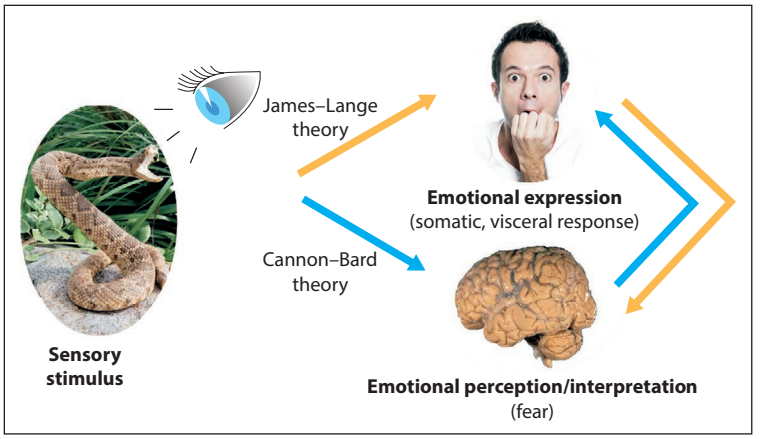

FIGURE 16.2: According to the James–Lange theory, bodily reactions occur first, and emotional processing occurs after (as the perception/interpretation of those reactions). According to the Cannon–Bard theory, the emotional perception/interpretation occurs first, and the bodily reaction occurs after.

bodily experiences do not create emotions (contrary to James–Lange), but they can enhance conscious emotional experiences.

There are several contemporary theories that bear similarity to the James–Lange theory, most notably Damasio's (1994) suggestion that bodily responses linked to emotions guide decision-making. This is the somatic marker hypothesis discussed in more detail in Chapter 14. Although the James–Lange theory states that these bodily responses must be consciously perceived, Damasio (1994) takes the different view that they are unconscious modifiers of behavior.

The **Cannon–Bard theory** of emotions that emerged in the 1920s argued that bodily feedback could not account for the differences between the emotions (Cannon, 1927). According to this view, the emotions could be accounted for solely within the brain, and that bodily responses occur *after* the emotion itself. The Cannon–Bard theory was inspired by neurobiology. Earlier research had noted that animals still exhibit emotional expressions (e.g., of rage) after removal of the cortex. This was considered surprising given that it was known that cortical motor regions are needed to initiate most other bodily movements (Fritsch & Hitzig, 1870). In a series of lesion studies, Cannon and Bard concluded that the hypothalamus is the centerpiece of emotions. They believed that the hypothalamus received and evaluated sensory inputs in terms of emotional content and then sent signals to the autonomic system (to induce the bodily feelings discussed by James) and to the cortex (giving rise to conscious experiences of emotion).

KEY TERMS

Cannon–Bard theory
Theory centered on the hypothalamus' role in emotions in which bodily responses occur after the emotion itself.

Papez circuit
A limbic-based circuit that was once thought to constitute a largely undifferentiated "emotional" brain.

Papez circuit and the limbic brain

Papez (1937) drew upon the work of Cannon–Bard in arguing that the hypothalamus was a key part of emotional processing, but extended this into a circuit of other regions that included the regions of the cingulate cortex, hippocampus, hypothalamus, and anterior nucleus of the thalamus. Papez argued that the feeling of emotions originated in the subcortical **Papez circuit**, which was hypothesized to be involved in bodily regulation. A second circuit, involving the cortex, was assumed to involve a deliberative analysis that retrieved memory associations about the stimulus. The work of MacLean (1949) extended this idea to incorporate regions such as the amygdala and orbitofrontal cortex, which he termed the "limbic brain." The different regions were hypothesized to work together to produce an integrated "emotional brain."

There are a number of reasons why these earlier neurobiological views are no longer endorsed by contemporary cognitive neuroscience. First, some of the key regions of the Papez circuit can no longer be considered to carry out functions that relate primarily to the emotions. For example, the role of the hippocampus in memory was not appreciated until the 1950s (Scoville & Milner, 1957), and the hypothalamus is not a central nexus of emotions, although it does regulate bodily homeostasis. Second, contemporary research tends to suggest that these different regions perform different

emotion-related functions (e.g., relating to fear versus disgust) rather than all regions being equivalent. Finally, most contemporary theories acknowledge the importance of the cortex in emotion which acts, as a network, in concert with these limbic regions.

Contemporary views of emotion: categories, dimensions, and constructions

Contemporary views propose that emotional processes can be broken down into different elements, distributed amongst various regions of the brain. But there is disagreement as to how these are structured, as illustrated in Figure 16.3, which shows three possibilities. Emotions might be organized along some continuous space defined by different dimensions (left) or might be organized around different categories of emotion (middle). For instance, there might be separate regions or circuits for fear versus anger. Finally, there might be separate regions that are engaged in different kinds of information processing relevant to emotions (right) – so one region that codes the feelings and one region involved in emotional learning. It is important to note that these three options are not mutually exclusive: it is possible that all three might be true to some extent.

KEY TERM

Basic emotions
Different categories of emotions assumed to be independent of culture and with their own biological basis (in terms of evolution and neural substrate).

With regards to a categorical representation of emotions, one of the most influential ethnographic studies of the emotions concluded that there are six **basic emotions** that are independent of culture (Ekman & Friesen, 1976; Ekman et al., 1972): happy, sad, disgust, anger, fear, and surprise. These are shown in Figure 16.4. This study was based on comparisons of the way that facial expressions are categorized and posed across diverse cultures. Participants from

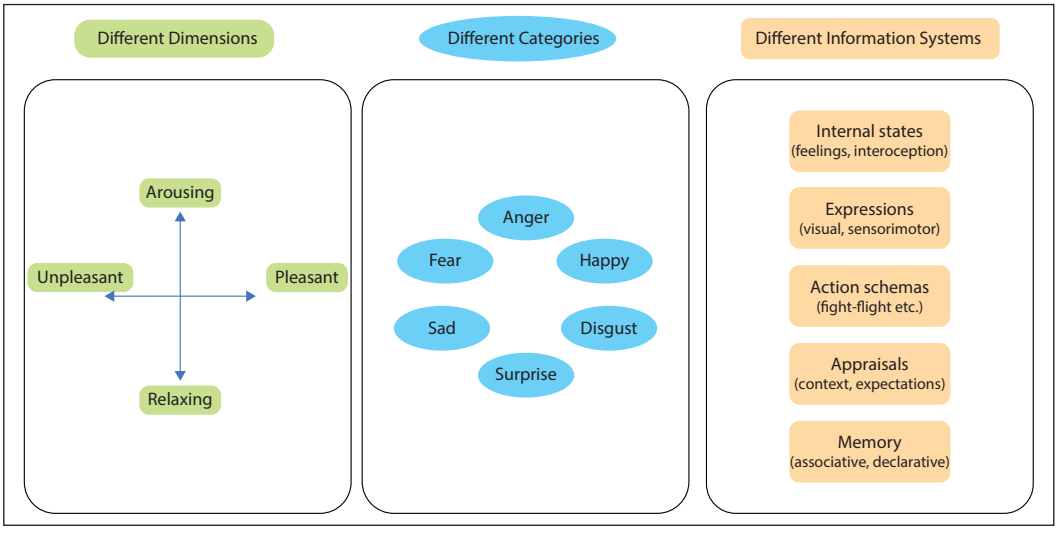

FIGURE 16.3: How are emotions represented in the brain? Different emotions could be represented by brain systems that represent different dimensions (left), different categories (right), or different kinds of information systems (right). It is possible that all three possibilities could be correct, to some degree.

Papua New Guinea, never exposed to other cultures, could recognize expressions posed by Westerners. Conversely, Westerners could recognize posed expressions generated by this group in response to narratives (e.g., "a family member just died"). Ekman (1992) considers other characteristics for classifying an emotion as "basic" aside from universal facial expressions, such as, each emotion having its own specific neural basis; each emotion having evolved to deal with different survival problems; and occurring automatically. Other research has argued in favor of cross-cultural universality whilst not necessarily endorsing Ekman's original list of six. Jack et al. (2016) used facial movements, rather than static photos, and data-driven techniques for clustering expressions into categories to identify four basic expressions (merging fear and surprise into a single high arousal category and merging anger and disgust into a low valence pattern linked to stimulus avoidance). Others have found cultural invariance in facial expressions for pain versus orgasm (Chen et al., 2018) and different social functions of smiling (Rychlowska et al., 2015). It is possible to decode, significantly above chance, different categories of emotion from fMRI multivariate pattern analysis, and these are not reducible to dimensions such as arousal and valence (Kragel & Labar, 2016). But the complex nature of the patterns, across many brain regions, does not support the simple view the different categories of emotions are supported by highly specialized circuits or regions (Wager et al., 2015).

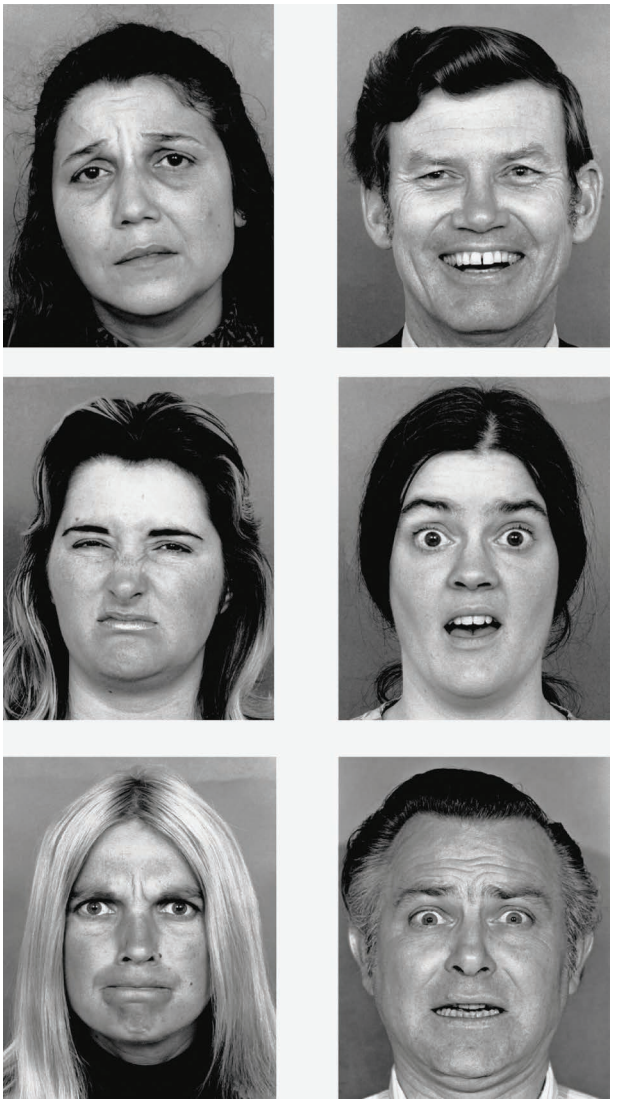

FIGURE 16.4: Paul Ekman tested a wide range of different cultures and concluded that there are six basic types of emotion expressed in faces: sad, happy, disgust, surprise, anger, and fear.

Rather than assuming basic categories of emotion, other models postulate different *dimensions* that underpin emotions. For example, the model of Rolls (2005) defines emotions in terms of the extent to which stimuli are rewarding or punishing (as opposed to categories such as anger or fear). Barrett and colleagues (Barrett, 2006; Lindquist & Barrett, 2012) argue that all emotions tap into a system termed core affect that is organized along two dimensions: pleasant–unpleasant and high-low arousal. This is illustrated in Figure 16.5. Evidence that emotional experience can be classified

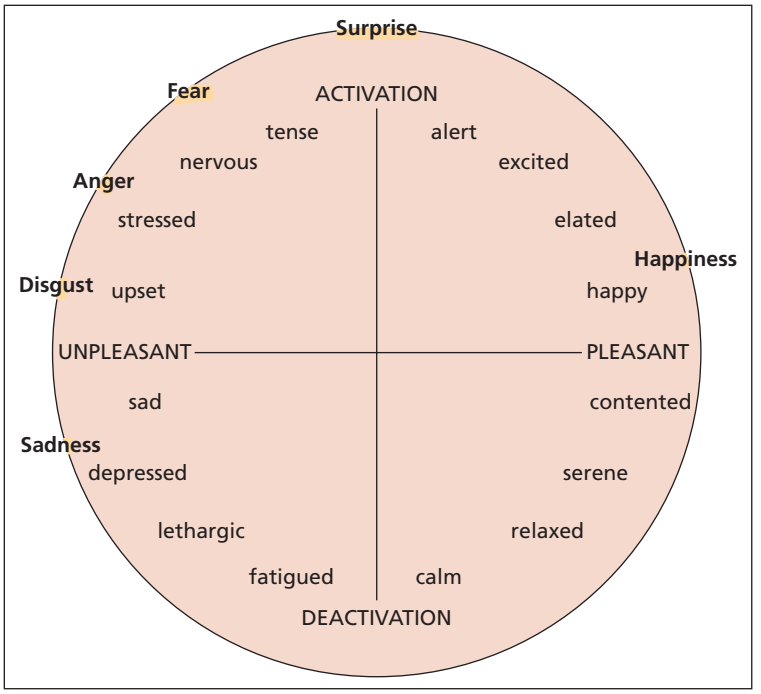

FIGURE 16.5: In the model of Feldman-Barrett, all emotions (and mood) involve a "core affect" system that is organized along two dimensions corresponding to pleasantness and arousal (/activation). Different categories of emotion are points in that space (and linked to associated cognitions – language, memory, perception, theory of mind) but are not afforded a special status.

From Russell and Feldman-Barrett (1999). Journal of Personality and Social Psychology.

along these two dimensions comes from studies employing factor analysis of current mood ratings (Yik et al., 1999). In biological terms, core affect is linked to bodily feelings of emotion and linked to limbic structures such as medial temporal lobes, cingulate and orbitofrontal cortex (Lindquist & Barrett, 2012). Note that this model does not entirely reject the idea of emotion categories but, instead, argues that the categories are constructed from other elements (as opposed to being the basic elements in themselves). So "fear" is related to low pleasantness and high arousal (in the core affect system) plus high-level conceptual knowledge derived from language and personal experience (i.e., drawing on other systems in the brain). The idea that emotions are constructed in this way is rooted in a longer tradition of linking emotions to **appraisals** (i.e., contextual evaluations) rather than simple stimulus-response associations.

KEY TERM

Appraisal
An evaluation of both the content (e.g., negative feeling) and the context (e.g., likely source of content) which combine to generate an emotion.

A controversial claim of Barrett's constructed emotion theory is that even facial expressions are culturally constructed based on experience rather than innate (i.e., contrary to Darwin and Ekman). Language differences due to cross-cultural variation (e.g., the Himba tribe of Namibia; Gendron et al., 2014) or loss of conceptual knowledge in semantic dementia (Lindquist et al., 2014) lead to differences in sorting images of facial expressions; for instance, sorting them into positive versus negative affect rather than six categories. This runs counter to the view that these categories are basic and independent of

language/culture. However, it would be important to test these ideas on more indirect measures of facial expression processing (e.g., via subliminal presentation of fear v. anger), which are less likely to depend on language than tasks such as sorting faces into categories.

It is important to note that advocates of the basic emotions approach do not deny that *some* emotions are constructed, but they differ from theories such as those of Barrett (2006) and Rolls (2005) that assume that *all* emotions are constructed. One possibility within the basic emotion approach is to consider some emotions as being composed of two or more basic emotions: for example, joy + fear = guilt, and fear + surprise = alarm (Plutchik, 1980). Another possibility is that some emotions are constructed from a basic emotion(s) plus a non-emotional cognitive appraisal. For example, a similar feeling could be appraised as either shame or guilt depending on whether it is contextualized relative to the self (shame) or other (guilt). Haidt (2003) has used the term **moral emotions** to refer to emotions that are related to the behavior of oneself (in relation to others) or the behavior of others (in relation to oneself or others). It implies the existence of some normative benchmark with which to evaluate our actions. These norms could be a product of both innate mechanisms (e.g., an instinctive desire not to harm others) and culturally accepted norms (e.g., law and religion). In this view, the existence of moral emotions depends on an evolutionarily older set of emotional processes together with an evolutionarily newer ability to reflect on the behavior of self and others.

ONLINE RESOURCES

Test your ability to categorize the six basic emotions from facial expressions (www.testable.org/ward).

KEY TERM

Moral emotions
Emotions that are related to the behavior of oneself (in relation to others) or the behavior of others (in relation to oneself or others).

Evaluation

Although there are many different theories of emotion, there are a core set of ideas concerning emotions that have stood the test of time. This includes the idea that emotions have an evolved adaptive value, and this is largely conserved across species. It also includes the notion that emotions are multifaceted: they contain both conscious (at least in humans) and unconscious processes; they involve the interplay of brain and body via the autonomic system (although emotions cannot be reduced to bodily sensations); and that (at least in humans) some emotions are constructed from both affective mechanisms and cognitive ones (e.g., appraisal). A good example of the latter is moral emotions (e.g., guilt, pride). Contemporary theories emphasize categorical distinctions between emotions (such as anger, fear, sadness) but differ with regards to whether these categories represent natural kinds (i.e., innately specified categorical differences, as in the basic emotion approach) or are themselves constructed from different combinations of building blocks of other kinds of core processes (e.g., reward/punishment, pleasure, arousal, appraisals).

MORALITY IN THE BRAIN

Moral judgments involve an evaluation of actions and intentions (either our own or that of others) against some standard of acceptable behavior. Moral emotions occur when we compare behavior against those standards (Haidt, 2003). For instance, if our own actions exceed our standards, then we may feel pride, but if they fall below those standards, we may feel shame, guilt, or embarrassment. If other people's behavior falls below those standards, then we may feel anger or disgust. The question of where the moral standards come from is an interesting one. It is likely to derive from a core set of instincts around love for one's family, need for affiliation, empathy, and fairness (including retribution against unfairness). Cultural norms, including religion and the law, tend to reinforce these instincts (can you think of a successful religion that does not preach love for one's family?). But they may extend moral norms in more idiosyncratic ways (e.g., what to eat and wear).

There is evidence consistent with the view that processing of moral emotions involves brain structures involved in both emotion and cognitive appraisal (Figure 16.5). Moll et al. (2002) presented pictures of three kinds of emotional scenes to participants undergoing fMRI: images of moral violations (e.g., images of physical assaults, abandoned children), images of aversive scenes (e.g., a dangerous animal), and pleasant images. These were matched for their self-reported arousal. The moral-violation and aversive images were matched in terms of how negatively they were judged, but the moral-violation images were judged as more morally unacceptable than the other affective stimuli. All affective stimuli (relative to a neutral set of images) tended to activate regions linked to emotional processing such as the amygdala and insula, but moral emotions (relative to other affective stimuli) additionally activated regions such as the orbitofrontal cortex, the medial prefrontal cortex, and the right posterior superior temporal sulcus (STS). The medial prefrontal cortex and right posterior STS have been linked to theory of mind (Amodio & Frith, 2006; Saxe, 2006), whereas the orbitofrontal cortex is implicated in the regulation of social behavior. Similar results were obtained by reading verbal narratives for the moral emotions of embarrassment (Berthoz et al., 2002) and guilt (Takahashi et al., 2004); for example, "I left the restaurant without paying" (guilt) and "I mistook a stranger for my friend" (embarrassment).

Patients with acquired lesions to the orbitofrontal (and ventromedial prefrontal) cortex often display poor social functioning (see Chapter 14 for more discussion). These patients are judged by family members to exhibit low levels of empathy,

FIGURE 16.6: What regions of the brain are activated when viewing (or thinking about) scenes involving moral transgressions, such as domestic violence? Is it the same pattern found when viewing other emotional stimuli that do not involve a transgression?

lolostock/iStock

embarrassment, and guilt (Koenigs et al., 2007). That is, their impairments extend to moral emotions. When given certain moral dilemmas they tend to perform atypically. For instance, if asked whether they would be willing to push one person under a train to save the lives of five people, they are inclined to agree with this course of action (Koenigs et al., 2007). The explanation for this is that there are two conflicting answers in this dilemma. There is a numerically logical answer that killing one life is better than killing five lives. There is also a more emotionally loaded proposition, namely, that it would be wrong to push someone under a train. In patients with orbitofrontal lesions, logic may win when pitted against a moral emotion.

NEURAL SUBSTRATES OF EMOTION PROCESSING

This section introduces many of the key brain regions involved in emotional processing and considers their possible functions. The section will show how the same brain networks are used to process both social stimuli (our perceptions and interactions with others) as well as nonsocial stimuli with affective properties (such as snakes, food, electric shocks). Another aim of the section is to use this evidence to adjudicate between various theories in the field: for instance, to determine whether there are basic emotions with distinct neural substrates.

The amygdala: emotional learning, arousal, and fear

The **amygdala** (from the Latin word for almond) is a small mass of gray matter that lies buried in the tip of the left and right temporal lobes (Figure 16.6). It lies to the front of the hippocampus and, like the hippocampus, is believed to be important for memory – particularly for the emotional content of memories (Richardson et al., 2004) and for learning whether a particular stimulus/response is rewarded or punished (Gaffan, 1992). In monkeys, bilateral lesions of the amygdala have been observed to produce a complex array of behaviors that have been termed the **Kluver–Bucy syndrome** (Kluver & Bucy, 1939; Weiskrantz, 1956). These behaviors include an unusual tameness and emotional blunting, a tendency to examine objects with the mouth, and dietary changes. This is explained in terms of objects losing their learned emotional value. The monkeys typically also lose their social standing (Rosvold et al., 1954).

The role of the amygdala in fear conditioning is well established (Le Doux, 1996; Phelps, 2006). If a stimulus that does not normally elicit a fear response, such as an auditory tone (unconditioned stimulus, CS–), is paired with a stimulus that does normally evoke a fear response (termed conditioned response), such as an electric shock, then the tone will come to elicit a fear response by itself (it becomes a conditioned stimulus, CS+). This is illustrated in Figure 16.7. If the amygdala is lesioned in mice (specifically the

ONLINE RESOURCES

Scan the QR code or visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience) for selected videos on emotion, including the TED talk by Lisa Feldman-Barrett and interviews with Paul Ekman.

KEY TERMS

Amygdala
Part of the limbic system, implicated in learning the emotional value of stimuli (e.g., in fear conditioning).

Kluver–Bucy syndrome
In monkeys after bilateral amygdala and temporal lesions, an unusual tameness and emotional blunting, a tendency to examine objects with the mouth, and dietary changes.

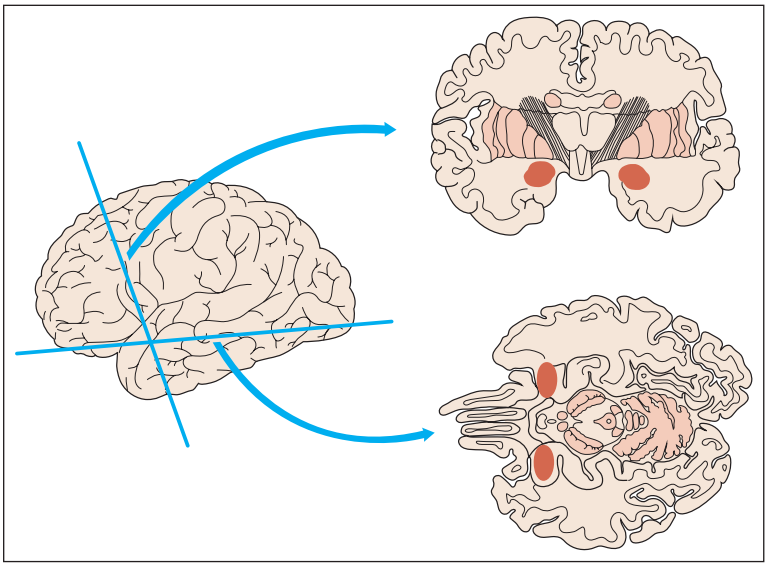

FIGURE 16.7: The amygdala is buried, bilaterally, in the anterior portion of the temporal lobes.

basolateral nucleus of the amygdala), then the animal does not show this learning, and if the lesion is performed after the animal has been trained, then this learned association is lost (Phillips & Ledoux, 1992). That is, the amygdala is important for both learning and storing the conditioned fear response (although for a different view see Cahill et al., 1999). Single-cell recordings suggest that different cells within the amygdala could be involved in learning versus storage of the association (Repa et al., 2001). Animals with lesions to the amygdala still show a fear response to normal fear-evoking stimuli (such as shocks). This suggests that its role is in learning and storing the emotional status of stimuli that are initially emotionally neutral, and that it isn't the fear center of the brain in any global sense.

In humans, a comparison of learned fear responses to a shock (CS+) with neutral stimuli (CS–) reveals amygdala activation during fMRI that correlates with the degree of conditioned response, in this instance a skin conductance response (LaBar et al., 1998). The **skin conductance response** is a measure of autonomic arousal and, hence, a body-based measure of emotion processing (see Figure 16.9). Bechara et al. (1995) report that humans with amygdala damage fail to show this conditioned response but nevertheless are able to verbally learn the association ("when I saw the blue square I got a shock"), whereas amnesic patients with hippocampal damage show a normal conditioned response but cannot recall the association. This suggests that the association is stored in more than one place: in the amygdala (giving rise to the conditioned fear response) plus in the hippocampus (giving

KEY TERM

Skin conductance response (SCR)
Changes in electrical conductivity on a person's skin, triggered by certain stimuli (e.g., emotional or familiar stimuli).

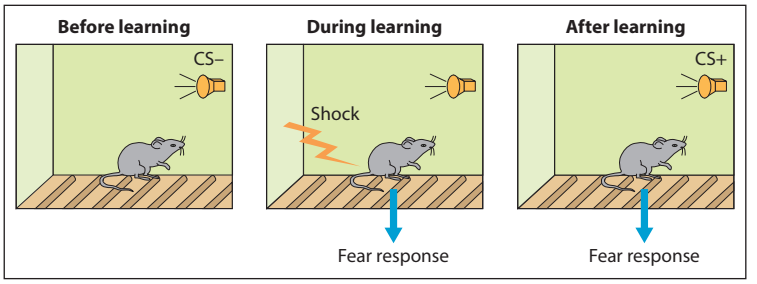

FIGURE 16.8: The basic procedure in fear conditioning involves presenting an initially neutral stimulus (the CS–, e.g., a tone) with a shock. After sufficient pairings, the stimulus will elicit a fear response without an accompanying shock (it has become a CS+).

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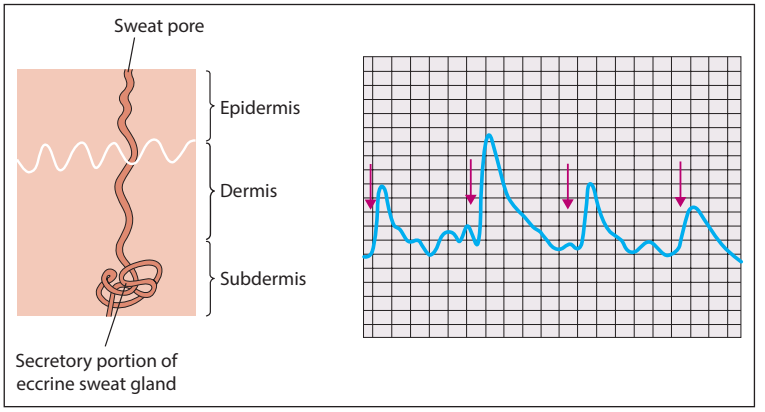

FIGURE 16.9: The skin conductance response (SCR) method involves recording changes in electrical conductivity on a person's skin on the hand. Heightened arousal can lead to more sweat even without overt sweating taking place. A person's SCR can be plotted as a continuous trace throughout the experiment. A peak SCR occurs between 1 and 5 s after face presentation.

rise to declarative memories of the association). fMRI studies also show that the amygdala may be important for fear-related conditioning in social settings in which participants learn fear associations by watching someone else receive a shock (Olsson & Phelps, 2004).

Amygdala lesions in humans can selectively impair the ability to *perceive* fear in others but not necessarily the other Ekman categories of emotion (Adolphs et al., 1994; Calder et al., 1996). For example, patient DR suffered bilateral amygdala damage and subsequently displayed a particular difficulty with recognizing fear (Calder et al., 1996). She was also impaired to a lesser degree in recognizing facial anger and disgust. She could imagine the facial features of famous people, but not of emotional expressions. She could recognize famous faces and match different views of unfamiliar people, but could not match pictures of the same person when the expression differed (Young et al., 1996). While it has been suggested that selective impairments in fear may arise because of a failure to attend closely to the eyes (Adolphs et al., 2005), this cannot account for the fact that some patients fail to recognize fear in speech (Scott et al., 1997) or music (Gosselin et al., 2007).

Electrophysiological recordings from the human amygdala show that neurons respond to various aspects of faces (Rutishauser et al., 2015), and whilst some neurons respond more to fear than happy, others also show the reverse profile (Wang et al., 2014). So it is certainly not the case that the amygdala only responds to facial fear. (The lesion data could still be explained if happiness, relative to fear, had a more diffuse distribution throughout the brain.) In fMRI, facial expressions of fear and happy activates the amygdala more during emotional learning (i.e., when paired with neutral objects) than passive viewing of the same expressions (Hooker et al., 2006). This is consistent with the amygdala using facial expressions (e.g., in learning) and not merely perceiving them.

Some researchers have argued that the ability to detect threat is so important, evolutionarily, that it may occur rapidly and without conscious awareness (Le Doux, 1996). In terms of neural pathways, it is generally believed that there is a fast subcortical route from the thalamus to the amygdala and a slow route to the amygdala via the primary visual cortex (Adolphs, 2002; Morris et al., 1999), as shown in Figure 16.10. Functional imaging studies suggest that the amygdala is indeed activated by unconscious fearful expressions in both healthy participants (Morris et al., 1999) and in a "blindsight" patient with damage to their primary visual cortex (Tamietto et al., 2012). This is consistent with a subcortical route to the amygdala, although it is to be noted that the temporal resolution of fMRI does not enable any conclusions to be drawn about whether the route is fast or slow.

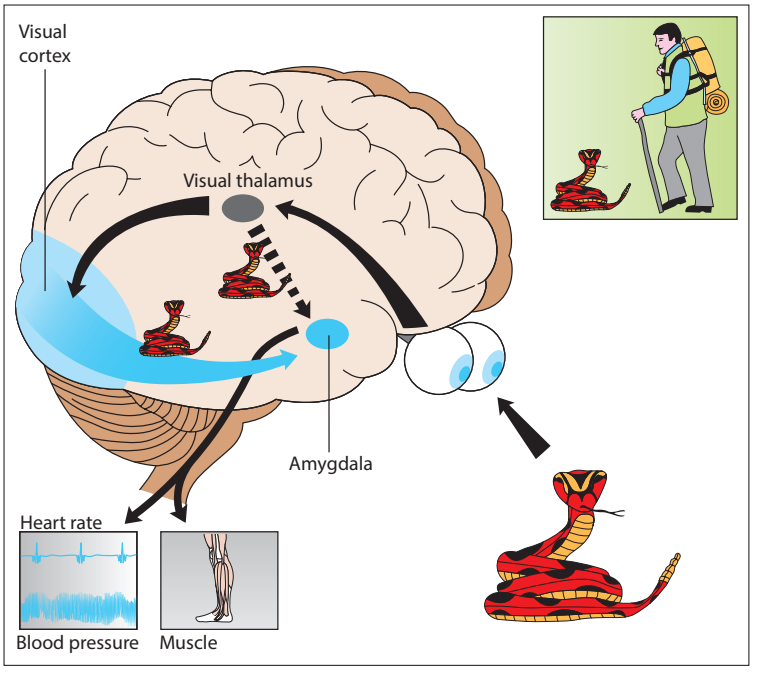

FIGURE 16.10: Le Doux has argued that the amygdala has a fast response to the presence of threatening stimuli such as snakes.

With regards to learning of stimulus–emotion associations there is evidence that the amygdala is involved in learning positive associations, based on food rewards, as well as fear conditioning (Baxter & Murray, 2002). However, the amygdala system for positive associations operates somewhat differently to fear conditioning and depends on different nuclei (Hatfield et al., 1996). Functional imaging studies that compare stimuli with learned positive and negative associations relative to emotionally neutral ones but do not rely on facial expressions have revealed amygdala activation to negative and positive affective stimuli (Figure 16.11); for instance, comparing positive, negative, and neutral tastes (Small et al., 2003), smells (Winston et al., 2005), pictures, and sounds (Anders et al., 2008). However, most fMRI studies do not have the spatial resolution to reliably distinguish between subregions within the amygdala.

The insula: disgust and interoception

The **insula** is a small region of cortex buried beneath the temporal lobes (it literally means "island"), as shown in Figure 16.12. The insula is generally considered to have a wider role in perceiving the state of one's own body (Craig, 2009; Singer et al., 2009): including the sense of taste (it contains the primary gustatory cortex), pain perception, and interoception (somatic sensing of the internal organs such as heart rate, breathing, and stomach). Internal feelings, such as nausea or visceral pain, may disrupt ongoing activities to demand attention in the same way as it would be adaptive to respond to external threats (e.g., a snake).

Most contemporary accounts of interception emphasize not only the bottom-up signaling of bodily states, but also the importance of top-down predictions of bodily states (Seth &

KEY TERM

Insula
A region of cortex buried beneath the temporal lobes; involved in body perception and contains the primary gustatory cortex; responds to disgust.

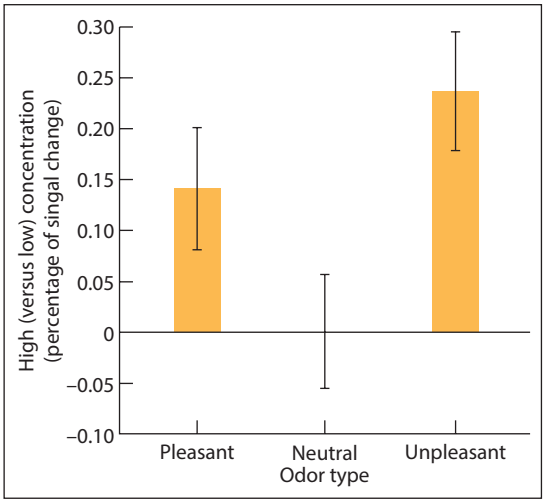

FIGURE 16.11: There is evidence that the amygdala responds to pleasant and unpleasant smells (but not neutral smells). This suggests a wider role of the amygdala in emotion processing, in contrast to the commonly held assumption that it is specific to fear.

Adapted from Dolan, R. J. (2007). The human amygdala and orbitofrontal cortex in behavioral regulation. *Philosophical Transactions of the Royal Society of London Series B, 362*, 787–799. Used with permission of The Royal Society. Permission conveyed through Copyright Clearance Centre, Inc.

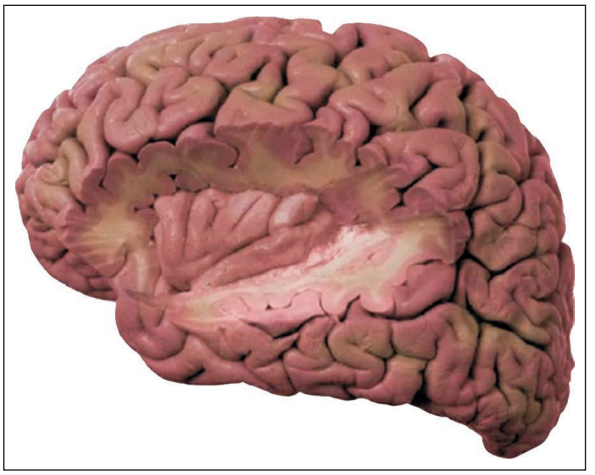

FIGURE 16.12: The insula is an island of cortex lying, bilaterally, underneath the temporal lobes. It is implicated in the creation of bodily feelings associated with emotions, and in the perception of disgust in particular.

Adapted from Singer et al. (2009).

KEY TERM

Depersonalization
The feeling of being outside yourself and observing your actions, feelings, or thoughts from a distance.

Friston, 2016). Problems in the ability to predict our internal states might give rise to symptoms such as anxiety (e.g., panic attacks) or **depersonalization** (Phillips et al., 2001). Conscious bodily experiences may constitute the "feeling" of an emotion. Damasio et al. (2000) report insula activity in response to recalling emotional memories from various categories (sadness, happiness, anger, fear) relative to emotionally neutral memories. Neural activity within the insula, measured with fMRI, can distinguish finer-grained feeling states such as between disgust-associated nausea and light-headedness (Harrison et al., 2010) and can also distinguish pain from negative affect (Wager et al., 2013). The insula might also support some aspects of empathy via a sharing of feelings. Seeing disgust and seeing pain in other people activates similar regions of the insula as feeling disgusted and being in pain oneself, with pain and disgust linked to separate sub-regions with the insula (Corradi-Dell'Acqua et al., 2016). This suggests that the insula represents qualitatively different aspects of emotions and feelings rather than broader emotional dimensions such as valence and arousal.

Aside from this broader role in emotion, there is a suggestion that the insula has a more specific role in the emotional category of disgust. The word disgust literally means "bad taste," and this category of emotion may be evolutionarily related to contamination and disease through ingestion (noting that both signals from the tongue and stomach have pathways to the insula). Patients with Huntington's disease can show difficulty in recognizing disgust via facial expressions (Sprengelmeyer et al., 1997) and vocalizations (Sprengelmeyer et al., 1996) as well as via taste and smell (Mitchell et al., 2005). Huntington's disease is a genetic disorder with symptoms arising in mid-adulthood and including excessive movements, cognitive decline, and structural atrophy in the brain, particularly in regions such as the basal ganglia. However, the degree of the disgust-related impairments in this group correlates with the amount of damage in the insula (Kipps et al., 2007).

We use the word "disgust" in at least one other context, namely, to refer to social behavior that violates moral conventions. Disgusting behavior is said, metaphorically, to "leave a bad taste in the mouth." But is there more to this than metaphor? Some have argued that moral disgust has evolved out of non-social, contamination-related disgust (e.g., Tybur

et al., 2009). Moral disgust also results in activity in the insula (Moll et al., 2005), and moral disgust is associated with subtle oral facial expressions characteristic of disgust more generally (Chapman et al., 2009).

Orbitofrontal cortex: contextualized emotions and emotional feelings

One general function of the orbitofrontal cortex is in computing the *current* value of a stimulus, that is, how rewarding the stimulus is within the current context. For example, chocolate may be a rewarding stimulus, but it may not be *currently rewarding* if one is full up or if eating it may incur the anger of someone else (Figure 16.13). Small et al. (2001) asked participants to eat chocolate between several blocks of functional imaging. Initially, the chocolate was rated as pleasant and participants were motivated to eat it, but the more they ate, the less pleasant it became and they were less motivated to eat it. This change in behavior was linked to changes in activity in orbitofrontal regions. Specifically, there was a shift in activity from medial regions (pleasant/wanting) to lateral regions (unpleasant/not-wanting). Other studies are consistent with different regions of orbitofrontal cortex coding rewards and punishments (e.g., for a review see Berridge & Kringelbach, 2015). For instance, activation of lateral orbitofrontal cortex is found when a rewarding smile is expected, but an angry face is instead presented (Kringelbach & Rolls, 2003), and activity in this lateral orbitofrontal region is correlated with the amount of monetary loss on a trial (O'Doherty et al., 2001).

The orbitofrontal cortex may enable flexible changes in behavior to stimuli that are normally rewarding (or recently rewarding) but suddenly cease to be. This can account for its role in reversal learning (in which rewarded and non-rewarded stimuli are reversed) and **extinction** (in which a rewarded stimulus is no longer rewarded). Eating chocolate until it is no longer pleasant can be regarded as a form of extinction. Lesions in these regions in humans lead to difficulties on related tasks, and the amount of difficulty in reversal learning correlates

KEY TERM

Extinction learning
Learning that a previously rewarded stimulus is no longer rewarded.

FIGURE 16.13: The same stimulus can elicit pleasure or aversion depending on context (e.g., the person's motivational state). Chocolate is normally pleasant, but if you have just eaten two bars of it you probably do not want any more. The orbitofrontal cortex computes the current emotional status of a stimulus (i.e., whether it is *currently* desired or not), thus enabling flexible behavior. Other regions in the brain may code the long-term value of a stimulus (i.e., whether it is *normally* desired or not).

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with the level of socially inappropriate behavior of the patients (Rolls et al., 1994).

Activity in the orbitofrontal cortex has been linked to participants' subjective reports of pleasantness to stimuli such as tastes (McClure et al., 2004b) and music (Blood & Zatorre, 2001). Importantly, these ratings of pleasantness are affected not just by the stimulus itself but also by the participants' beliefs about the product. Being told the price of a wine affects ratings of pleasantness upon tasting it – more expensive wines taste nicer – and perceived pleasantness was again related to activity in the medial part of the orbitofrontal cortex (Plassmann et al., 2008). Of course, the experimenters administered some of the same wines twice, giving the participants different prices so the stimuli were physically identical, but their beliefs about the quality of the wine were not identical. There appears to be a similar neural mechanism for computing pleasure across very diverse stimuli (Berridge & Kringelbach, 2015). This is sometimes described as "common currency" that can compute rewards, or punishments, across the full spectrum of stimuli (Levy & Glimcher, 2012). For example, a common currency enables us to compare a monetary value (e.g., cheating in poker) against a moral cost (e.g., feelings of guilt) to guide behavior.

Anterior cingulate: response evaluation, autonomic responses, and pain

In Chapter 14, it was noted that the anterior cingulate has previously been described in terms of primarily non-emotional functions such as monitoring for errors and response conflicts. However, more recent theories emphasize its importance in a much wider range of scenarios, including the processing of social and emotional stimuli. Specifically, it has been linked to motivation (Kouneiher et al., 2009) and determining the costs and benefits of actions (Shenhav et al., 2013). Rushworth et al. (2007) argue that the function of the anterior cingulate is to assess the value of responses, that is, whether an *action* is likely to elicit a reward or punishment. This may differ from the function of the orbitofrontal cortex which computes whether a given *stimulus* is currently rewarded or punished. Male monkeys with anterior cingulate lesions fail to adjust their responses, when reaching for food, when simultaneously shown a dominant male or a female in estrus, whereas most control monkeys will pay close attention to these social stimuli, and hence take longer to respond to the food (Rudebeck et al., 2006).

The anterior cingulate cortex, like the insula, is involved in processing bodily signals that characterize emotions, but whereas the insula is more concerned with the input (and awareness) of these signals, the anterior cingulate is more concerned with the output of bodily responses. Lesions in this area disrupt the skin conductance

response (Tranel & Damasio, 1995) and changes in heart rate and blood pressure (Critchley et al., 2003) to emotional stimuli.

The anterior cingulate also receives inputs (via the thalamus) relating to pain and may regulate feelings of pain via output connections to the periaqueductal gray (a region that is rich in endogenous opioids). As well as responding (e.g., in fMRI) to physically painful stimuli, such as mild electric shocks, watching someone else in pain activates some of the same regions (Singer et al., 2004). Thus, it responds to the perception of pain in others as well as to physical pain in oneself. This idea is returned to in later discussions on empathy. It has also been claimed that being separated from a loved one or being socially excluded in general is "painful," and these more social forms of pain may indeed involve the pain circuitry of the brain. Eisenberger et al. (2003) conducted an fMRI study of a Cyberball game involving three players, including the one person being scanned (Figure 16.14). Players could opt to throw the ball to one of the two other players. However, after a while the game was fixed such that two players consistently threw to each other, excluding the person in the scanner. There were two other conditions: one in which the player was included, and one in which they were excluded but given the cover story of "due to technical difficulties." Activity in the anterior cingulate correlated with self-reported distress during social exclusion. A region in the prefrontal cortex (right ventro-lateral prefrontal cortex) was linked to social exclusion, but not exclusion due to "technical difficulties" which they interpret as playing a controlling role in limiting the distress of social exclusion.

Ventral striatum and reward

The dorsal region of the striatum has more sensorimotor properties (e.g., involved in habit formation), whereas the ventral region may be more specialized for emotions, although the distinction is relative, not absolute (Voorn et al., 2004). There are several loops that connect regions within the frontal cortex to the basal ganglia and on to the thalamus before returning to the frontal cortex (Alexander & Crutcher, 1990). The loops modulate brain activity within these frontal structures and, hence, increase or decrease the probability of a particular behavior. The loop that is of particular relevance to reward-based learning (the "limbic circuit") starts and ends in the orbitofrontal cortex and limbic regions (including the amygdala and anterior cingulate), passing through the basal ganglia (including the **ventral striatum**) and thalamus.

Neurons containing the neurotransmitter, dopamine, project from the midbrain to a region in the ventral striatum called the nucleus accumbens. Psychomotor stimulants such as amphetamine and cocaine may exert their effects via this system (Koob, 1992). Other rewarding stimuli activate this region. Dopamine release

KEY TERM

Ventral striatum
Part of the basal ganglia that includes the nucleus accumbens; involved in a "limbic circuit" connecting the orbitofrontal cortex, basal ganglia, and thalamus.

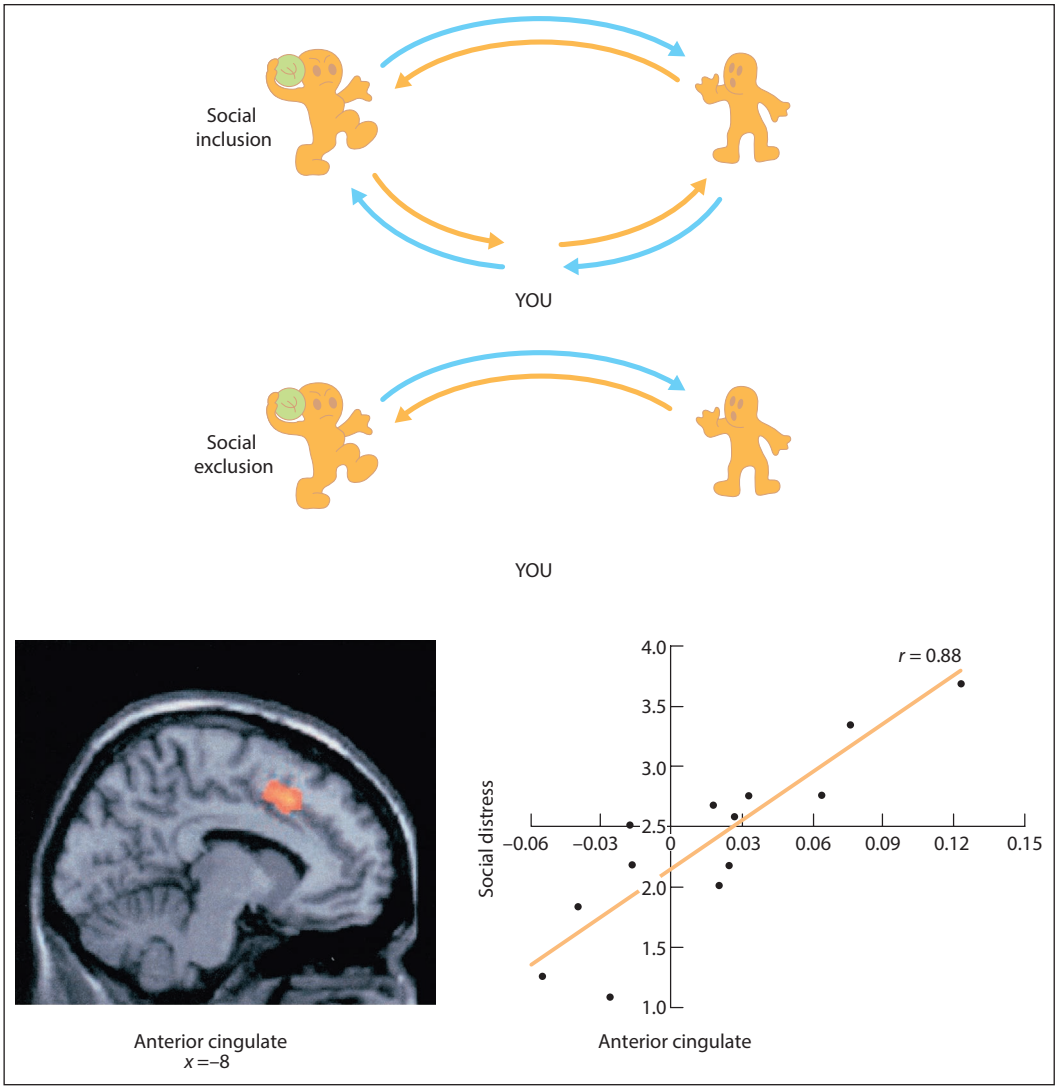


FIGURE 16.14: In the Cyberball game a participant must decide which of two other players to throw the ball to. In a social exclusion condition, two of the players always send the ball to each other and never to the participant. In a social inclusion condition, all players get to play. Social exclusion tends to activate the anterior cingulate, and this correlates with subjective levels of distress.

Bottom figures from Eisenberger et al. (2003). © 2003 American Association for the Advancement of Science. Reproduced with permission.

in the nucleus accumbens of male rats increases when a female is introduced to the cage and increases further if they have sex (Pfaus et al., 1990). Neutral stimuli previously associated with food increase the release of dopamine in the nucleus accumbens of rats (Robbins et al., 1989). In humans, an fMRI study shows that the greater the monetary reward that could be obtained in a task, the larger the activity in the ventral striatum (Knutson et al., 2001).

However, social stimuli are rewarding too, and activity in this region tends to be greater when a reward (e.g., monetary) is obtained via cooperation with another human than when it is obtained from noncooperation with a human or cooperation with a nonsocial agent such as a computer (Rilling et al., 2002).

One contemporary idea is that these dopaminergic neurons are not encoding reward per se but the difference between the *predicted* reward and *actual* reward (e.g., Schultz et al., 1997). After training to perform an action when presented with a light or tone cue, dopaminergic neurons in monkeys eventually respond to the conditioned cue itself rather than the subsequent reward (Schultz et al., 1992). If no subsequent reward appears, then their activity drops below baseline, indicating that a reward was expected (Figure 16.15). Some fMRI studies of decision-making in humans also suggest that activity in the ventral striatum is greater when a reward is better than expected, rather than when a reward is high per se (Hare et al., 2008). Self-reported lonely people show less activity in the ventral striatum when shown photos of social scenes (relative to non-lonely people), arguably because they predict them to be less rewarding (Cacioppo et al., 2009).

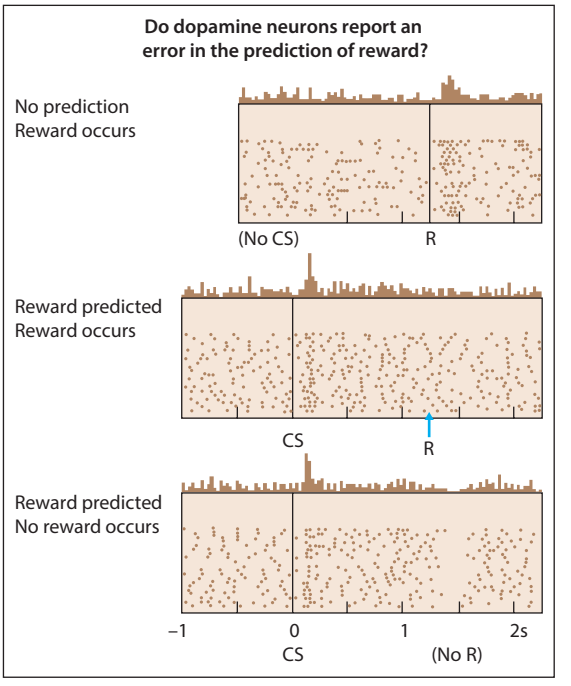


FIGURE 16.15: Single-cell recordings of dopamine neurons in the ventral striatum of monkeys show that the neuron responds when an unexpected reward of fruit juice is given (top), but if the reward is predicted by a cue (the conditioned stimulus), then the neuron responds to the cue and not the reward (middle). If an expected reward is omitted (bottom), the firing of the neuron falls below baseline. The results suggest that these neurons code the difference between the predicted reward and actual reward, rather than reward itself.

From Schultz et al. (1997). © 1997 American Association for the Advancement of Science. Reproduced with permission.

Evaluation

This section has outlined a set of regions that are critically involved in the processing of emotions. In social animals, such as humans, these emotional brain regions play a key role in evaluating and responding to social stimuli. For instance, the amygdala is implicated not only in evaluating whether a tone will lead to a shock but also in evaluating whether another person is afraid; the anterior cingulate responds not only to physical pain but also to social pain relating to separation and social exclusion; and the nucleus accumbens responds not only to basic rewards (food, sex) but also when we opt to cooperate with another person.

The different regions of the emotional brain serve different functions, and this is at odds with earlier theories of emotion (e.g., the Papez circuit and MacLean's "limbic brain"). Nor is it the case that different brain regions are highly specialized for only one emotion, although some relative specializations are observed. An emotion, such as fear, is likely to be represented in multiple different brain systems involved in learning (fear conditioning), internal and external expressions of fear, episodic and semantic memories of fear, and so on. This is broadly consistent with the notion

that emotions are constructed (i.e., built up from multiple parts). Whether emotions are solely constructed via experience or has some innate elements remains debated, as exemplified by the debate over whether (some) human facial expressions are innate.

READING FACES

The visual processing of faces has been considered previously (see Chapter 7). However, a face is far more than a visual object – it is also a social object, denoting a **conspecific**. A face conveys important information about another person's feeling states (e.g., their current emotion), their intentions (e.g., eye gaze provides some clues), their membership of social categories (e.g., race, gender), and perhaps even their dispositions (e.g., trustworthiness). This section first considers facial expressions followed by gaze detection and finally considers race.

KEY TERM

Conspecific
Other members of the same species.

Recognizing facial expressions

The two models of face processing already considered in some detail in Chapter 7 are the cognitive model of Bruce and Young (1986) and the neuroanatomical model of Haxby et al. (2000). Both models assume that extracting socially relevant information from faces (e.g., knowing they are happy) is largely separable from recognizing facial identity (i.e., knowing who the person is). However, the two models make different assumptions as to how this is done. In Bruce and Young's (1986) model there is a dedicated route for recognizing emotional expressions. This route is also assumed to be different from the mechanism needed for tasks such as lip-reading or gaze detection. By contrast, the model of Haxby et al. (2000) makes a broad division between time-invariant representations of a face (needed for facial identity and linked to the fusiform face area, FFA) and time-varying representations of a face. The latter is assumed to be needed *both* for recognizing expressions and for gaze processing and is linked to the superior temporal sulcus (STS). Both the fusiform face area and the superior temporal sulcus are assumed to be part of the "core system" of face processing (i.e., relatively specialized for faces in particular), but for expressions, this would additionally involve the "extended system" dealing with emotions (including the amygdala, insula and so on).

In support of the Haxby et al. (2000) model, it has been shown that dynamic faces activate the STS more than static faces during fMRI, and this pattern is not found for regions such as the FFA (Pitcher et al., 2011). Multivariate pattern analysis of fMRI signals in this region can also distinguish better than chance between the six "basic" facial expressions, together with neutral expressions (Said et al., 2010). A region of the left posterior STS has also been shown to respond, using fMRI multi-voxel pattern analysis, to the same expression whether presented in the face, voice, or body (Peelen et al.,

2010). This study also found that the medial prefrontal cortex had a similar profile. Collectively, the posterior STS and medial prefrontal cortex are typically linked to "mentalizing" (attributing mental states, such as emotions, to others). If so, then it suggests that other mechanisms, beyond a visual analysis of dynamic faces, are important in expression recognition. For instance, these regions might convert continuous variation in facial movements to discrete expressions (a form of categorical perception).

Other evidence suggests that regions beyond the STS – in the "extended system" of the Haxby et al. (2000) model – play an important role in expression recognition. As noted before, lesions of the amygdala and insula can disproportionately disrupt the ability to recognize certain facial expressions. This is not predicted by the Bruce and Young (1986) model, which has a single route for expression analysis. But there are some brain regions that, when lesioned, do disrupt facial expression recognition (across multiple emotions) more than identity recognition. This includes lesions in regions such as orbital and ventromedial frontal cortex (Heberlein et al., 2008; Hornak et al., 1996) or somatosensory cortex (Adolphs et al., 2000). These regions might be important because they are involved in a process called simulation. We may understand other people's emotional states by simulating them in our own brain regions for emotional experience (orbital and ventromedial frontal) and feelings in our own face (somatosensory).

Simulation theory consists of a collection of somewhat different theories based around a unifying idea – namely, that we come to understand others (their emotions, actions, mental states) by vicariously producing their current state on ourselves (Heberlein & Adolphs, 2007). With regard to emotions, the claim is that when we see someone smiling we also activate our own affective pathways for happiness. Moreover, we may activate the motor programs needed to make us smile (this may make us smile back, or it may prepare a smile response) and we may simulate what this might feel like in terms of its sensory consequences (e.g., muscle stretch and tactile sensations on the face). As such, one could possibly recognize emotions such as happiness, fear, and disgust not just in terms of their visual appearance but also in terms of the way they activate the sensorimotor programs of the perceiver. This notion, now widely accepted, was not predicted by either the Bruce and Young (1986) or Haxby et al. (2000) models.

KEY TERM

Simulation theory
The theory that we come to understand others (their emotions, actions, mental states) by vicariously producing their current state in ourselves.

There is evidence from electromyographic (EMG) studies that viewing a facial expression produces corresponding tiny changes in our own facial musculature, even if the face is viewed briefly so as to be unconsciously perceived (Dimberg et al., 2000). However, this does not necessarily imply that this is used to recognize expressions. To address this, Oberman et al. (2007) report that biting a pen lengthways uses many of the same muscles involved in smiling. They subsequently showed that the bite task selectively disrupts the recognition of happiness (Figure 16.16). TMS over the

KEY TERM

Capgras syndrome
People report that their acquaintances (spouse, family, friends, and so on) have been replaced by "body doubles."

somatosensory cortex impairs the recognition of facial expressions of emotion (Pitcher et al., 2008), as do injections of Botox in the face which cause muscular paralysis (Neal & Chartrand, 2011). This suggests that emotion recognition involves, at least in part, simulating facial expressions either indirectly (in the brain) or directly (on one's face).

The extent to which facial mimicry of expressions occurs depends on situational and motivational factors such as desire to affiliate, power dynamics, and so on (Fischer & Hess, 2017). Thus, simulation may be related more to social bonding than expression recognition. To account for this, some researchers have proposed multi-route models of facial expression recognition some of which involve sensorimotor simulation and some that do not (Wood et al., 2016).

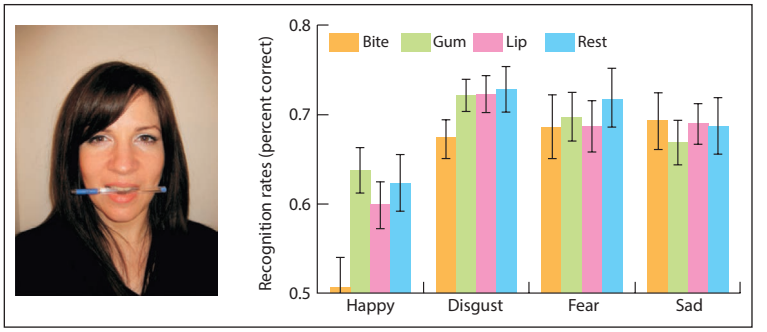


FIGURE 16.16: Placing a pen in the mouth horizontally and holding it with the teeth uses many of the same muscles as smiling. Performing this task can also disrupt recognition of facial expressions of happiness.

Data from Oberman et al. (2007).

"YOU LOOK LIKE MY WIFE, BUT YOU ARE AN IMPOSTER!"

In the **Capgras syndrome**, people report that their acquaintances (spouse, family, friends, and so on) have been replaced by "body doubles" (Capgras & Reboul-Lachaux, 1923; Ellis & Lewis, 2001). They will acknowledge that their husband/wife looks like their husband/wife. Indeed, they are able to pick out their husband/wife from a line-up while maintaining all along that he/she is an imposter. To account for this, Ellis and Young (1990) suggest that they can consciously recognize the person, but they lack an emotional response to them. As such, the person is

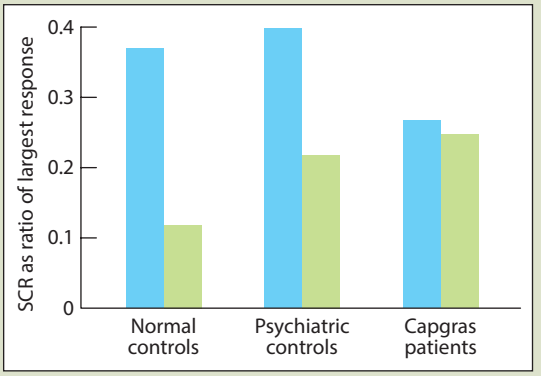


FIGURE 16.17: Most people produce a greater skin conductance response (SCR) to personally familiar faces, but patients with Capgras delusion do not.

Reprinted from Ellis and Lewis (2001). © 2001 with permission from Elsevier.

interpreted as an imposter. This explains why the people who are doubled are those closest to the patient, as these would be expected to produce the largest emotional reaction. This theory "makes the clear prediction that Capgras patients will not show the normally appropriate skin conductance responses to familiar faces" (Ellis & Young, 1990, p. 244). One general finding in the neurotypical population is that familiar faces, relative to unfamiliar faces, have an emotional component that reveals itself as a skin conductance response (Tranel et al., 1995). Subsequent research has confirmed that this skin conductance response to familiar people is disrupted in Capgras syndrome (Ellis et al., 1997), as shown in Figure 16.17.

Detecting and utilizing eye gaze information

The eye region distinguishes between many emotions, such as smiling or frowning. Moreover, making eye contact can be important for establishing one-to-one communication (dyadic communication), and the direction of gaze can be important for orienting attention to critical objects in the environment. Direct eye contact, in many primates, can be sufficient to initiate emotional behaviors. Macaques are more likely to show appeasement behaviors when shown a direct gaze relative to indirect or averted gazes (Perrett & Mistlin, 1990), and dominance struggles are often initiated with a mutual gaze and terminated when one animal averts its gaze (Chance, 1967).

Baron-Cohen argues that an "eye direction detector" is an innate and distinct component of human cognition (Baron-Cohen, 1995a). Babies are able to detect eye contact from birth, suggesting that it is not a learned response (Farroni et al., 2002). This ability is likely to be important for the development of social competence, because the eyes code relational properties between objects and agents (e.g., "mummy sees daddy," "mummy sees the box"). The superior temporal sulcus contains many cells that respond to eye direction (Perrett et al., 1985), and lesions in this area can impair the ability to detect gaze direction (Campbell et al., 1990). Functional imaging studies show that when participants are asked to make judgments about eye gaze (deciding whether the face is looking in the same direction as the last face) activity is increased in the superior temporal sulcus, but not the fusiform face area (Hoffman & Haxby, 2000). In contrast, when participants are asked to make judgments about face identity (deciding whether the face is the same as the last one presented) activity is increased in the fusiform face area, but not the superior temporal sulcus.

Children with autism can detect whether the eyes of another person are directed at them and, as such, do not appear to be impaired in the perception of gaze (Baron-Cohen et al., 1995). They do, however, have difficulties in using gaze information to

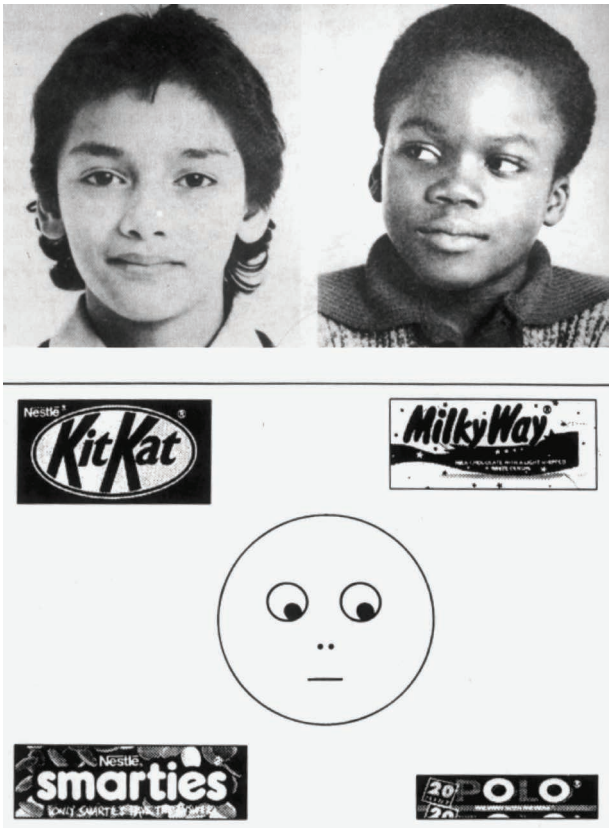


FIGURE 16.18: Children with autism are able to detect which person is looking at them (top) but are unable to infer behavior or desires from eye direction (bottom). For example, they are impaired when asked "which chocolate will Charlie take?" or "which one does Charlie want?"

Top photo from Baron-Cohen and Cross (1992). Reprinted with permission of Blackwell Publishing. Bottom panel from Baron-Cohen et al. (1995). Reproduced with permission from British Journal of Developmental Psychology. © British Psychological Society.

predict behavior or infer desire (Figure 16.18). In the four sweets task, a cartoon face of Charlie directs his gaze to one of the sweets. Children with autism are unable to decide: "which chocolate will Charlie take?" or "which one does Charlie want?" The difficulty in utilizing gaze information manifests itself as an absence of joint attention in the social interactions of autistic people (Sigman et al., 1986).

EVALUATION

Recognizing facial expressions depend on several mechanisms in the brain. Expressions may be recognized using regions of the brain specialized for emotional processing (including the amygdala and orbitofrontal cortex). However, sensorimotor simulation may also contribute to recognizing expressions. The superior temporal sulcus is important for recognizing eye gaze and facial/bodily movements, but it is presently unclear whether it is critically involved in expression recognition. The recognition of eye gaze provides important clues about the intentions of others and may interface with other regions involved in making mentalizing inferences.

PERCEIVING RACE IN FACES

The basic architecture of face processing should apply to all faces: a face is a face. However, race is such a socially salient category that basic visual mechanisms of face processing rapidly interface with other parts of the brain involved in emotional evaluations (e.g., amygdala) and the control of behavior (e.g., faster shooting of Black avatars by White participants; Mekawi & Bresin, 2015). This network is illustrated in the model of Kubota et al. (2012) shown in Figure 16.19.

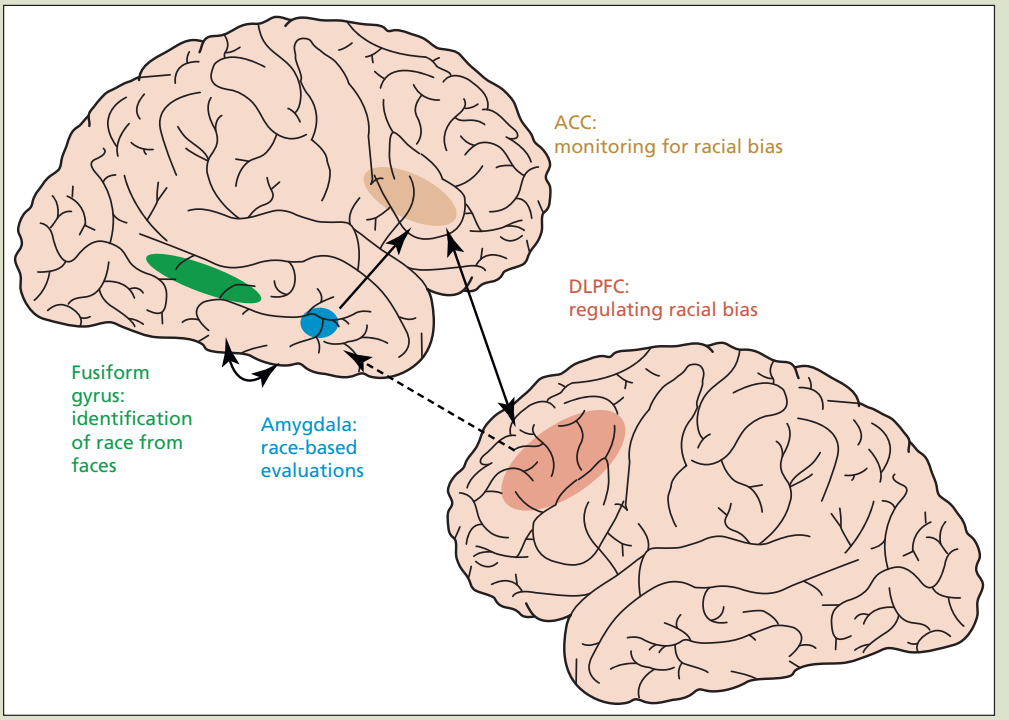


FIGURE 16.19: The neural processing of race is likely to begin in the fusiform gyrus, involved in face perception. Affective evaluations may be driven by the amygdala which itself may be regulated by regions such as the anterior cingulate cortex (ACC) and dorsolateral prefrontal cortex (DLPFC).

From Kubota et al. (2012). Reproduced with permission from Springer Nature

To some extent, racial differences in face perception could reflect differences in expertise. We are better at recognizing and remembering people from our own ethnic group, and this manifests itself as preferential activation in the FFA to one's ingroup by both Black and White participants (Golby et al., 2001). However, exactly the same effect is found if faces are arbitrarily assigned to teams regardless of race (Van Bavel et al., 2011). People belonging to "your team" elicit more FFA activity. This may reflect differences in processing strategy (a tendency to treat the ingroup as individuals and the outgroup as a category) rather than race or expertise.

White American participants tend to activate their amygdala more when viewing Black relative to White faces (Chekroud et al., 2014), and this can correlate with some reaction-time measures of racial bias (Phelps et al., 2000). One general interpretation of this finding is that it does reflect greater emotion-related processing but that this need not constitute prejudice in itself (Chekroud et al., 2014). For instance, the amygdala response may be driven by cultural stereotypes (e.g., of violence), which are not necessarily endorsed or acted upon by the perceiver (where the latter would constitute prejudice). The amygdala response also takes into account context beyond race itself. For instance, it does not show the same pattern when well-liked Black faces, such as Martin Luther King, are shown to White participants (Phelps et al., 2000).

UNDERSTANDING OTHER MINDS

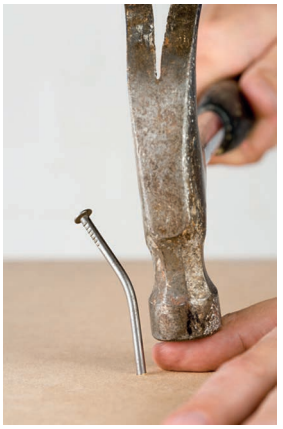
Facial expressions are only an outward manifestation of someone's unobservable mental state. The term *mental state* is used to refer to knowledge, beliefs, feelings, intentions, and desires. Being able to know the content of someone's mind is a good way of predicting their behavior. Humans, and other species, have evolved mechanisms for "mind reading." One mechanism that has already been touched upon is simulation. Simulation theories have in common the basic idea that we understand others through a self-centered approach. This may be achieved by a mirroring of states: for instance, seeing you afraid makes me afraid (by activating my fear-related circuits), and this enables me to infer your mental state. The most common version of simulation theory is linked to perception-action coupling and with the candidate neural mechanism being mirror neurons (Gallese, 2003; Gallese & Goldman, 1998). The other main explanation suggests that there is a mechanism for inferring and reasoning about the mental states of others that is commonly referred to as **theory of mind** (Dennett, 1978). One hallmark of theory of mind is that it enables the representation of different states of mind to one's own (e.g., "you think it is in the box, I know it is in the basket") – this is not straightforward for most simulation theories to explain. In some stronger accounts, it is assumed that there is a domain-specific module in the brain for theory of mind. The term mentalizing is used by some researchers instead of theory of mind to denote essentially the same thing, but without carrying the connotation that it may be a special mechanism. Although there are more nuanced theories, the debate between mirroring versus mentalizing offers a clear way of understanding this literature (Zaki & Ochsner, 2012).

KEY TERMS

Theory of mind
The ability to represent the mental states of others (e.g., their beliefs, desires, intentions).

Empathy
The ability to appreciate others' points of view and share their experiences.

FIGURE 16.20: Do you empathize with someone by simulating how you would feel in their situation? An image such as this one tends to activate parts of the brain involved in the physical perception of pain.



Empathy, mirroring, and simulation theory

Empathy refers, in the broadest sense, to an emotional reaction to another person's feelings (Figure 16.20). In experimental settings, empathy is often studied by presenting a stimulus relating to one person (e.g., an image or description of someone in distress) and measuring their response in various ways (brain activity, subjective report, bodily response). It is also possible to measure individual differences in empathy, that is, the tendency for different people to respond empathically, and this is most frequently done via questionnaire (Davis, 1980). From first principles, empathy could be related to either mirroring or mentalizing mechanisms or both. However, research on empathy typically differs from that done with theory of mind in that studies on theory of mind tend to directly probe knowledge of mental states (e.g., "what does Sally think?"), whereas studies on empathy tend not to.

Iacoboni (2009) has argued that the mirror system for action may be co-opted by other regions of the brain to support empathy.

Carr et al. (2003) examined a possible link between empathy and action perception/production using fMRI in humans. They showed participants emotional facial expressions under two conditions: observation versus deliberate imitation. They found increased activation for the imitation condition relative to observation in classical mirror-system areas such as the premotor cortex. In addition, they found increased activation in areas involved in emotion such as the amygdala and insula. Their claim was that imitation activates shared motor representations between self and other, but crucially, there is a second step in which this information is relayed to limbic areas via the insula. This action-to-emotion route was hypothesized to underpin empathy.

Simulation theories extend the notion of a mirror neuron (see Chapter 10) not only to action but also to sensation (such as pain and touch) and emotion. The term **mirror system** is used to convey the idea of neural circuits that disregard the distinction between self and other but need not necessarily imply action-coding mirror neurons. For example, the insula region is activated both when we are disgusted and when we look at someone else scrunching up their face in an expression of disgust (Phillips et al., 1997). Moreover, people who score higher on questionnaire measures of empathy show greater activation of their own disgust regions when watching other people being disgusted (Jabbi et al., 2007). This suggests that we may, in some literal sense, share the emotions of the people around us.

KEY TERM

Mirror systems
Neural circuits or regions that disregard the distinction between self and other.

Singer and colleagues (2004) investigated empathy for pain. The brain was scanned when anticipating and watching a loved one suffer a mild electric shock. There was an overlap between regions activated by expectancy of another person's pain and experiencing pain oneself, including the anterior cingulate cortex and the insula. In a follow-up to this study, participants in an fMRI scanner watched electric shocks delivered to people who were considered either good or bad on the basis of whether they had played fairly or unfairly in a game (Singer et al., 2006). The results are shown in Figure 16.21. While participants empathically activated their own pain regions when watching the "goodie" receive the electric shock, this response was attenuated when they saw the "baddie" receiving the shock. In fact, male participants often activated their ventral striatum (linked to better than expected rewards) when watching the baddie receive the shock – that is, the exact opposite of simulation theory. This brain activity correlated with their reported desire for revenge. This suggests that, although simulation may tend to operate automatically, it is not protected from our higher-order beliefs. Other research has shown that pain-related regions are activated differently when watching someone in pain depending on whether one takes a self-centered or other-centered perspective and depending on one's beliefs about whether the pain was necessary (Lamm et al., 2007). This suggests a significant amount of flexibility in mirroring that some simple versions of simulation theory would not predict.

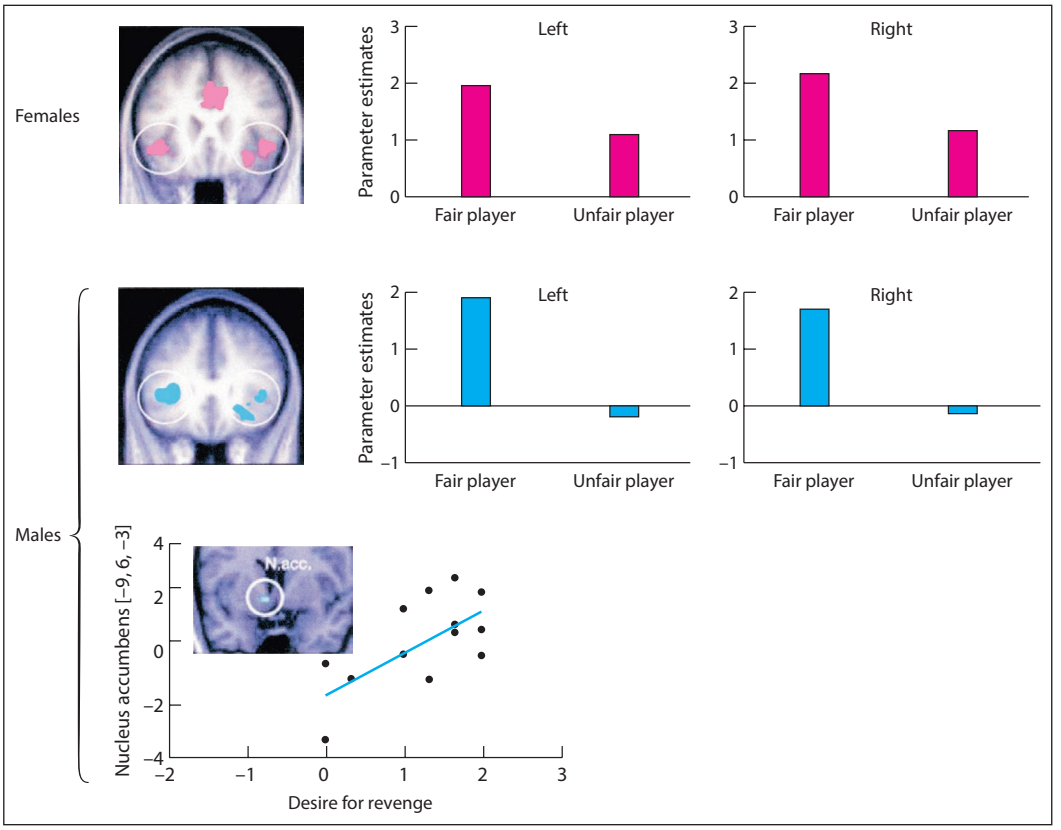


FIGURE 16.21: Females (pink) and males (blue) show reduced activity in brain regions that respond to pain when watching an unfair player receive a shock (shown here for the insula). In males, activity in the nucleus accumbens, measured while the unfair player received a shock, correlates with their self-reported desire for revenge.

From Singer et al. (2006). © 2006 Nature Publishing Group. Reproduced with permission from Springer Nature.

KEY TERM

Compassion
Non-shared feelings of support towards others (e.g., pity)

The fact that mirroring seems to occur in some contexts and not others implies that there are other mechanisms at play that regulate this aspect of empathy. Singer and Klimecki (2014) argue for a distinction between empathy and **compassion**, arguing that that these superficially similar concepts involve a shift in perspective. Mirroring involves a shared emotion between self and other, but compassion does not. Compassion can involve non-shared feelings: seeing someone suffering may evoke pity (promoting a desire to help) rather than shared suffering (which could provoke an avoidance response). Training people on compassion, by generating kind thoughts about other people (including people we are inclined to dislike), results in a shift in fMRI activity away from pain-related regions (insula, cingulate) to ventral striatum when observing distress (Klimecki et al., 2013). But training people to share the suffering of others only increased activity within the original pain network (Klimecki et al., 2014). Compassion training is an example of emotion regulation involving reappraisal: that

is, we simulate an alternative context in order to change how we feel (and, ultimately, how we behave). In this example, it results in prosocial behavior but reappraisals can also be used to engage in antisocial behavior, for example, by imagining that the other person's suffering is deserved. In both cases, it requires a mechanism to prevent mirroring which may involve a shift in perspective (possibly involving right temporoparietal junction) and executive functions (via lateral prefrontal cortex).

Mind-reading in autism

> He wandered about smiling, making stereotyped movements with his fingers, crossing them about in the air. He shook his head from side to side, whispering or humming the same three-note tune. He spun with great pleasure anything he could seize upon to spin . . . When taken into a room, he completely disregarded the people and instantly went for objects, preferably those that could be spun . . . He angrily shoved away the hand that was in his way or the foot that stepped on one of his blocks.

(This description of Donald, aged 5, was given by Leo Kanner [1943], who also coined the term "autism." The disorder was independently noted by Hans Asperger [1944], whose name now denotes a variant of autism.)

Autism has been formally defined as "persistent deficits in social communication and social interaction across multiple contexts" and "restricted, repetitive patterns of behavior, interests, or activities" (American Psychiatric Association, 2013, *Diagnostic and Statistical Manual*; DSM-V). It is a severe developmental condition that is evident before 3 years of age and lasts throughout life. There are a number of difficulties in diagnosing autism. First, it is defined according to behavior because no specific biological markers are known. Second, the profile and severity may be modified during the course of development. It can be influenced by external factors (e.g., education, temperament) and may be accompanied by other disorders (e.g., attention deficit and hyperactivity disorder, psychiatric disorders). As such, autism is now viewed as a spectrum of conditions spanning all degrees of severity. It affects 1.2 percent of the childhood population and is three times as common in males (Baird et al., 2006). **Asperger syndrome** falls within this spectrum, and used to be considered a special subgroup, but is now regarded as the normal to high end of the spectrum. Learning disability, defined as an IQ lower than 70, is present in around half of all cases of autism (Baird et al., 2006).

Much of the behavioral data have been obtained from high-functioning individuals in an attempt to isolate a specific core of deficits. One candidate deficit is the ability to represent mental states (Baron-Cohen, 1995b; Fodor, 1992). The first empirical evidence in favor of this hypothesis came with the development of a test of **false belief**, devised by Wimmer and Perner (1983) and tested on

ONLINE RESOURCES

Scan the QR code or visit the Instructor & Student Resources website (routledgelearning.com/wardcognitiveneuroscience) for selected videos including TED talks by Rebecca Saxe, Uta Frith on "Autism: The First Fifty Years" and Tania Singer on the neuroscience of compassion.

KEY TERMS

Autism
The presence of markedly abnormal or impaired development in social interaction and communication and a markedly restricted repertoire of activities and interests.

Asperger syndrome
A variant of autism linked to normal to high intelligence.

False belief
A belief that differs from one's own belief and that differs from the true state of the world.

autistic children by Baron-Cohen et al. (1985). In the version used with autistic children, the *Sally–Anne task* shown in Figure 16.22, the child is introduced to two characters, Sally and Anne. Sally puts a marble in a basket so that Anne can see. Anne then leaves the room, and Sally moves the marble to a box. When Anne enters the room, the child is asked: "Where will Anne look for the marble?" or "Where does Anne think the marble is?" Children with autism reply, "In the box," whereas normal children (aged 4+) and learning-disabled controls reply, "In the basket." The erroneous reply is not due to a failure of memory, because the children can remember the initial location. It is as if they fail to understand that Anne has a belief that differs from physical reality – that is, a failure to represent mental states. This has also been called "mind-blindness" (Baron-Cohen, 1995b). Adults with autism often pass false belief tasks but, nevertheless, show differences in eye-movements during these tasks (Senju et al., 2009), suggesting that these tasks remain challenging or are perhaps solved in different ways.

A number of other studies have pointed to selective difficulties in mentalizing compared with carefully controlled conditions. For example, people with autism can understand false photographs, but not false beliefs (Leekam & Perner, 1991); can sequence behavioral pictures, but not mentalistic pictures (Baron-Cohen et al., 1986); are good at sabotage, but not deception (Sodian & Frith, 1992); and tend to use desire and emotion words, but not belief and idea words (Tager-Flusberg, 1992). In all instances, the performance of people with autism is compared with mental-age controls to

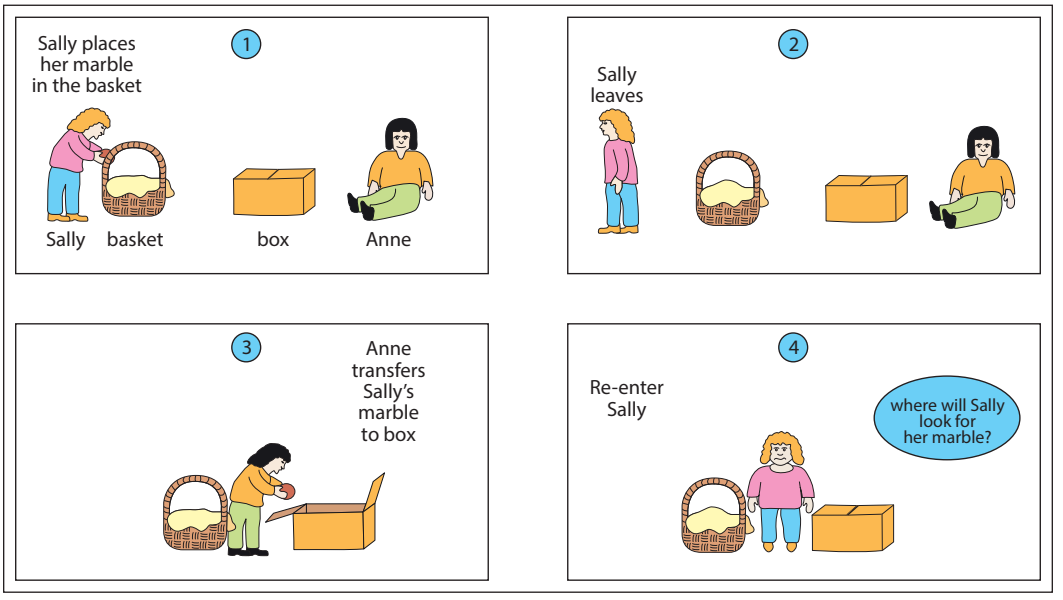


FIGURE 16.22: The Sally–Anne task requires an understanding of "false belief" and tends to be failed by children with autism.

Adapted from Wimmer and Perner (1983).

establish that the effects are related to autism and not general level of functioning.

There are several theories that attempt to explain the social deficits in autism without recourse to a deficit in mentalizing or without postulating the absence of a specialized theory of mind mechanism. An earlier suggestion is that the primary deficit in autism is one of executive functioning (e.g., Russell, 1997). For example, on false belief tasks the incorrect answer might be chosen because of a failure to suppress the strongly activated "physical reality" alternative. The **broken-mirror theory** of autism argues that the social difficulties linked to autism are a consequence of mirror-system dysfunction (e.g., Ramachandran & Oberman, 2006; Rizzolatti & Fabbri-Destro, 2010).

Several lines of evidence have been taken to support the broken mirror theory. Hadjikhani et al. (2006) found, using structural MRI, that autistic individuals had reduced gray matter in several regions linked to the mirror system, including the inferior frontal gyrus (Broca's region). Dapretto et al. (2006) conducted an fMRI study in which autistic children and matched controls either observed or imitated emotional expressions. The imitation condition produced less activity in the inferior frontal gyrus of the autistic children relative to controls, and this was correlated with symptom severity. Oberman et al. (2005) used EEG to record mu waves over the motor cortex of high-functioning autistic children and controls (see Figure 16.23). **Mu oscillations** occur at a particular frequency (8–13 Hz) and are greatest when participants are doing nothing. However, when they perform an action there is a decrease in the number of mu waves, a phenomenon termed mu suppression. Importantly, in typical controls mu suppression also occurs when people *observe* actions, and as such, it has been regarded by some as a measure of mirror-system activity (Pineda, 2005). Oberman et al. (2005) found that the autistic children failed to show as much mu suppression as controls during action observation (watching someone else make a pincer movement) but did so in the control condition of action execution (they themselves make a pincer movement). Finally, watching someone perform an action increases one's own motor excitability, measured as a motor-evoked potential (MEP) on the body, when TMS is applied to the motor cortex. However, this effect is reduced in autistic people, even though their motor cortex behaves normally in other contexts (Theoret et al., 2005).

In sum, there is convincing evidence for mirror-system dysfunction in autism. What is less clear is whether this represents the core deficit and whether it is sufficient to account for the full range of social impairments (including false belief). First, tasks involving imitation and empathy do not rely solely on these kinds of simulation mechanisms but also involve deliberate perspective taking, knowledge of social rules and cognitive control (Dinstein et al., 2008; Southgate & Hamilton, 2008). Second, a core deficit elsewhere (e.g., in representing mental states) could nevertheless affect the functioning of the mirror system, and perhaps even lead

KEY TERMS

Broken-mirror theory
An account of autism in which the social difficulties are considered as a consequence of mirror-system dysfunction.

Mu oscillations
EEG oscillations at 8–13 Hz over the sensorimotor cortex that are greatest when participants are at rest.

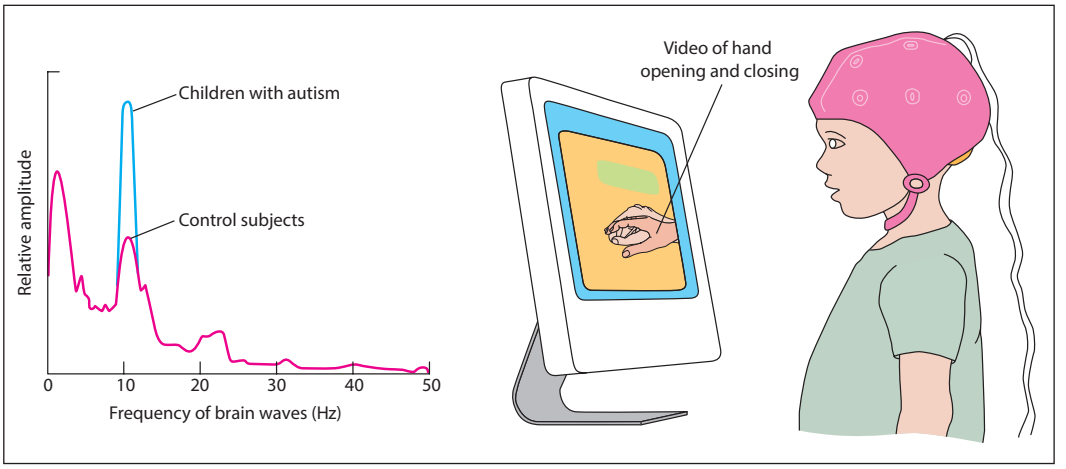


FIGURE 16.23: Mu waves are EEG oscillations in the 8–13 Hz range that are reduced both when performing an action and when watching someone else perform an action (relative to rest). As such, they may provide a neural signature for human mirror neurons. Autistic children show less mu suppression when watching others perform a hand action, which provides evidence in support of broken-mirror theory.

From Ramachandran and Oberman (2006). Reproduced with permission from Lucy Reading-Ikkanda for Scientific American Magazine.

to structural changes within that system. Heyes (2010) argues that the properties of mirror neurons may be learned as a result of social interactions. So impoverished social interactions may cause mirror-system dysfunction, as well as vice versa.

Neural basis of theory of mind

Evidence for the neural basis of theory of mind has come from two main sources: functional imaging studies of normal participants and behavioral studies of patients with brain lesions. Numerous tasks have been used, including directly inferring mental states from stories (e.g., Fletcher et al., 1995), from cartoons (Gallagher et al., 2000) or when interacting with another person (McCabe et al., 2001). A review and meta-analysis of the functional imaging literature was provided by Frith and Frith (2003), who identified three key regions involved in mentalizing (see Figure 16.24). Subsequent reviews reveal a similar general pattern but with some important differences depending on the nature of the theory of mind test that is used (Schurz et al., 2014).

Temporal poles

This region is normally activated in tasks of language and semantic memory. Frith and Frith (2003) suggest that this region is involved with generating schemas that specify the current social or emotional context, as well as in semantics more generally. Zahn et al. (2007) report an fMRI study suggesting that this region responds to

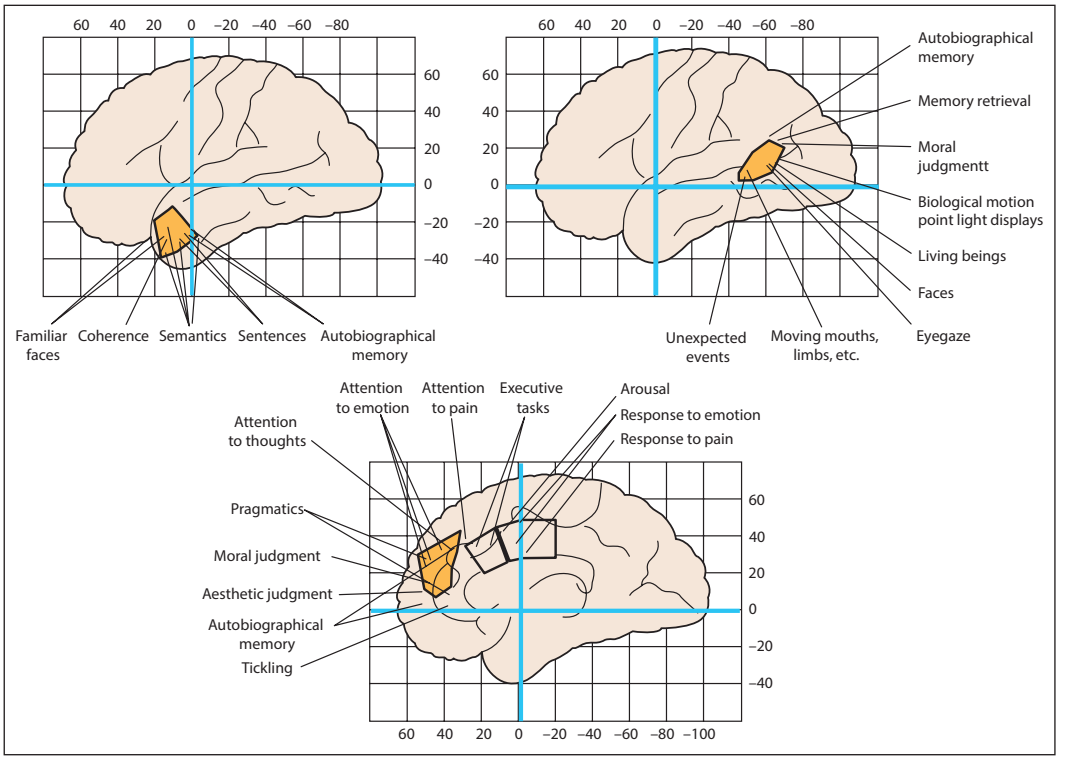


FIGURE 16.24: Functional imaging and lesion studies implicate three important regions in theory of mind (shaded): temporal poles (top left), temporoparietal junction (top right), and the medial frontal lobes including a portion of the anterior cingulate (bottom; note the anterior cingulate is drawn as divided into functionally separate areas).

From Frith and Frith (2003). Used with permission of The Royal Society. Permission conveyed through Copyright Clearance Center, Inc.

comparisons between social concepts (e.g., brave–honorable) more than matched non-social concepts (e.g., nutritious–useful). Not all the tests of mentalizing that activated this region involved linguistic stimuli. For example, one study used triangles that appeared to interact by, say, chasing or encouraging each other (Castelli et al., 2000).

Medial prefrontal cortex

Functional imaging studies reliably show that this region responds more to thinking about people than thinking about other entities such as computers or dogs (e.g., Mitchell et al., 2002, 2005) and thinking about the *minds* of people than thinking about their other attributes such as their physical characteristics (Mitchell et al., 2005). Some studies of patients with frontal lobe damage have suggested that the medial regions are necessary for theory of mind (Roca et al., 2011). This region also seems to be implicated in the pragmatics of language such as irony ("Peter is well read.

He has even heard of Shakespeare") and metaphor ("your room is a pigsty"; Bottini et al., 1994). Interestingly, people with autism have difficulties with this aspect of language (Happé, 1995). In such instances, the speaker's *intention* must be derived from the ambiguous surface properties of the words (e.g., the room is not literally a pigsty). Functional imaging suggests that this region is involved both in theory of mind and in establishing the pragmatic coherence between ideas/sentences, including those that do not involve mentalizing (Ferstl & von Cramon, 2002). The region is part of the default mode network which is characterized by responding more to rest than then presence of task (Raichle et al., 2001), and this is consistent with the region being involved for some aspect of inner thought (given that rest is rarely the absence of any cognition).

Krueger et al. (2009) argue that the function of this region is to bind together different kinds of information (actions, agents, goals, objects, beliefs) to create what they term a "social event." They note that within this region some subregions respond more when participants make judgments about themselves and also judgments about others who are considered to be similar to themselves. This suggests that this region is not attributing mental states per se but is considering the self in relation to others. The notion of creating internal social events could also explain some of the findings of the role of this region in linking ideas in story comprehension (Ferstl & von Cramon, 2002).

Temporoparietal junction (TPJ)

This region tends to be not only activated in tests of mentalizing but also in studies of the perception of biological motion, eye gaze, moving mouths and living things in general. A meta-analysis of fMRI data (neurotypical participants) on a wide range of tasks showed that whilst activity in the TPJ is found across diverse tasks, a more anterior region tends to be activated when using observable agents (e.g., inferring mental states from faces) and a more posterior region for non-observed agents (e.g., verbal false belief tasks) (Schurz et al., 2014). Patients with lesions in the TPJ region fail theory of mind tasks that can't be accounted for by difficulties in body perception (Samson et al., 2004). Saxe and Kanwisher (2003) found activity in this region, on the right, when comparing false belief tasks (requiring mentalizing) with false photograph tasks (not requiring mentalizing but entailing a conflict with reality). The result was also found when the false photograph involved people and actions, consistent with a role in mentalizing beyond any role in action/person perception. Saxe and Powell (2006) have shown that this region responds to attribution of contentful mental states (such as thoughts and beliefs) rather than subjective states (such as hunger or tiredness). This suggests that it may have a role over and above "thinking about others." Saxe and Powell (2006) claim this region is specific to thinking about mental states.

Other accounts propose more general functions to the TPJ that are relevant to theory-of-mind but without assuming it represents mental states as such. It may serve a general functioning of orienting of attention to a stimulus (Corbetta & Shulman, 2002; Mitchell, 2008) that, in social terms, may include orienting attention to other people and away from the self (Spengler et al., 2009).

Evaluation

Performance on tasks of theory of mind typically requires the use of several nonspecialized (i.e., domain general) processes, including language processing, executive functions, and action perception. The controversy lies in whether these mechanisms are the *only* ones that are needed to account for theory of mind (in some forms of simulation theory) or whether there is additionally the need for a specialized (i.e., domain-specific) mechanism that is specific to representing the mental states of others. Functional imaging and brain-lesion studies highlight the importance of several key regions in theory of mind, but the extent to which these regions are specific to theory of mind is controversial.

SUMMARY AND KEY POINTS OF THE CHAPTER

- Contemporary models of emotion differ with respect to whether there are a finite number of discrete emotions or whether there is a continuous range of emotional processes but with categories of emotion being constructed through interactions with non-affective processes (e.g., appraisal, language).
- Different regions of the "emotional brain" have different functions, although these functions do not precisely map onto discrete categories of emotion (such as fear, happiness, etc.). The amygdala has a key role in emotional learning and memory (e.g., fear conditioning); the insula and anterior cingulate have key roles in bodily related aspects of emotion experience; the orbitofrontal cortex is crucial for the appraisal and control of social and emotional stimuli; and the ventral striatum has a key role in reward prediction.
- The functions of the emotional brain described previously operate in both the social realm (e.g., when the stimuli consist of conspecifics) and the non-social realm.
- Recognizing facial expressions, processing eye gaze and recognizing facial identity depend on different neural mechanisms. The superior temporal sulcus

is particularly important for gaze detection, whereas recognizing expressions depends, at least in part, on simulating the affective and sensorimotor components of that expression.
- Mirroring (and simulation theory) is an important aspect of explaining empathy, but there is more to empathy than this. Empathy is modulated by social knowledge of others and may also require a mentalizing component.
- People with autism may lack a theory of mind mechanism, but impaired theory of mind alone cannot explain the full pattern of strengths and weaknesses in autism. It is unclear whether theory of mind is the core deficit in autism or whether a defective mirror system is the core deficit.
- Thinking about the mental states of others involves a core network of regions (including the temporoparietal junction and medial prefrontal cortex) that differ from those involved in executive functions more generally, or involved in emotional evaluation or person perception.

EXAMPLE ESSAY QUESTIONS

- Are there discrete categories of different emotions?
- Contrast the different roles of the amygdala and orbitofrontal cortex in emotion processing.
- Can autism be explained as "mind-blindness"?
- To what extent can empathy and theory of mind be explained by a process of simulation?
- To what extent are recognizing facial identity, expression recognition, and gaze recognition served by different mechanisms?
- What is the role of mirror systems in social cognition?

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