JAMIE WARD

The Student's Guide to Cognitive Neuroscience

FOURTH EDITION

A **Psychology Press** Book

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ROUTLEDGE

The Student's Guide to Cognitive Neuroscience

Reflecting recent changes in the way cognition and the brain are studied, this thoroughly updated fourth 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.

New to this edition:

- Increased focus on the impact of genetics on cognition
- New coverage of the cutting-edge field of connectomics
- Coverage of the latest research tools including tES and fNIRS and new methodologies such as multi-voxel pattern analysis in fMRI research
- Additional content is also included on network versus modular approaches, brain mechanisms of hand–eye coordination, neurobiological models of speech perception and production and recent models of anterior cingulate function.

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.

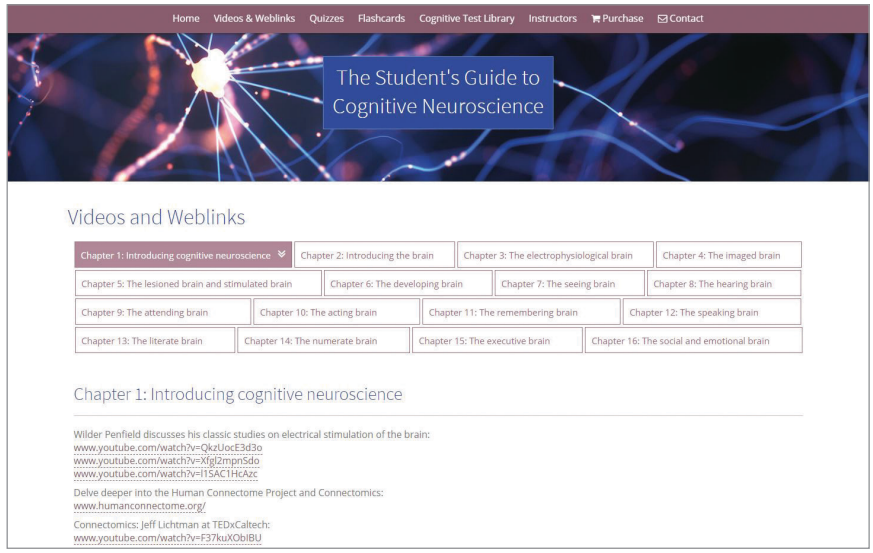
This textbook is supported by an extensive companion website for students and instructors, including lectures by leading researchers, links to key studies and interviews, interactive multiple-choice questions and flashcards of key terms.

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

To find additional tools to master the concepts and terminology covered in *The Student's Guide to Cognitive Neuroscience*, visit the companion website for the fourth edition, available at:

www.routledge.com/cw/ward



What you will find on this website:

For students:

- Videos and links to interviews, lectures, documentaries, and studies
- Simulations of key experiments
- Interactive multiple-choice quizzes for each chapter
- Flashcards to test your knowledge of key terms.

For instructors:

- Lecture guides
- Downloadable PowerPoint teaching slides
- Additional quiz questions and answers.

THE STUDENT'S GUIDE TO COGNITIVE NEUROSCIENCE

Fourth Edition

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Preface to the fourth 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 newer methodologies. I suspect that students who are new to the field will approach the topic with open-mindedness rather than skepticism, but I hope that they will nevertheless be able to gain something from this debate.

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. This fourth edition has been updated to include the latest research tools (such as tES, transcranial electrical stimulation) and the latest research methodology (such as multi-voxel pattern analysis, MVPA, in fMRI research).

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 fourth edition represents a substantial update. The order of the chapters has been changed to bring development much earlier on (as it deals with general issues relating to brain structure and function). These chapters were also extensively updated to take into account the rapid changes in this field, notably the links with genetic methods and connectomics. Vision and hearing are now consecutive chapters (Chapters 7 and 8), which link well to the following chapters on attention and action.

The following topics have either been added for the first time or extensively updated: network versus modular approaches (Chapter 1), magnetoencephalography (MEG) (Chapter 3), functional near-infrared spectroscopy (fNIRS) (Chapter 4), visual imagery (Chapter 7), parietal lobe mechanisms of sensorimotor transformation (Chapter 10), recent neurobiological models of speech perception and production (Chapter 12), developmental dyslexia (Chapter 13) and the neuroscience of racial biases (Chapter 16).

In addition, we have created a demonstration library of cognitive tests (www.testable.org/ward) with thanks to Constantin Rezlescu. Within the textbook, we provide more guidance to web resources via new feature boxes in the text, as well as via our dedicated webpage (www.routledge.com/cw/ward).

Jamie Ward
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Brighton, UK, March 2019

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 theatre. 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.

This book tells the emerging story of how mental processes such as thoughts, memories and perceptions are organized and implemented by the

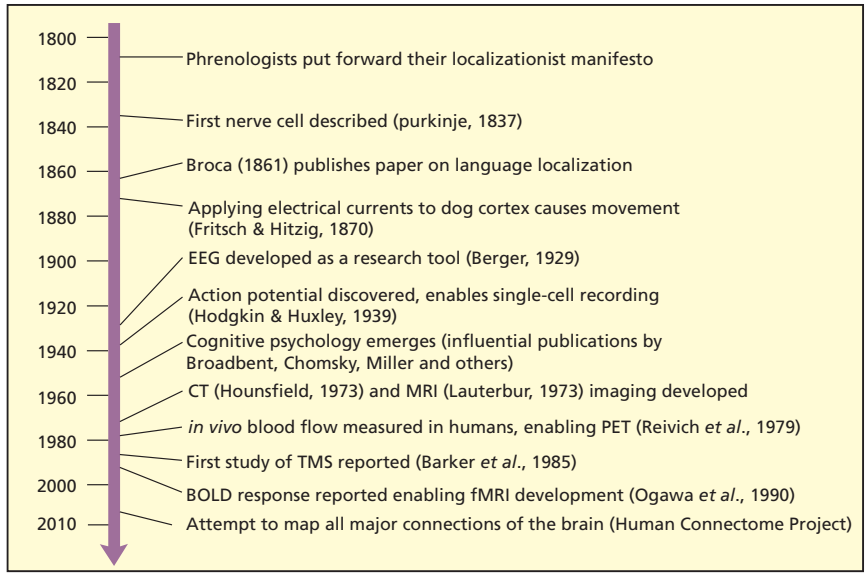

FIGURE 1.1: A timeline for the development of methods and findings relevant to cognitive neuroscience, from phrenology to present day.

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ONLINE RESOURCES

To discover more about Wilder Penfield and his pioneering research, watch the videos found on the companion website (www.routledge.com/cw/ward).

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.

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

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

KEY TERMS

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.

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.

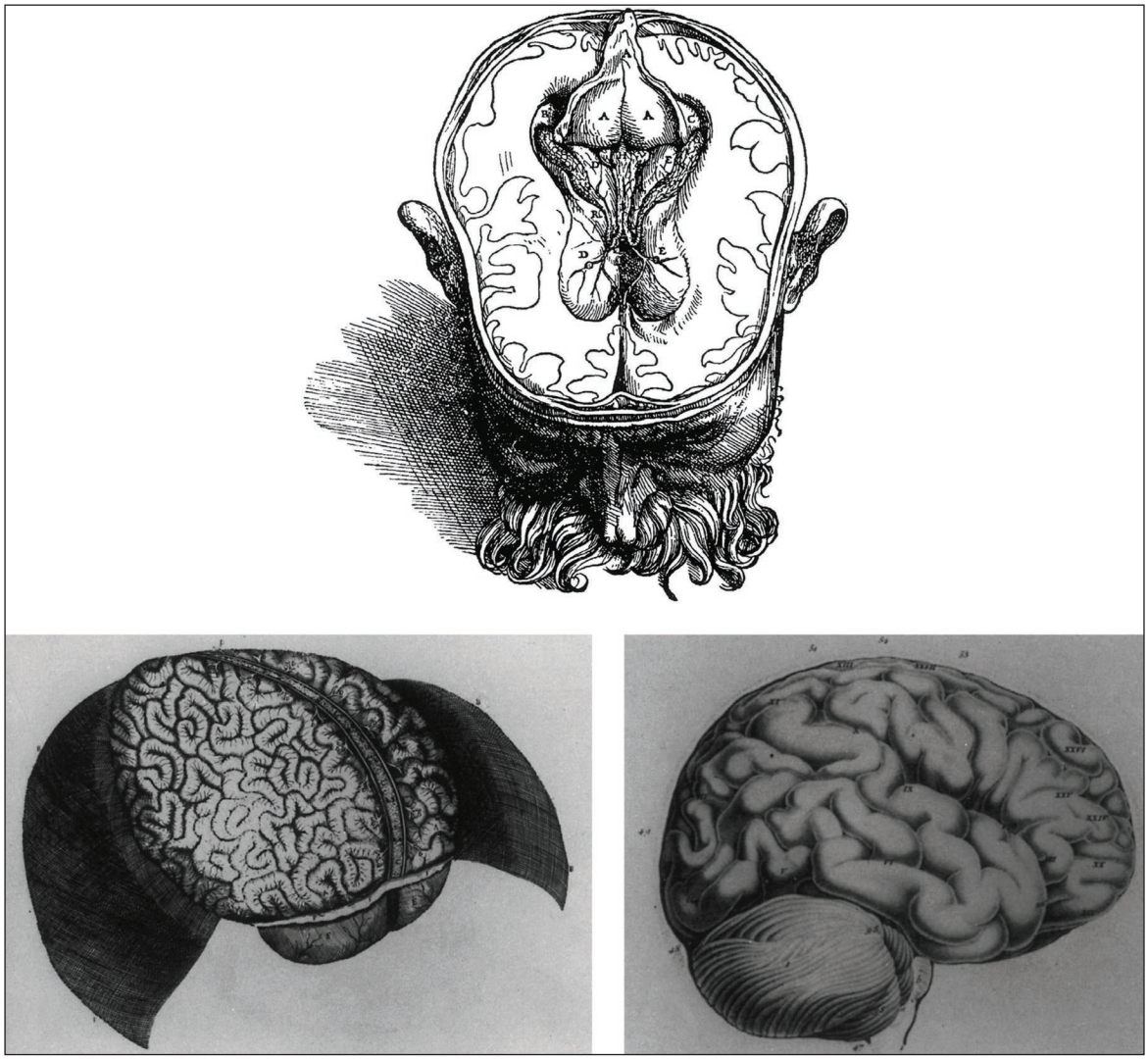

FIGURE 1.2: Drawings of the brain from Vesalius (1543) (top), de Viessens (1685) (bottom left) and Gall and Spurzheim (1810) (bottom right). Note how the earlier two drawings emphasized the ventricles and/or misrepresented the cortical surface.

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 co-workers 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.

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.

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 relatively 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 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

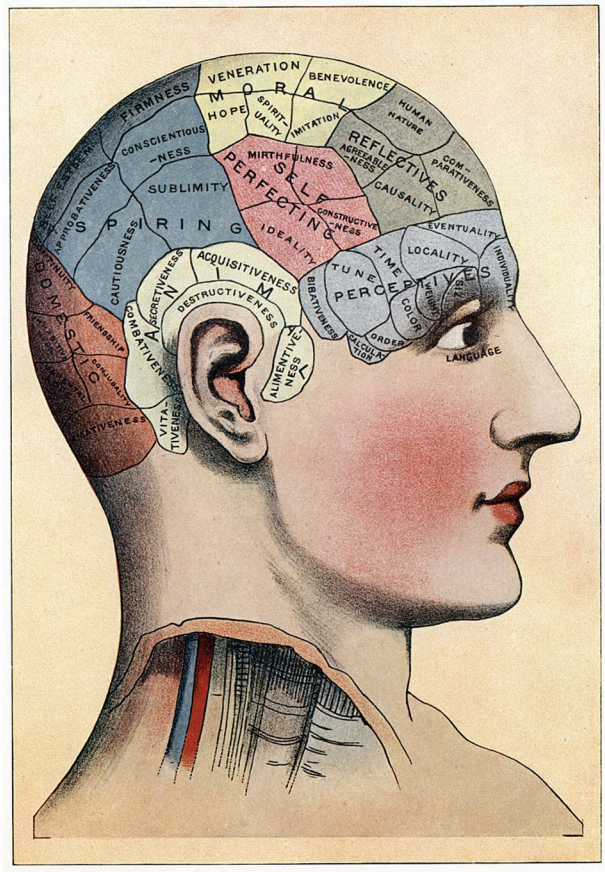

FIGURE 1.3: The phrenologist's head was used to represent the hypothetical functions of different regions of the brain.

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.

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

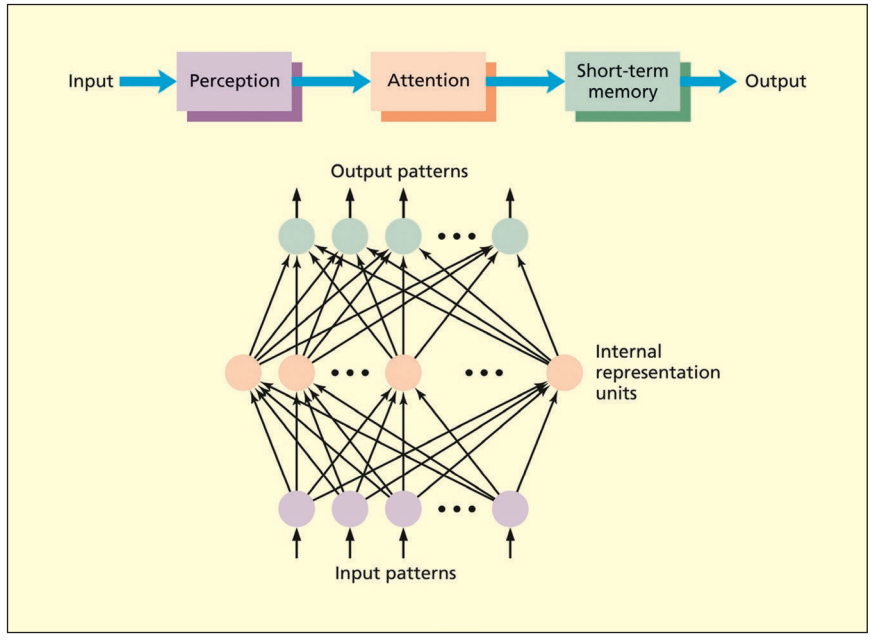

FIGURE 1.4: Examples of box-and-arrow and connectionist models of cognition. Both represent ways of describing cognitive processes that need not make direct reference to the brain.

could understand the series of steps performed by a computer program, and without reference to the brain.

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 of information processed is non-specific (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).

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

KEY TERMS

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).

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).

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

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.

KEY TERM

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

The birth of cognitive neuroscience

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

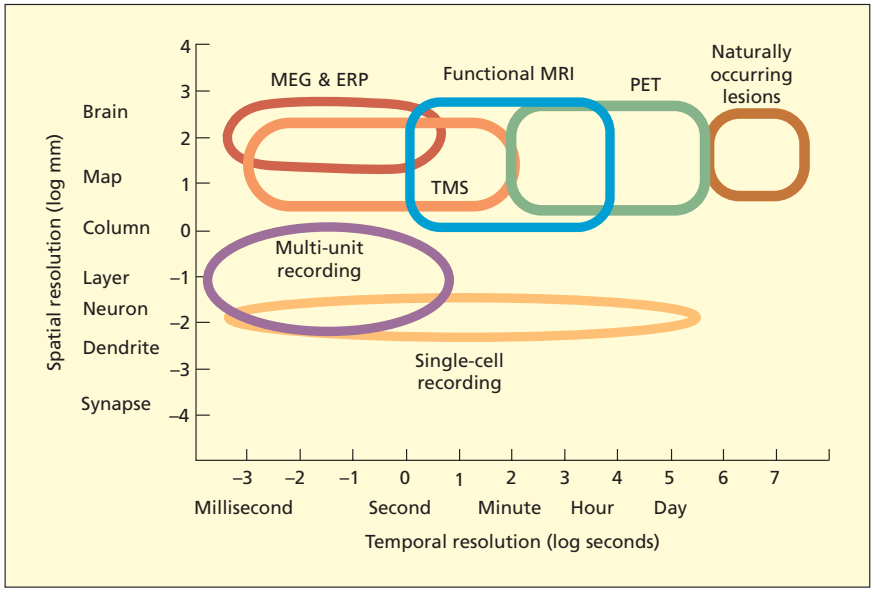

FIGURE 1.5: The methods of cognitive neuroscience can be categorized according to their spatial and temporal resolution.

Adapted from Churchland and Sejnowski, 1988.

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.

The methods of cognitive neuroscience can be placed on a number of dimensions (see Figure 1.5):

- 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.

KEY TERM

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

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

KEY TERM

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

- 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 *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 non-human animals.

DOES COGNITIVE PSYCHOLOGY NEED THE BRAIN?

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.

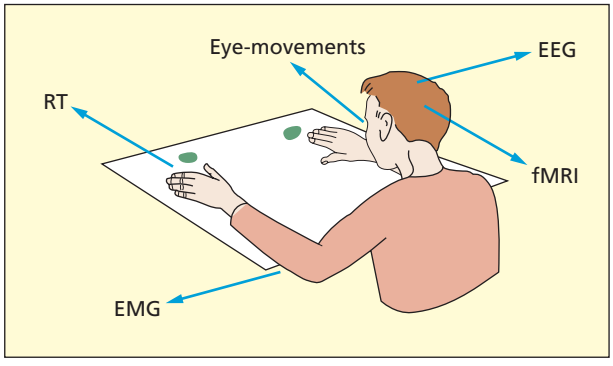

FIGURE 1.6: One could take many different measures in a forced-choice response task: behavioral (reaction time [RT], errors, eye-movements) or biological (electromyographic [EMG], BOLD response in fMRI or electrical activity in EEG). All measures could potentially be used to inform cognitive theory.

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

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 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 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

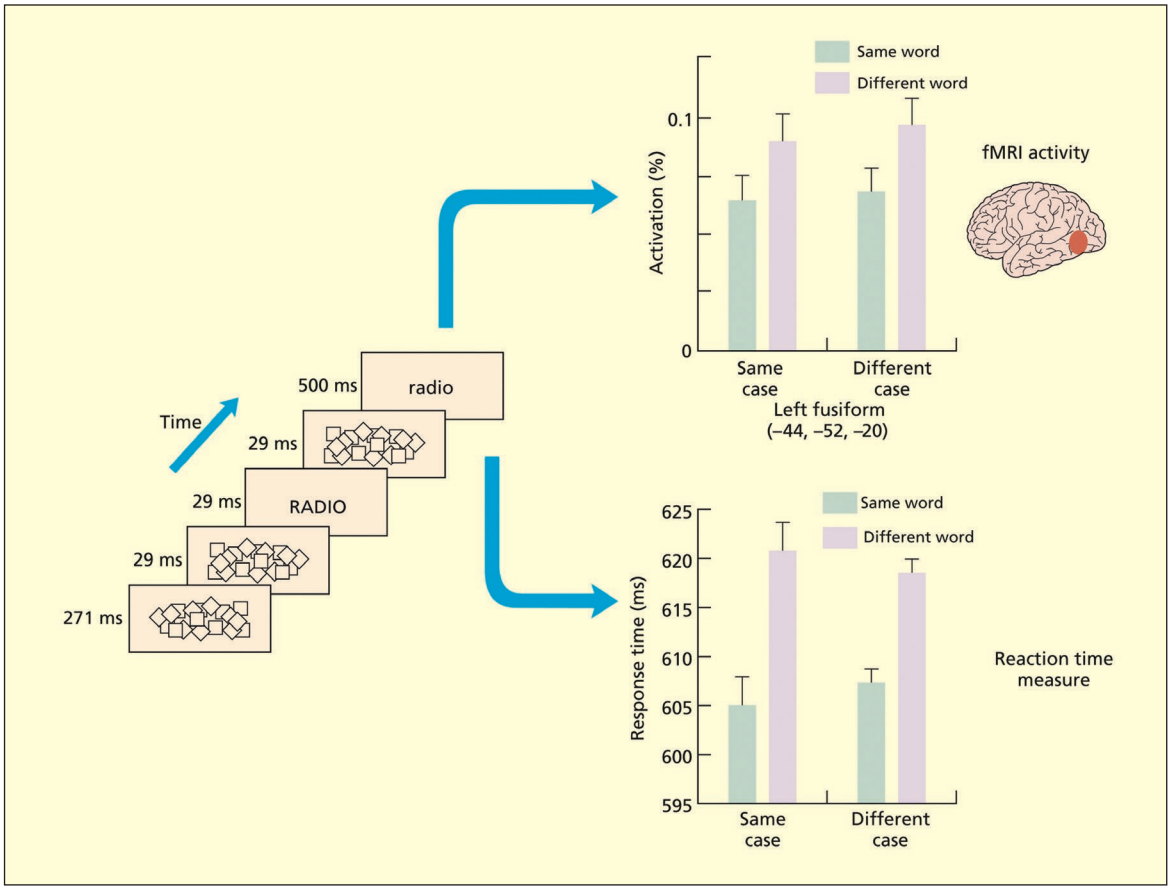

FIGURE 1.7: Both reaction times and fMRI activation in the left fusiform region demonstrate more efficient processing of words if they are preceded by subliminal presentation of the same word, irrespective of case. Adapted from Dehaene *et al*., 2001.

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 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. 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

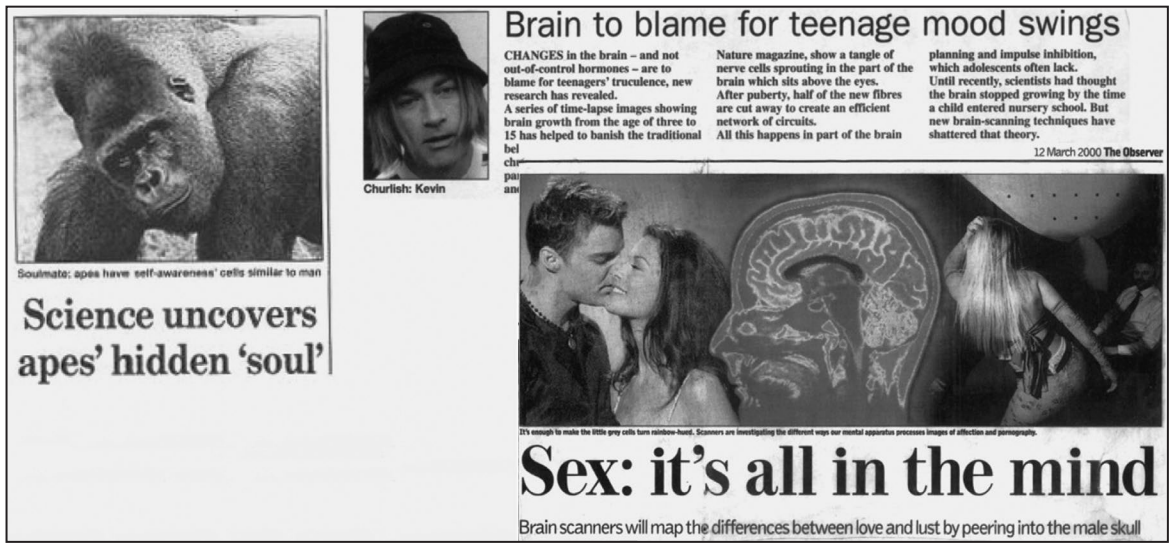

FIGURE 1.8: The media loves to simplify the findings of cognitive neuroscience. Many newspaper stories appear to regard it as counterintuitive that sex, pain and mood would be products of the brain.

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

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.

FROM MODULES TO NETWORKS

What does the future of cognitive neuroscience look like? Although nobody knows for sure, much current research is centered on understanding the mind and brain as a network. 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, i.e., millimeter, scale (rather

KEY TERM

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

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 companion website at www.routledge.com/cw/ward.

KEY TERM

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

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. 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 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).

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.

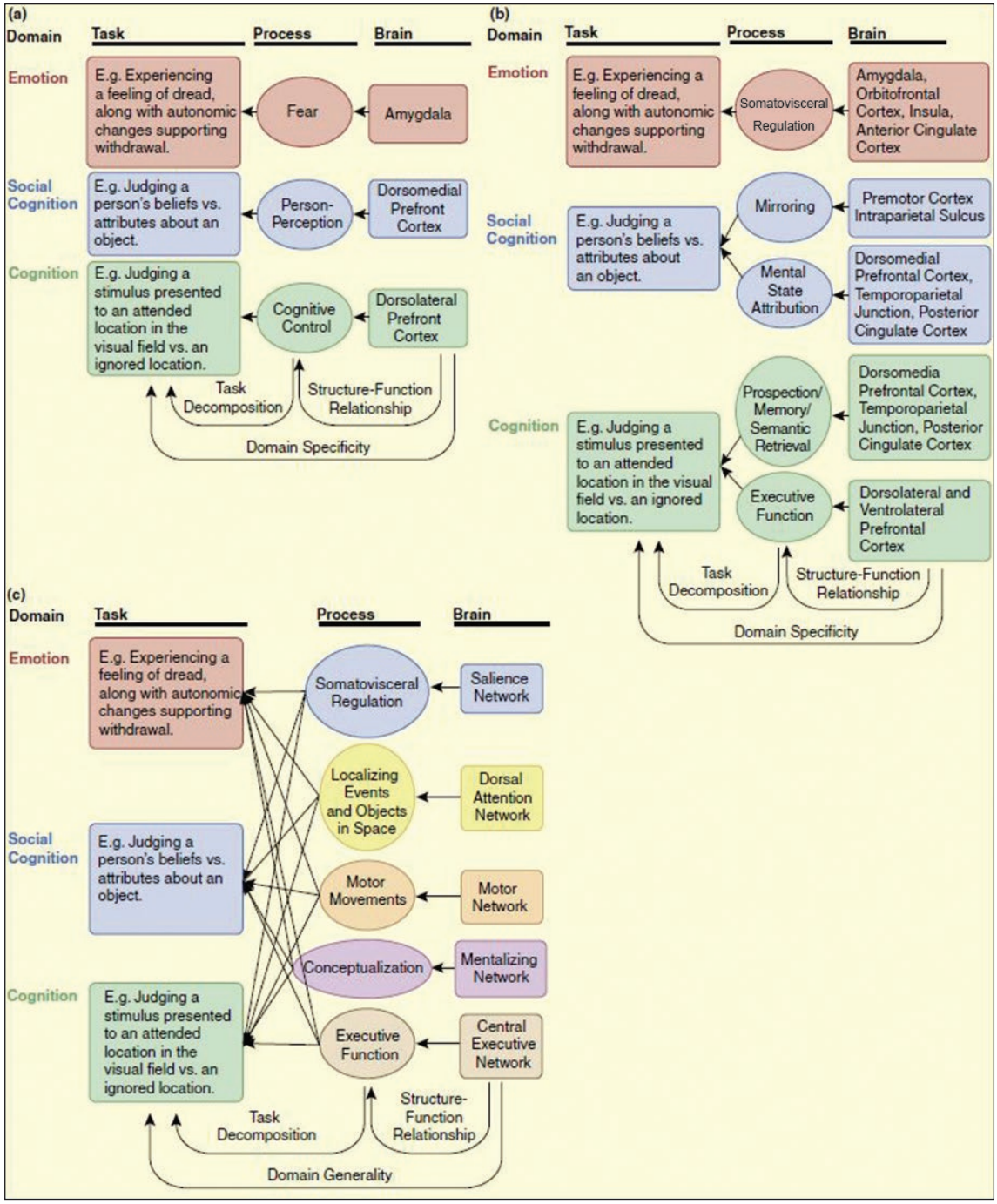

FIGURE 1.9: Three different ways in which different brain structures might be mapped to different functions (tasks and processes). In (a) there is a one-to-one association between brain structure and function whereas in both (b) and (c) a network of regions may make different contributions to a given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

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) 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 & Hamann, 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.

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?

ONLINE RESOURCES

Visit the companion website at www.routledge.com/cw/ward for:

- References to key papers and readings
- Video interviews on key topics with leading neuroscientists Wilder Penfield and Michael Gazzaniga, and philosopher Ned Block
- Multiple-choice questions and interactive flashcards to test your knowledge
- Downloadable glossary

RECOMMENDED FURTHER READING

- Henson, R. (2005). What can functional neuroimaging tell the experimental psychologist? *Quarterly Journal of Experimental Psychology*, 58A, 193–233. An excellent summary of the role of functional imaging in psychology and a rebuttal of common criticisms. This debate can also be followed in a series of articles in *Cortex* (2006, 42, 387–427).
- Shallice, T., & Cooper, R. P. (2011). *The organisation of mind*. Oxford, UK: Oxford University Press. The chapters on "conceptual foundations" deal with many of the issues touched on in the present chapter in more detail.
- Uttal, W. R. (2001). *The new phrenology: The limits of localizing cognitive processes in the brain*. Cambridge, MA: MIT Press. An interesting overview of the methods and limitations of cognitive neuroscience.
- Wickens, A. P. (2015). *A history of the brain: How we have come to understand the most complex object in the universe*. New York: Psychology Press. A good place to start for the history of 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. They consist of three components: a **cell body** (or soma), **dendrites** and an **axon**, as shown in Figure 2.1. Although neurons have the same basic structure and function, it is important to note that there are some significant differences between different types of neurons in terms of the spatial arrangements of the dendrites and axon.

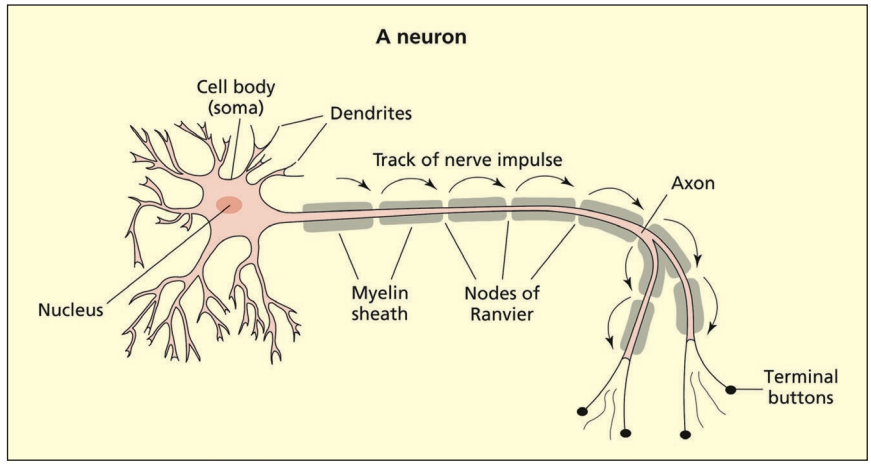


FIGURE 2.1: Neurons consist of three basic features: a cell body, dendrites that receive information and axons that send information. In this diagram the axon is myelinated to speed the conduction time.

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.

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. There is unlikely to be a simple relationship between brain size and intellect (most people with autism have low IQ), and brain efficiency may be unrelated to size.
(10) Men have larger brains than women, but the female brain is more folded, implying an 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 "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.

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.

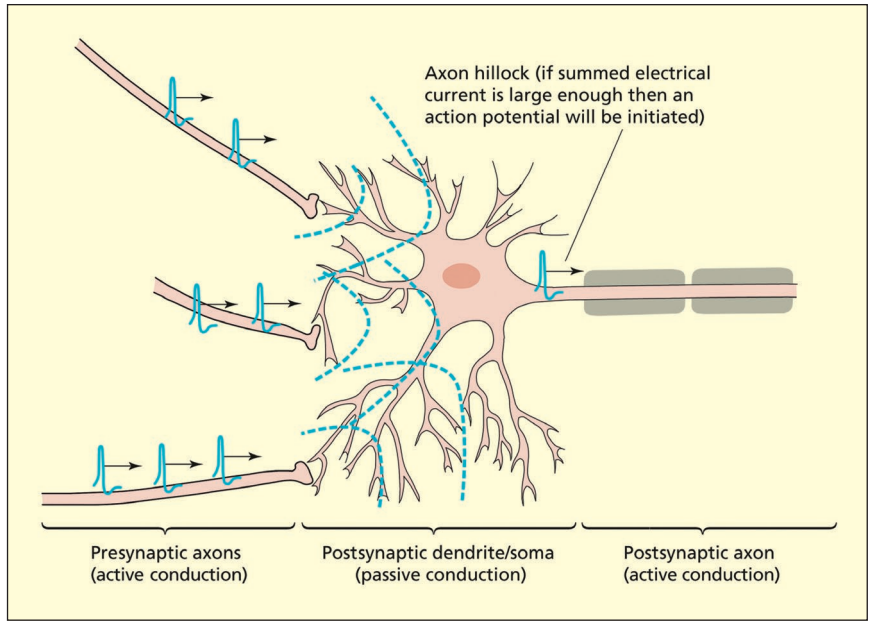


FIGURE 2.2: Electrical currents are actively transmitted through axons by an action potential. Electrical currents flow passively through dendrites and soma of neurons, but will initiate an action potential if their summed potential is strong enough at the start of the axon (called the hillock).

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 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.

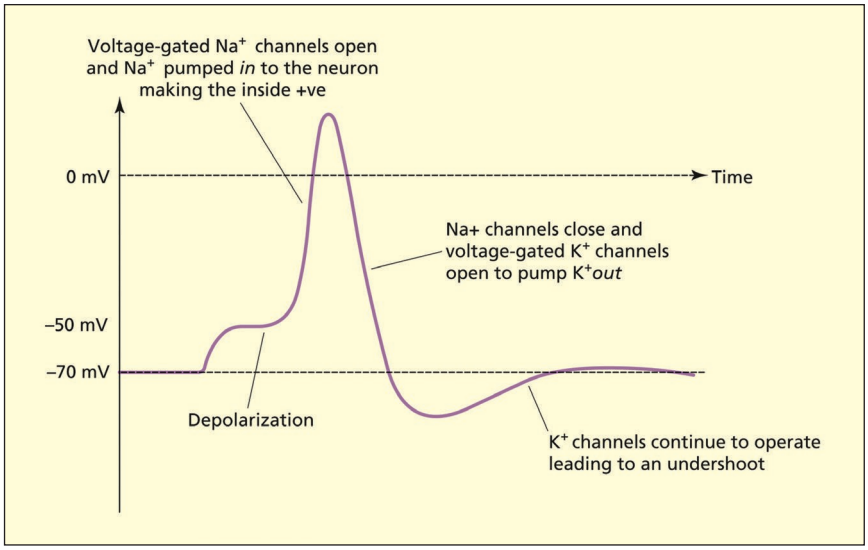


FIGURE 2.3: The action potential consists of a number of phases.

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

ONLINE RESOURCE

Do you need to get up to speed on your neuroscience basics? Take a look at the companion website (www.routledge.com/cw/ward) for links to a YouTube neuroscience crash course and a free online Fundamentals of Neuroscience module from Harvard University.

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 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.

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).

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.

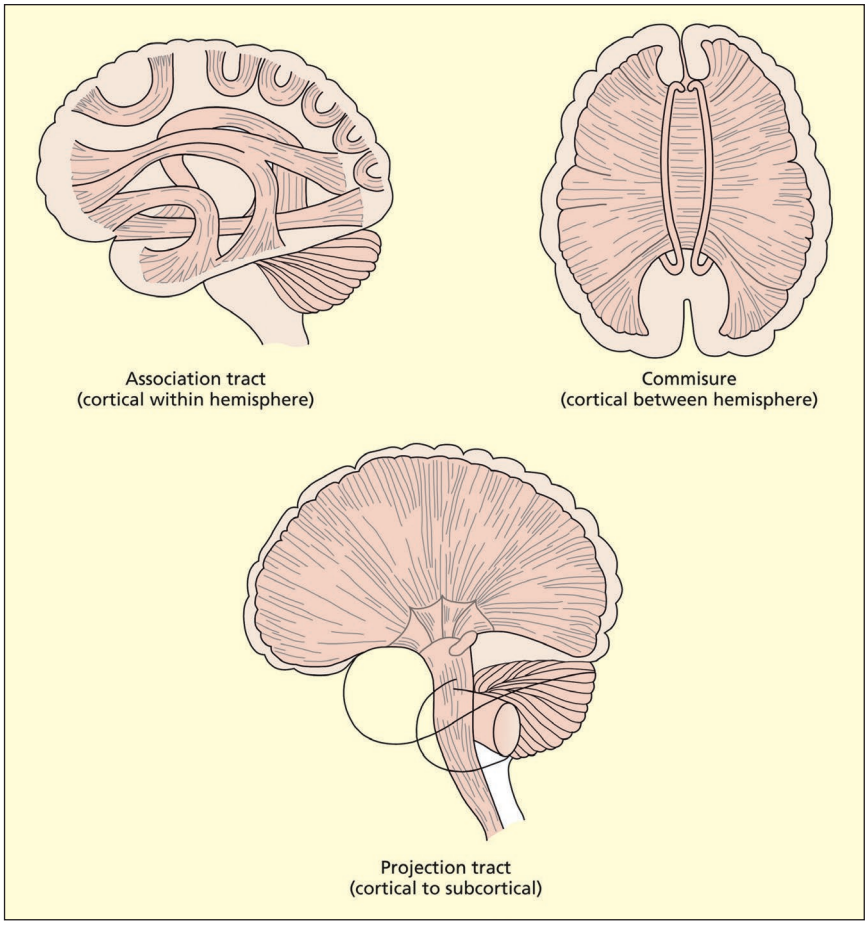
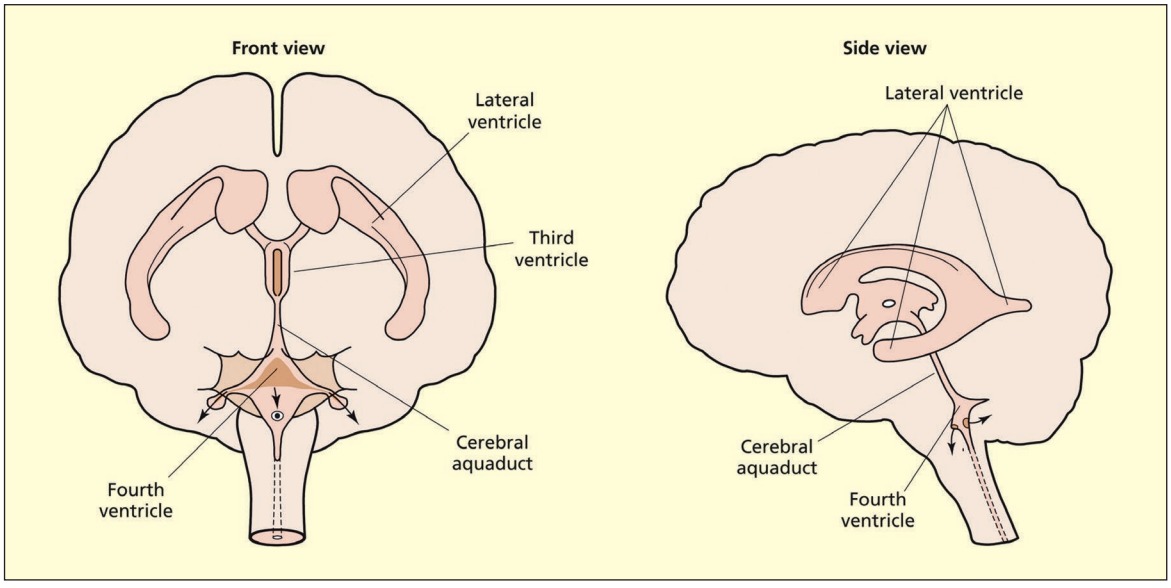


FIGURE 2.4: There are three different kinds of white matter tract, depending on the nature of the regions that are connected.

Adapted from Diamond *et al.*, 1986. © 1986 by Coloring Concepts, Inc. Reprinted by permission of HarperCollins Publishers.

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).



KEY TERMS

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

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

Anterior
Toward the front.

Posterior
Toward the back.

Superior
Toward the top.

Inferior
Toward the bottom.

Dorsal
Toward the top.

Ventral
Toward the bottom.

Lateral
The outer part (cf. medial).

Medial
In or toward the middle.

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.

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).

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 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 in another context. Although it is used to refer to the center of the brain, 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.

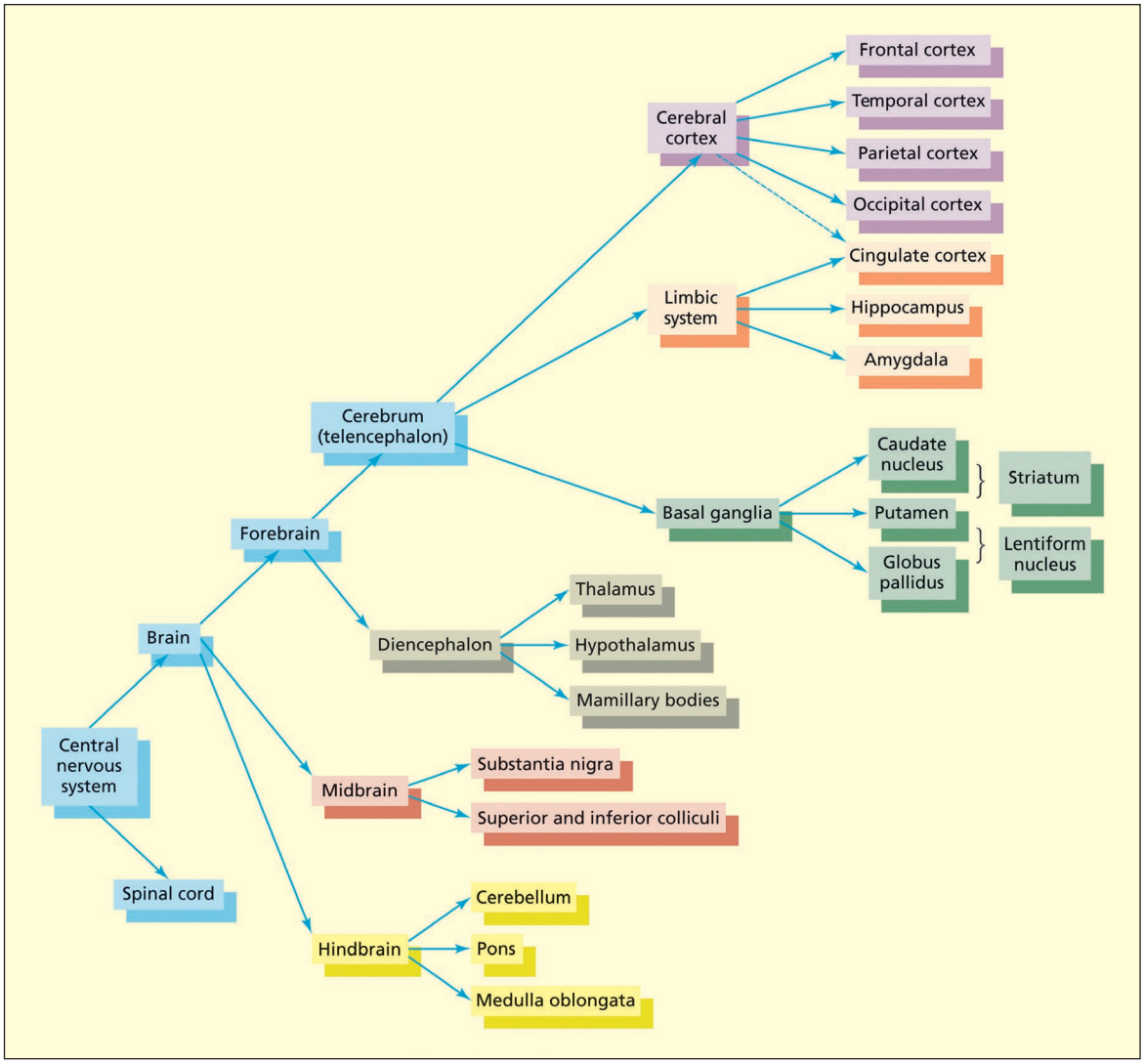


FIGURE 2.6: The central nervous system (CNS) is organized hierarchically. The upper levels of the hierarchy, corresponding to the upper branches of this diagram, are the newest structures from an evolutionary perspective.

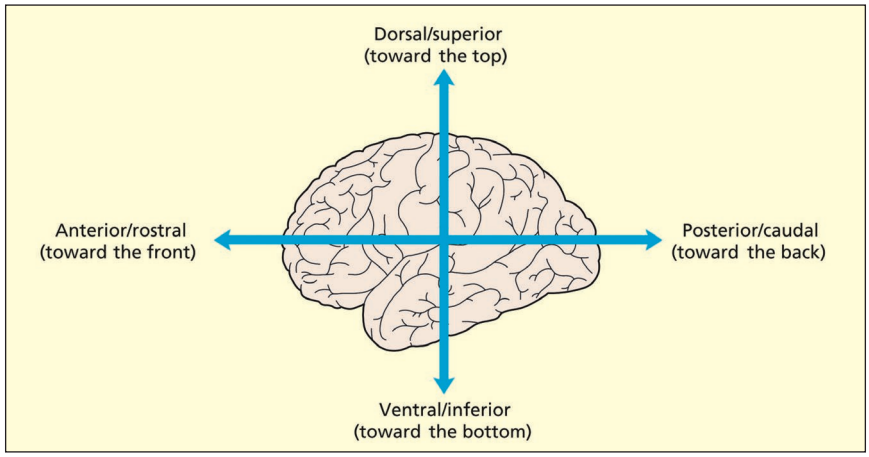


FIGURE 2.7: Terms of reference in the brain. Note also the terms *lateral* (referring to the outer surface of the brain) and *medial* (referring to the central regions).

KEY TERMS

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

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

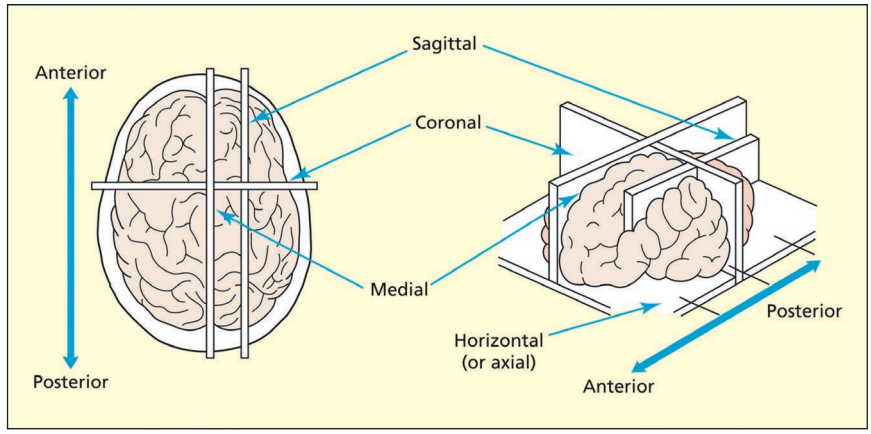


FIGURE 2.8: Terms of sections of the brain.

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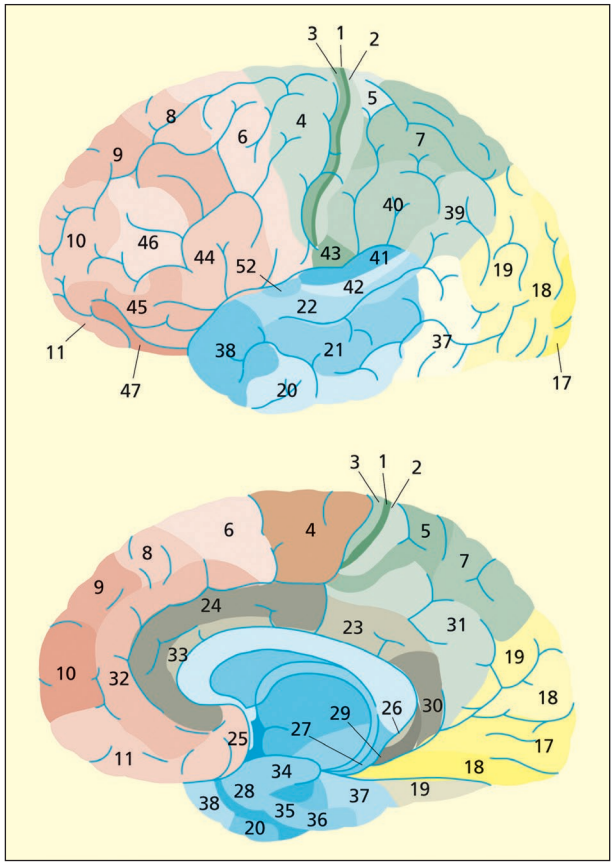


FIGURE 2.9: The main gyri of the lateral (top) and medial (bottom) surface of the brain. The cortical sulci tend to be labeled according to terms of reference. For example, the superior temporal sulcus lies between the superior and medial temporal gyri.

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**.

KEY TERM

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

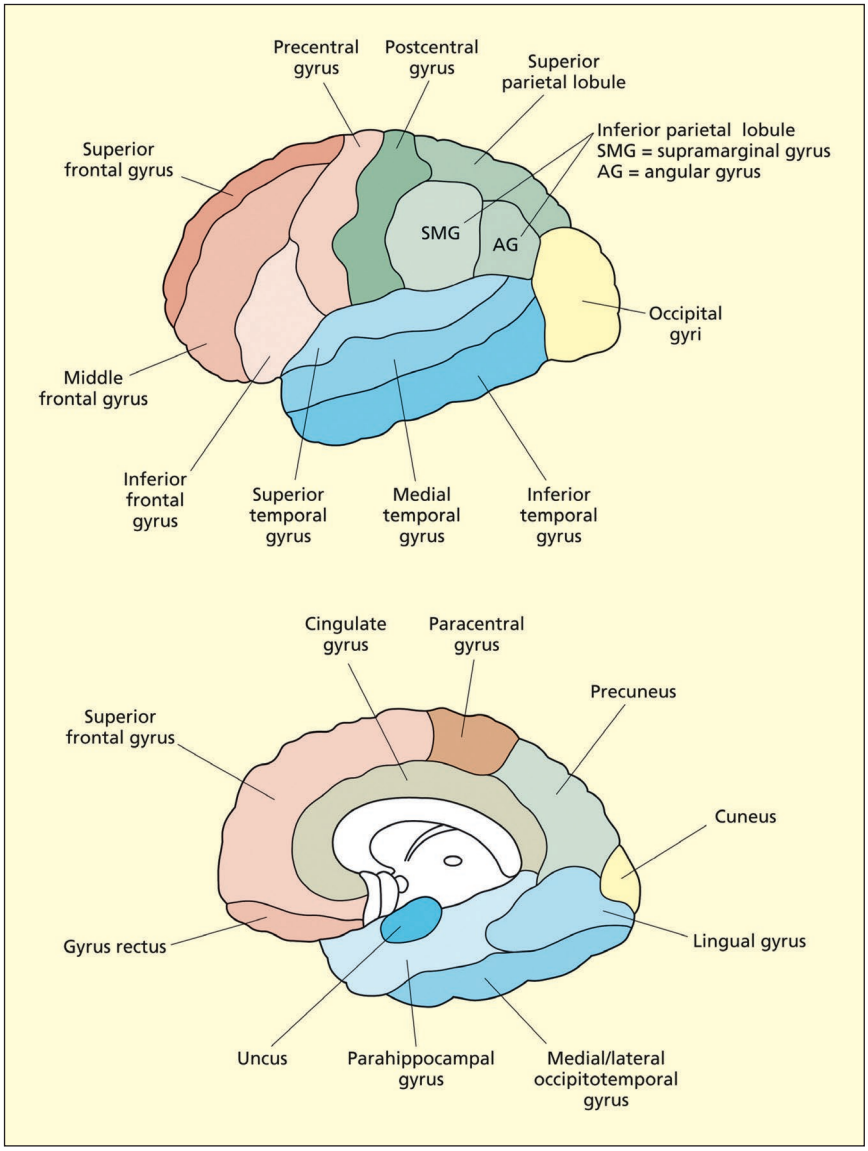


FIGURE 2.10: The Brodmann areas of the brain on the lateral (top) and medial (bottom) surface.

ONLINE RESOURCE

Check out the companion website (www.routledge.com/cw/ward) for a link to the 3D Brain App from Google Play or Neuroanatomy Online.

KEY TERM

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.

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.

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).

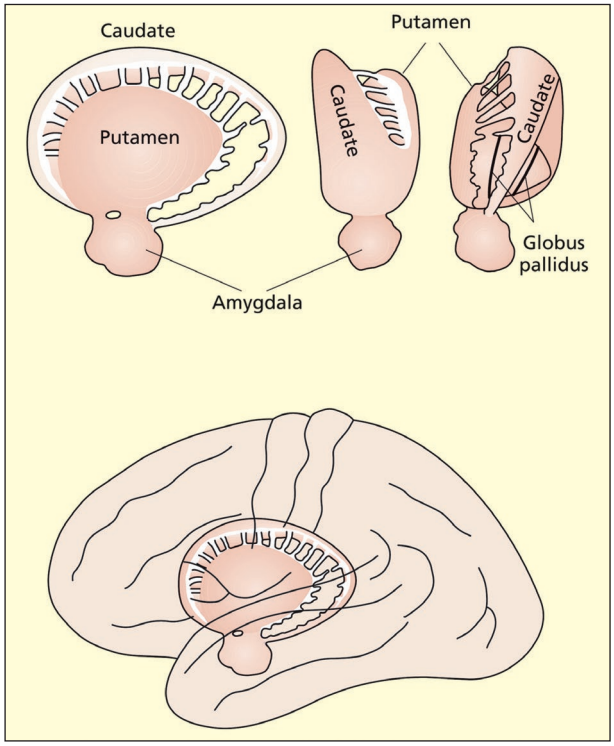
THE SUBCORTEX

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).

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



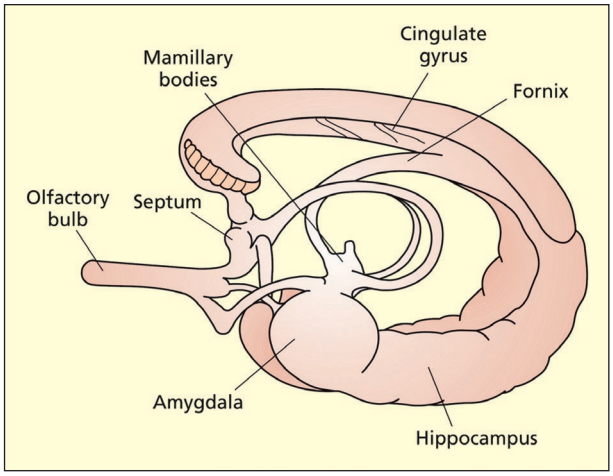


FIGURE 2.12: The limbic system.

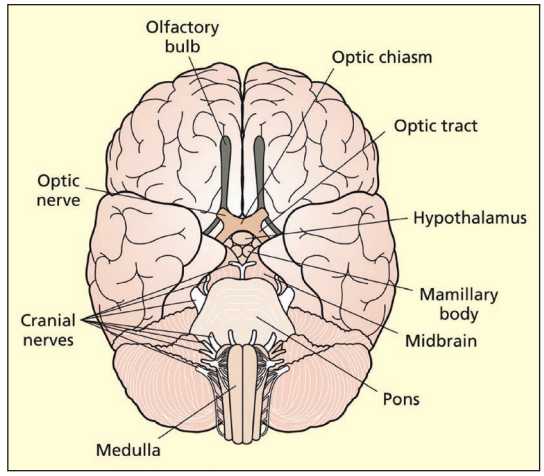


FIGURE 2.13: The ventral surface of the brain shows the limbic structures of the olfactory bulbs and mamillary bodies. Other visible structures include the hypothalamus, optic nerves, pons and medulla.

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 needs and the present situation, and based on 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 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.

KEY TERMS

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.

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

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.

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. It also contains projections to almost all parts of the cortex and the basal ganglia. At the posterior end

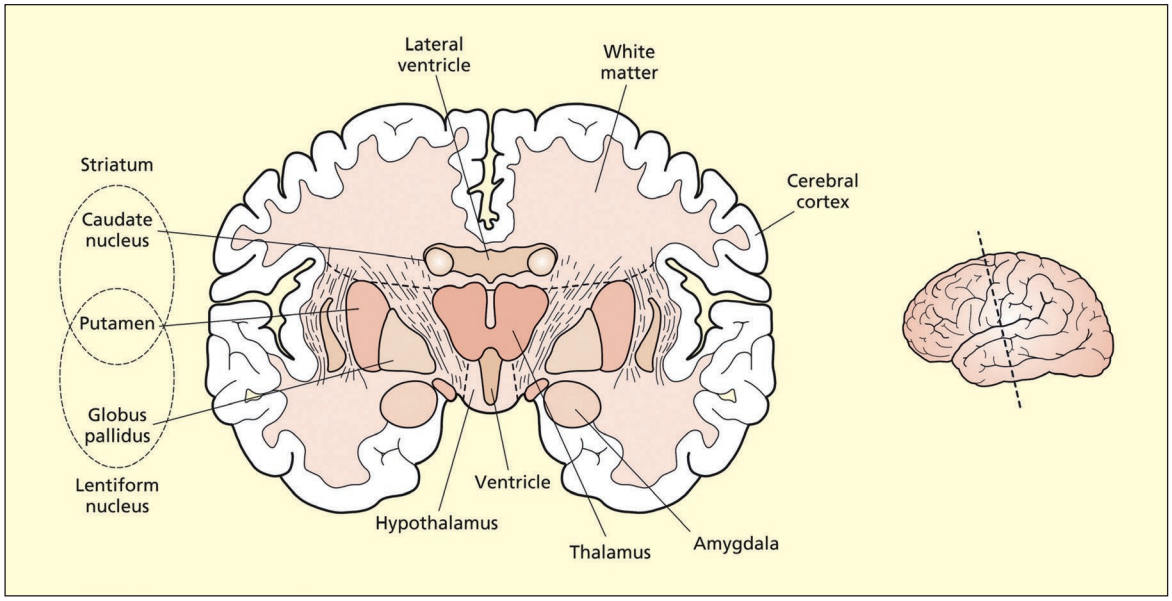


FIGURE 2.14: A coronal section through the amygdala and basal ganglia shows the thalamus and hypothalamus as prominent in the midline.

KEY TERMS

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

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.

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.

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 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 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.

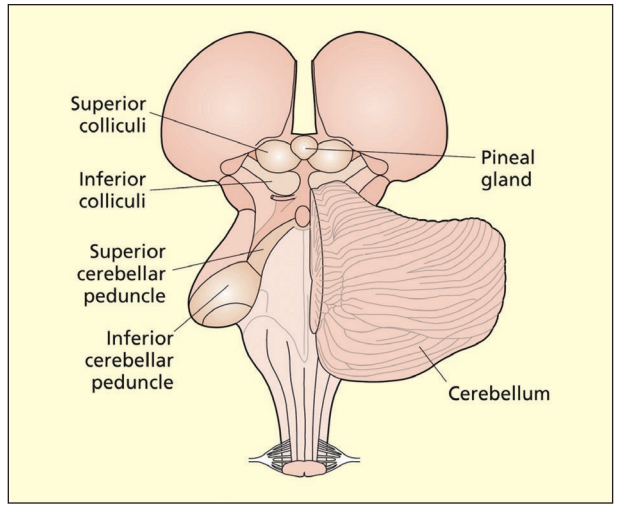


FIGURE 2.15: A posterior view of the midbrain and hindbrain. Visible structures include the thalamus (the two egg-shaped masses at the top), pineal gland, superior colliculi, inferior colliculi, cerebellum, cerebellar peduncle and medulla oblongata (the pons is not visible but lies on the other side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

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 hemostatic 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.

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.

ONLINE RESOURCE

Visit the companion website at www.routledge.com/cw/ward for:

- References to key papers and readings
- Video interviews on key topics
- Links to the Interactive Neuroanatomy website and Harvard's *MRI Brain Atlas*
- Multiple-choice questions and interactive flashcards to test your knowledge
- Downloadable glossary

RECOMMENDED FURTHER READING

- Bear, M. F., Connors, B. W., & Paradiso, M. A. (2015). *Neuroscience: Exploring the brain* (4th edition). Baltimore, MD: Lippincott Williams & Wilkins. A detailed book that covers all aspects of neuroscience. It is recommended for students whose degree contains significant neuroscience components. The book may be beyond the need of many psychology students.
- Crossman, A. R., & Neary, D. (2014). *Neuroanatomy: An illustrated colour text* (5th edition). Edinburgh: Harcourt Publishers. A good and clear guide that is not too detailed.
- Pinel, J. P. J., & Edwards, M. (2007). *A colorful introduction to the anatomy of the human brain: A brain and psychology coloring book* (2nd edition). New York: Pearson. An active way of learning your way around the brain.

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).

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

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**.

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 animal 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.

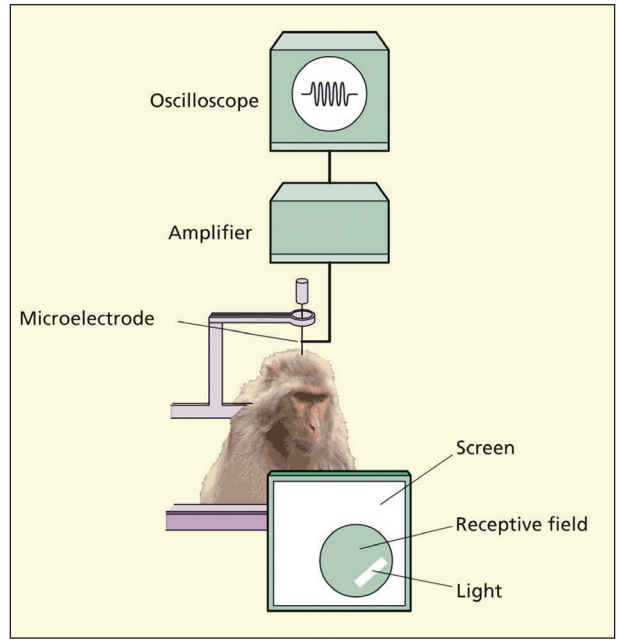


FIGURE 3.1: A typical experimental set-up for single-cell recording.

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.

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. It is also commonly referred to as a cell that responds to the sight of her (although from any viewpoint) (Figure 3.2).

KEY TERMS

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.

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