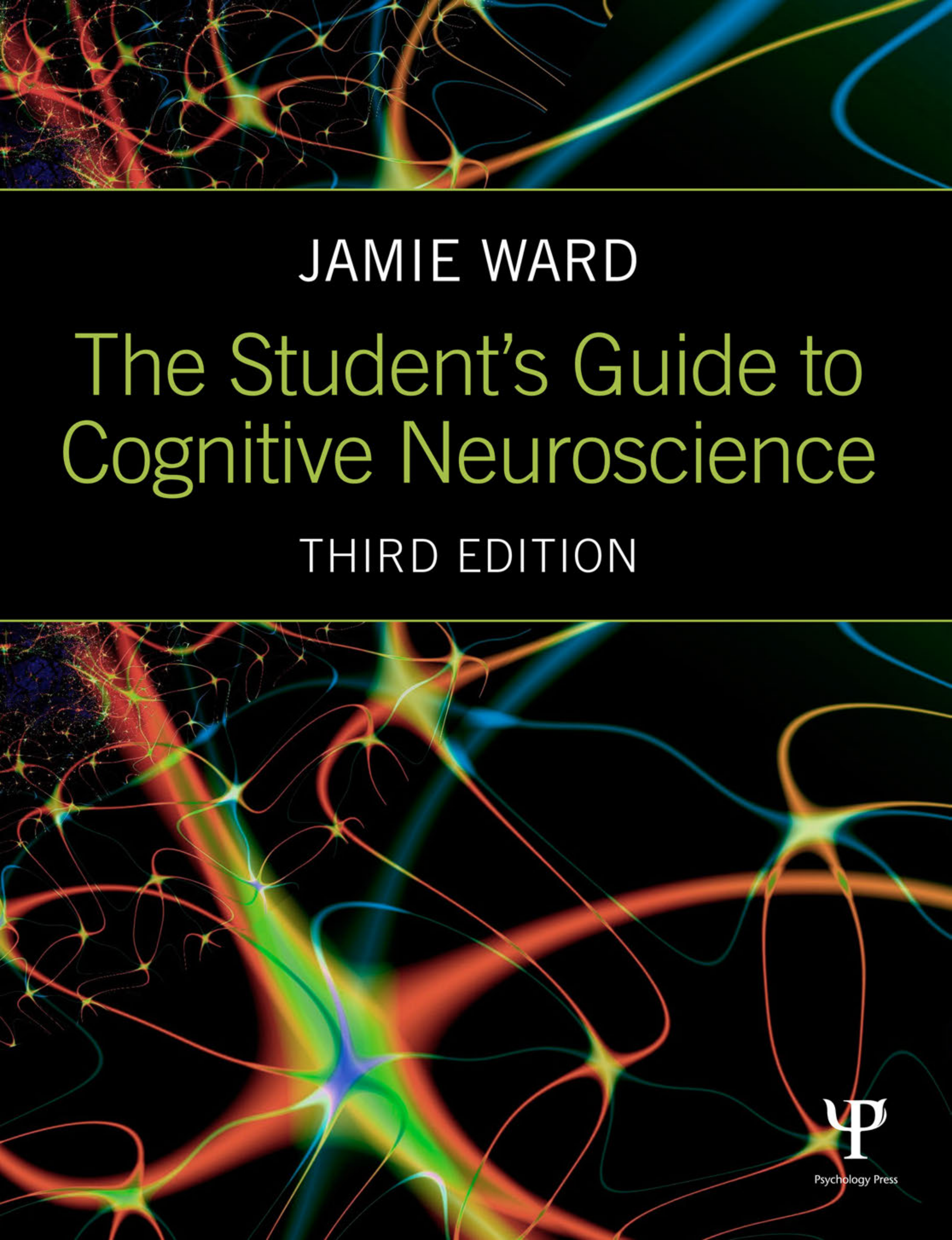

JAMIE WARD

The Student's Guide to Cognitive Neuroscience

THIRD EDITION

Psychology Press

The Student's Guide to Cognitive Neuroscience

Reflecting recent changes in the way cognition and the brain are studied, this thoroughly updated third edition of the best-selling 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 an up-to-date overview of the latest theories and findings in all the key topics in cognitive neuroscience, including vision, memory, speech and language, hearing, numeracy, executive function, social and emotional behavior and developmental neuroscience, as well as a new chapter on attention. Throughout, case studies, newspaper reports and everyday examples are used to help students understand the more challenging ideas that underpin the subject.

In addition each chapter includes:

- Summaries of key terms and points
- Example essay questions
- Recommended further reading
- Feature boxes exploring interesting and popular questions and their implications for the subject.

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.

The Student's Guide to Cognitive Neuroscience, Third Edition is supported by a companion website, featuring helpful resources for both students and instructors.

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 synaesthesia, and is the Founding Editor of the journal *Cognitive Neuroscience*.

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THE STUDENT'S GUIDE TO COGNITIVE NEUROSCIENCE

Third Edition

JAMIE WARD

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Preface to the third 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, 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 third edition has been updated to include the latest research tools (such as tDCS, transcranial direct current 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. Although no new chapters have been added, this third edition represents a substantial update. Chapter 7 is now rewritten to focus specifically on attention, rather than spatial cognition more generally. The content relating to working memory now appears in Chapter 9, “The Remembering Brain,” rather than in the chapter on executive functions, and the “cognitive map” theory of the hippocampus (place cells, etc.) is integrated within the memory chapter, too. The hot-topic of embodied cognition is introduced in more detail and critically evaluated, notably in Chapter 10 (e.g. motor theories of speech perception), Chapter 11 (e.g. sensorimotor grounding of semantic features), and Chapter 15 (e.g. understanding others via simulation). Chapter 14, “The Executive Brain,” has been substantially rewritten and reorganized to take into account newer theories concerning the organization of control systems in the prefrontal cortex.

Jamie Ward
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Brighton, UK, July 2014

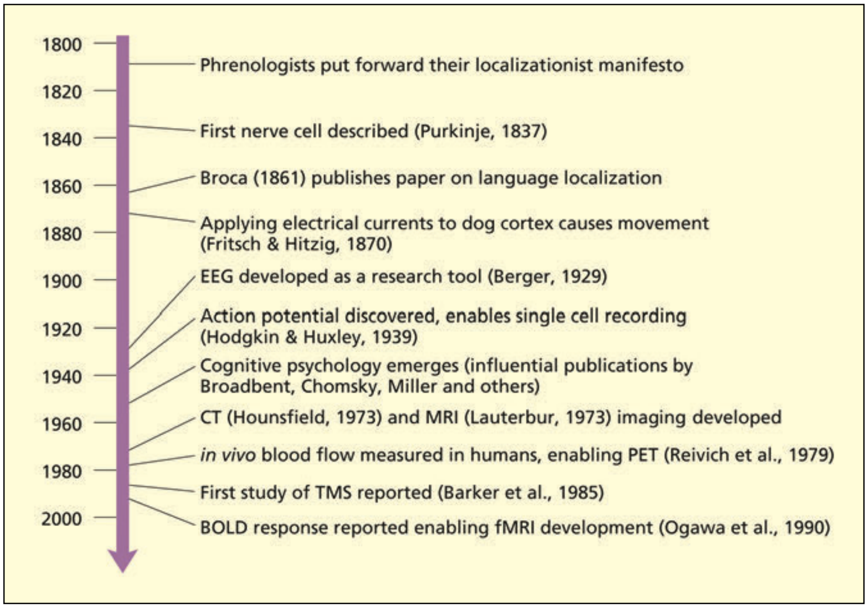
CHAPTER 1

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 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



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

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. 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 an 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.

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).

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

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 will 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

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

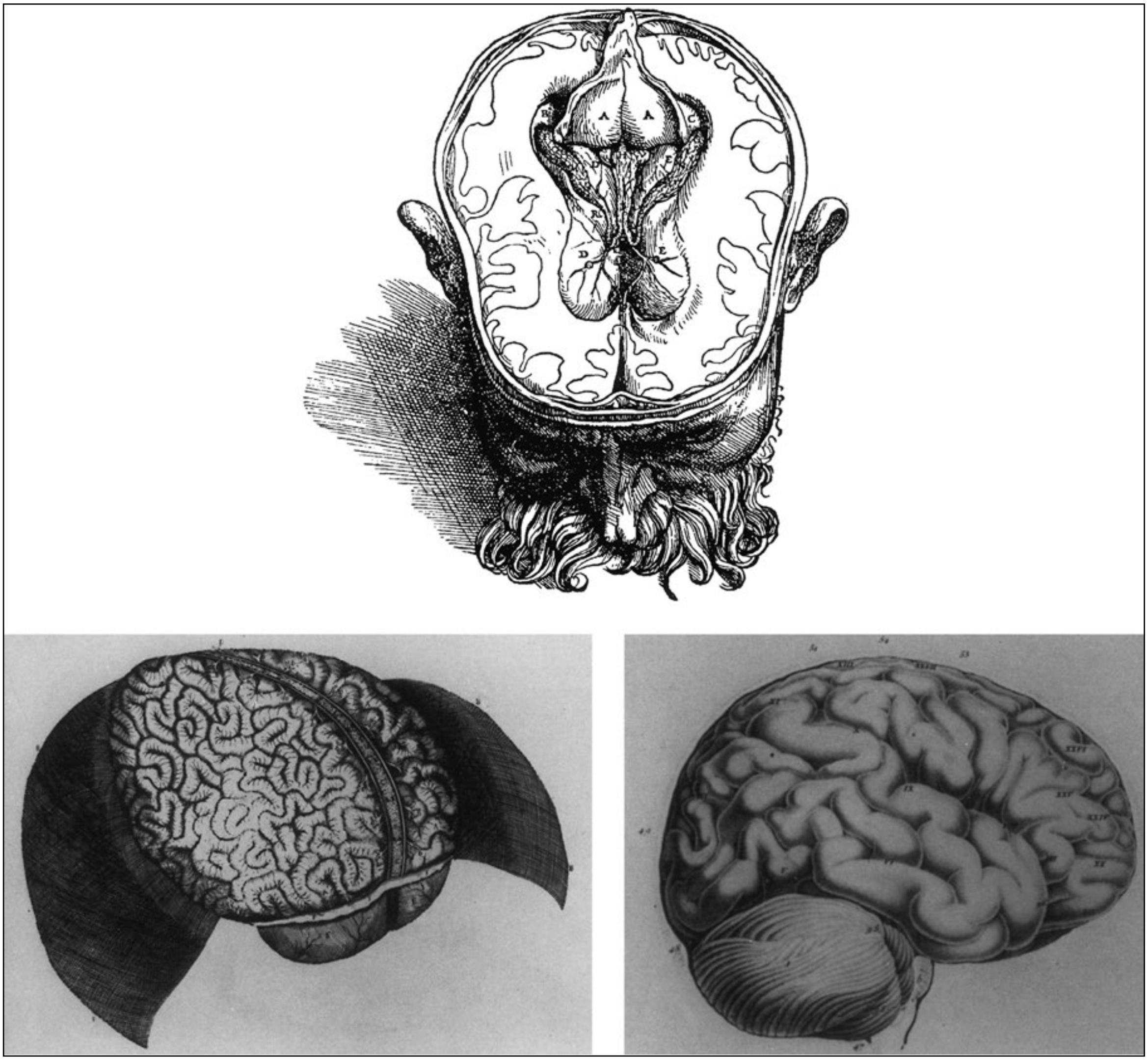
Our understanding of the brain emerged historically late, largely in the nineteenth century, although some important insights were gained during classical times. Aristotle (384–322 BC) noted that the ratio of brain size to body size was greatest in more intellectually advanced species, such as humans. 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,

KEY TERM

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

published his plates of dissected brains, the ventricles were drawn in exacting detail, whereas the cortex was drawn crudely and schematically. Others followed in this tradition, often drawing the surface of the brain like the intestines. This situation probably reflected a lack of interest in the cortex rather than a lack of penmanship. It is not until one looks at the drawings of Gall and Spurzheim (1810) that the features of the brain become recognizable to modern eyes.

Gall (1758–1828) and Spurzheim (1776–1832) received a bad press, historically speaking, because of their invention and advocacy of **phrenology**. Phrenology had two key assumptions; first, that different regions of the brain perform different functions and are associated with different behaviors; and second, that the size of these regions produces distortions of the skull and correlates with individual differences in cognition and personality. Taking these two ideas



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.

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 empirically derived 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." Moreover, skull shape has nothing to do with cognitive function.

Although phrenology was fatally flawed, the basic idea of different parts of the brain serving different functions paved the way for future developments in the nineteenth century, the most notable of which are Broca's (1861) reports of two brain-damaged patients. Broca documented two cases in which acquired brain damage had impaired the ability to speak but left other aspects of cognition 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 11 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 what the building blocks of cognition are (is language a single faculty?) 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 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.

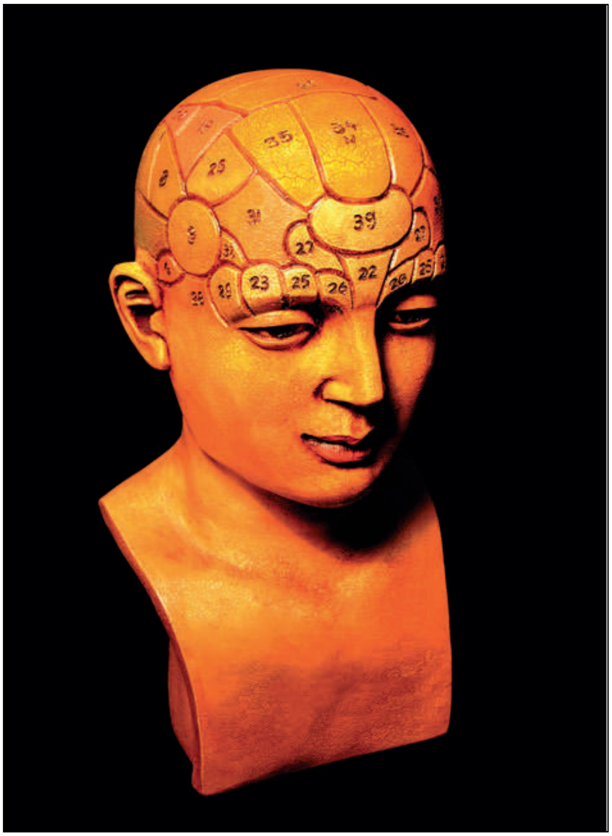
Whereas discoveries in the neurosciences continued apace throughout the nineteenth and twentieth centuries, the formation of psychology as a discipline at the end of the nineteenth century took the study of the mind away from its biological underpinnings. This did not reflect a belief in dualism. It was due, in part, to some pragmatic

KEY TERMS

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

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

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



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. The implication was that one could understand the cognitive system in the same way as one could understand the series of steps performed by a computer program, and without reference to the brain. The idea of the mind as a computer program has advanced over the years along with advances in computational science. 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**). **Parallel processing** refers to the fact that lots of different information can be processed simultaneously (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 (Ellis & Humphreys, 1999).

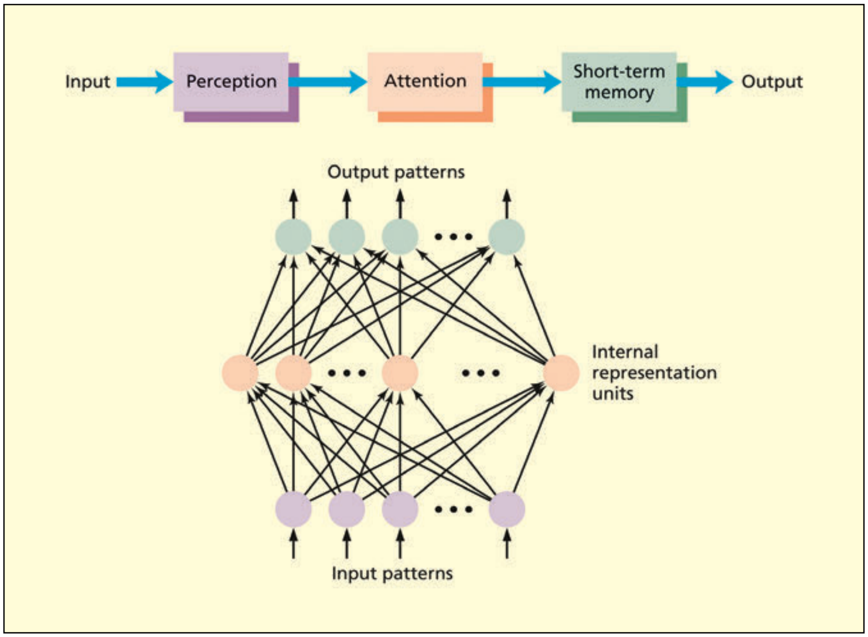
KEY TERMS

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

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).

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



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.

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. Whether or not the brain actually *does* implement cognition in that particular way will ultimately be a question for empirical research in cognitive neuroscience.

The 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 post mortem).

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. The modern-day equivalent of these studies uses stimulation across the skull rather than directly to the brain (i.e. transcranially). This includes

KEY TERMS

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

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

transcranial magnetic stimulation (TMS) and transcranial direct current stimulation (tDCS). 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 and fMRI) record physiological changes associated with blood supply to the brain, which evolve more slowly over time. These are called hemodynamic methods and are considered in Chapter 4.

The methods of cognitive neuroscience can be placed on a number of dimensions:

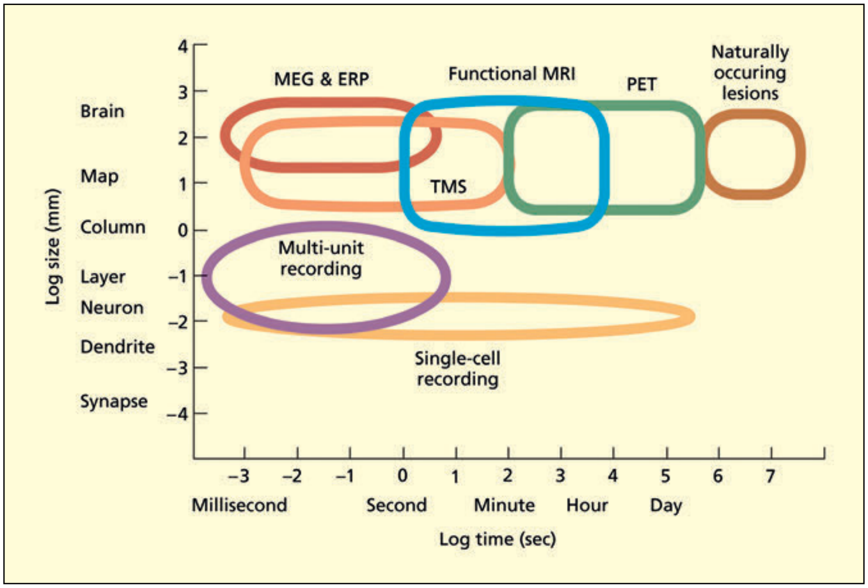
- The **temporal resolution** refers to the accuracy with which one can measure *when* an event is occurring. The effects of brain damage are permanent and so this has no temporal resolution as such. Methods such as EEG, MEG, TMS,

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	Non-invasive	Electrical
Single-cell (and multi-unit) recordings	Recording	Invasive	Electrical
TMS	Stimulation	Non-invasive	Electromagnetic
tDCS	Stimulation	Non-invasive	Electrical
MEG	Recording	Non-invasive	Magnetic
PET	Recording	Invasive	Hemodynamic
fMRI	Recording	Non-invasive	Hemodynamic



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

Adapted from Churchland and Sejnowski, 1988.

and single-cell recording have millisecond resolution. fMRI has a temporal resolutions of several seconds that reflects the slower hemodynamic response.

- The **spatial resolution** refers to the accuracy with which one can measure *where* an event is occurring. Lesion and functional imaging methods have comparable resolution at the millimeter level, whereas single-cell recordings have spatial resolution at the level of the neuron.
- The *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.

KEY TERM

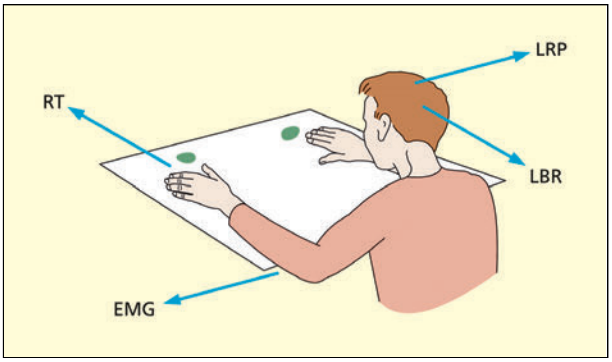
Spatial resolution
The accuracy with which one can measure where an event (e.g. a physiological change) is occurring.

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). Each measure will relate to the task in some way and can be used to inform theories about the task.

To illustrate this point, consider an example. One could ask a simple question such as: Does visual recognition of words and letters involve computing a representation that is independent of case? For 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 or different case (e.g. radio-RADIO, RADIO-RADIO) and compare this with



One could take many different measures in a forced-choice response task: behavioral (reaction time [RT], errors) or biological (electromyographic [EMG], lateralized readiness potential [LRP], lateralized BOLD response [LBR]). All measures could potentially be used to inform cognitive theory.

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