

# CHAPTER 1

# INTRODUCTION AND HISTORY

## KEY THEMES

- Although the phenomenon consciousness and the related construct of *cognition* (i.e., thinking) are the focus of many different scholarly disciplines, what distinguishes cognitive neuroscience is its grounding in the methods and traditions of neuroscience, and the primacy that it places on understanding *the neurobiological bases* of mental phenomena.
- There are two levels at which the term “cognitive neuroscience” is used: broadly, it has come to refer to the neuroscientific study of most domains of human behavior; narrowly, it refers to the study of neural bases of *thinking* – what influences it, what it consists of, and how it is controlled.
- The roots of cognitive neuroscience can be traced back to a nineteenth-century debate over two ways of thinking about brain function that both remain relevant today: localization of function vs. mass action.
- Mid-to-late nineteenth-century research established the validity of localization for three functions: motor control (localized to frontal lobes); vision (localized to occipital lobes); speech production (localized to the left posterior inferior frontal gyrus).
- The motor control research introduced the principle of *topographic representation*, that adjacent parts of the body can be represented on adjacent parts of the cerebral cortex.
- Studying an aspect of cognition requires careful thought about the validity of the function to be studied; and not all aspects of human behavior are equally amenable to cognitive neuroscience research.
- The discipline of cognitive neuroscience could not exist without discoveries yielded by research with nonhuman animals.
- At the dawn of the twentieth century, scientists were studying the brain and behavior from three related, but distinct, perspectives that would eventually give rise to cognitive neuroscience as we know it today: systems neuroscience; behavioral neuroneurology/neuropsychology; and experimental psychology.

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REFERENCES

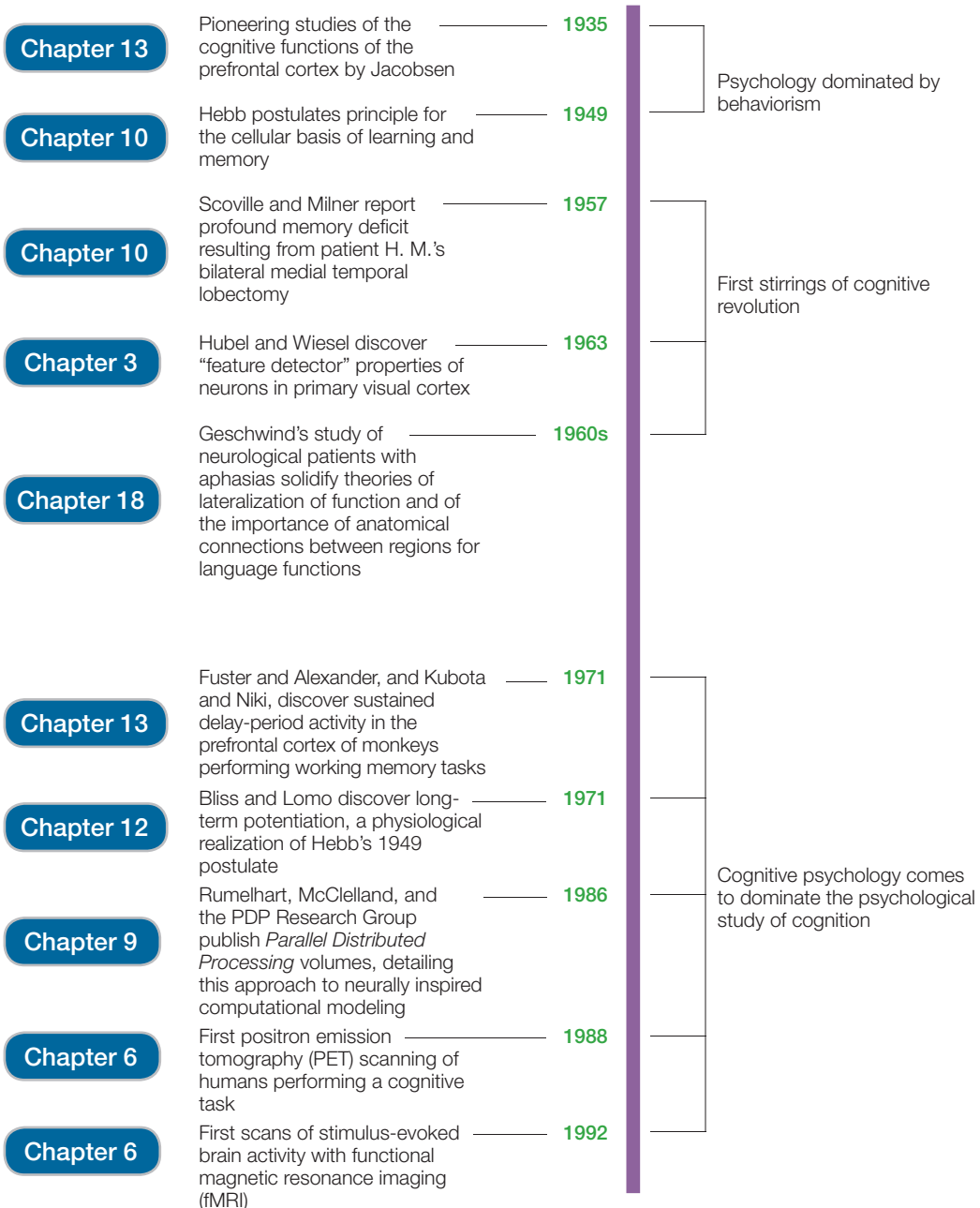
OTHER SOURCES USED

FURTHER READING

# TIMELINE: NINETEENTH- AND TWENTIETH-CENTURY ORIGINS OF COGNITIVE NEUROSCIENCE

	Event	Dates	Contemporaneous developments in the psychological study of cognition*
Chapter 1	Gall promotes his treatise on phrenology	1790–1820s	Philosophy dominates scholarship in psychology
Chapter 1	Flourens performs experiments refuting phrenology-based localization	1820s–1850s	
	Jackson proposes somatotopic organization of motor cortex	1860s	Pioneering experimentation in perception by Weber and Helmholtz gives rise to psychophysics
Chapter 1	Broca, based on work with Tan and other patients, localizes speech to left posterior inferior frontal gyrus.	1863	
Chapter 1	Fritsch and Hitzig demonstrate, with electrical stimulation, the localization of motor functions to posterior frontal cortex	1870	
Chapter 18	Wernicke describes receptive aphasia, thereby localizing speech comprehension	1874	
Chapter 1	Studies of Munk and of Schäfer establish conclusively the localization of visual perception to the occipital cortex	1880s	Wundt founds Institute of Experimental Psychology
Chapter 3	Brodmann publishes cytoarchitectonic map of anatomical organization of the human brain	1909	Dawn of behaviorism
Chapter 3	Berger records human alpha rhythm with extracranial electroencephalography (EEG)	1929	Psychology dominated by behaviorism
Chapter 4	Penfield's electrical stimulation studies map somatosensory homunculus to postcentral gyrus	1930s	

\*Note that, although these are not considered in any detail in this textbook, they are provided for historical context.



## A BRIEF (AND SELECTIVE) HISTORY

Although the term “cognitive neuroscience” as a moniker for a scientific discipline has only been with us for a few decades, the field has roots that extend back thousands of years. Ancient Egyptians, Greeks, and Romans all had ideas about the corporeal bases of human thoughts and emotions, although many of these did not specify a role for the brain. In preparing the bodies of deceased nobles for the afterlife, for example, ancient Egyptians removed and discarded the brain as an early step in the mummification process. The internal organs that were deemed to be important were preserved in urns that were entombed along with the body. In most ancient civilizations for which there are records, up through and including Roman civilization, the heart was believed to be the organ of thought. By the time we get to Enlightenment-era Europe, however, the central importance of “neuro” for cognition was widely accepted. One highly influential (and, more recently, ridiculed) example was that of German anatomists Franz Josef Gall (1758–1828) and Johann Caspar Spurzheim (1776–1832), who developed a highly detailed scheme, known as **phrenology**, for how the shape of different parts of the skull related to one’s personality and mental capacities. The underlying premise was that the relative bigness or smallness of various parts of the brain would produce convexities or concavities in the overlying skull. A skilled phrenologist, then, could learn something about an individual by palpating that person’s skull. A bulge in the cheekbone below the eye would mean a predilection toward language, whereas an indentation near the left ear would correspond to a relative absence of the trait of “destructiveness” (*Figure 1.1*). One can see how such a scheme, if it had any validity, would have obvious utility for diagnosing maladies of the brain, as well as for assessing personality and aptitude. (Indeed, for a period during the 1800s it was (mis)used in this way quite extensively, particularly in England and in the United States.)

For at least the past 100 years, the psychology and neuroscience communities have viewed virtually all tenets of the phrenological enterprise as being

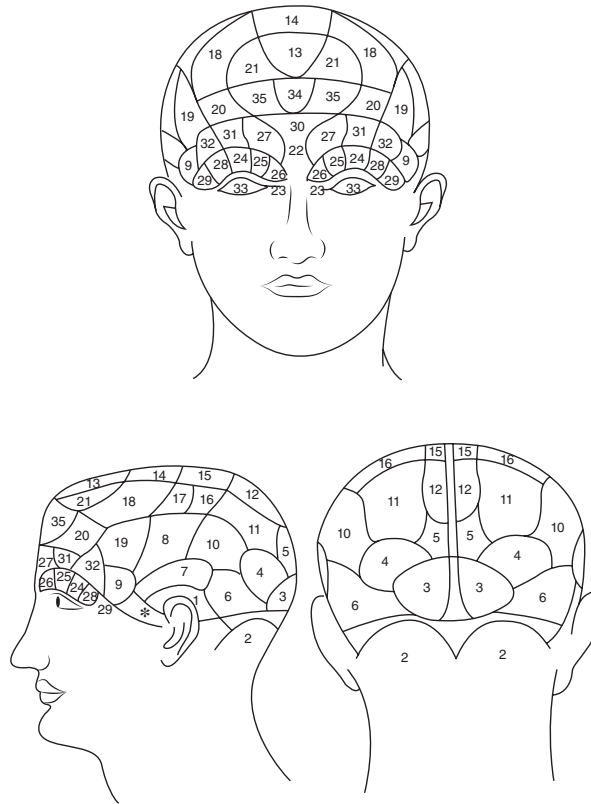
### Tip 1.1

Cognitive neuroscience is grounded in the governing assumption that all cognitive functions arise from the physical, chemical, and physiological properties of the brain and **central nervous system**. Thus, all differences between individuals must reduce to physical factors. In **typically developed** humans, however, these will be microscopic (e.g., connections between **neurons** (*Chapter 2* and *Chapter 10*); varying levels of concentration of chemical transmitters (*Chapter 2*)), and underlain by differences in genetics and/or life experience.

scientifically invalid. From one perspective, we have come to know that subtle, idiosyncratic variations in gross shape from one brain to another have little, if anything, to do with the “kind of person” that one is (however, see *Tip 1.1* for qualification of this point). We also recognize that the assignments of function that Gall gave to various parts of the brain were not based on rigorous science, and turned out to be altogether wrong. A third point, that merits additional elaboration in *Thought Box 1.1*, is that the very selection and definition of functions that phrenologists mapped onto the brain lacked systematicity and rigor. There was, however, at the core of the phrenological enterprise, a powerful idea that has continued to animate many debates about brain function up to the present time – the idea of **localization of function**.

### Localization of function vs. mass action

The principle of localization of function refers to the idea that different aspects of brain function, such as visual perception vs. the control of our emotions vs. our talents as musicians, are governed by, and therefore localizable to, different “centers” in the brain. An analogy might be that different functions of the body – extracting oxygen from blood vs. pumping blood vs. filtering blood – are each accomplished by a different organ (i.e., the lungs, the heart, and the kidneys) that



**FIGURE 1.1** A phrenological map of the anatomical organization of mental faculties. They are organized into two primary categories (bold), with subcategories (underlined) under each. The first primary category is **Affective Faculties**: Propensities: \* – Alimentiveness; 1 – Destructiveness; 2 – Amativeness; 3 – Philoprogenitiveness; 4 – Adhesiveness; 5 – Inhabitiveness; 6 – Combativeness; 7 – Secretiveness; 8 – Acquisitiveness; 9 – Constructiveness; Sentiments: 10 – Cautiousness; 11 – Approbativeness; 12 – Self-Esteem; 13 – Benevolence; 14 – Reverence; 15 – Firmness; 16 – Conscientiousness; 17 – Hope; 18 – Marvelousness; 19 – Ideality; 20 – Mirthfulness; 21 – Imitation. The second primary category is **Intellectual Faculties**: Perceptive: 22 – Individuality; 23 – Configuration; 24 – Size; 25 – Weight and Resistance; 26 – Coloring; 27 – Locality; 28 – Order; 29 – Calculation; 30 – Eventuality; 31 – Time; 32 – Tune; 33 – Language; Reflective: 34 – Comparison; 35 – Causality. Source: Spurzheim, 1834.

are located in different parts of the body. This notion can be contrasted with an alternative idea, **mass action**, according to which a particular function can't necessarily be localized to a specific area of the brain and, conversely, any given area of the brain can't be thought of as a "center" that is specialized for any one function. To stick with our analogy to familiar parts of the body below the neck, we can illustrate the principle of mass action by zeroing in on the kidney. The overall function of the kidney – filtering blood – is

carried out in the same way by the top portion and the middle portion and the bottom portion. To understand how the kidney does its job, one could study in detail the inner workings of only the top, or only the middle, or only the bottom of this organ, and one would learn the same thing from each. In effect, then, different zones of the kidney are "interchangeable" with respect to understanding their function. Now project yourself back in time a few centuries to a time when what I've just written hasn't yet been

## THOUGHT BOX

### 1.1 What's a function? (And what qualities make the neural bases of a function amenable to experimental study?)

A quick inspection of an iconic phrenological bust, such as that illustrated in *Figure 1.1*, often elicits giggles: *Acquisitiveness? Conscientiousness? Amativeness?* On what basis can one assert that any of these labels actually correspond to a unitary, discrete “function”?

Near the end of this chapter we'll note that the functions of motor control and vision are relatively easy to observe and to measure. The fact that they also turn out to be localizable with a high degree of anatomical specificity reinforces the idea that each can be considered a discrete function of the brain. But can the same be said about, say, *conscientiousness*? It is true, of course, that an organism without a brain cannot exhibit conscientiousness, and, therefore, the phenomenon could not exist without a brain. However, might it not be the case that “conscientiousness” is just a label that we, as denizens of highly organized societies, have given to a certain collection of attributes that doesn't correspond to any single discrete mental capacity? For example, if a student sends me a thank-you note for writing a letter of recommendation, I will consider her to have displayed conscientiousness. But could it not be the case that she was conditioned during her upbringing to seek positive reinforcement from her parents (*You're such a good girl for writing those thank-you notes!*), and that her note to me is “merely” the product of an association that she has formed between writing a thank-you note and this reinforcement? Were this the case, it wouldn't be possible to localize conscientiousness, per se, and any attempt to do so would be destined to yield erroneous conclusions.

This exercise illustrates a fundamental shortcoming of phrenology: many, if not all, of the “functions” that it sought to map onto the brain were simply not valid, because they were derived from nothing more than Gall's intuition. More generally, it illustrates two principles that are highly relevant to contemporary cognitive neuroscience. The first is that a model of the neural instantiation of a cognitive function depends critically on the validity of the function that it seeks to explain. The question of **construct validity** will be important for every domain of behavior that we consider in this book. For many, the formal models of the construct under study will come from one of the “different scholarly disciplines” invoked in the Introduction to Section I. A second principle is that not all aspects of cognition and behavior are equally amenable, with current theories and methods, to a neural level of explanation. To illustrate, we can return again to conscientiousness. It so happens that in the field of personality psychology, *conscientiousness* is a valid construct, one of the “big five” dimensions along which an individual's personality can vary (along with *agreeableness*, *extroversion*, *openness*, and *neuroticism*). Each of these is formalized as a statistical factor to which many traits contribute. (For *conscientiousness*, these include the extent to which one “follows a schedule,” “forgets to put things back in their proper place,” etc.) However, none of this alters the reasoning from the preceding paragraph, which is that not all describable traits are easily reduced to a neural level of analysis.

discovered. It is an era when biomedical research techniques are limited, and the best tool that you have for studying the function of an organ is to damage a portion of it and then observe the consequent impact of this damage on its function. Your kidney research

would indicate that damaging comparable-sized regions of upper vs. middle vs. lower kidney has the same effect in all cases: an overall decline in the efficacy of blood filtration. Thus, you would have discovered that a principle of mass action applies to the

**Tip 1.2**

Some scientists reserve the use of *neuropsychology* to refer to studies with humans who have sustained damage to the brain, and refer to analogous experiments with nonhuman animals simply as *lesion studies*.

kidney: a larger **lesion** results in a larger diminishment of the rate of blood filtration; smaller lesions result in a smaller diminishment of the rate of blood filtration; and, critically, the location of the damage doesn't seem to matter.

Now, let's return to the functions of the brain. In the decades following the introduction of phrenology, and in some instances in reaction to it, scientists and physicians began pursuing the idea of localization of function in the brain with methods reflecting the maturation of the scientific method that was occurring in many branches of science, from biology to chemistry to physics. At this general level, this entailed the a priori articulation of falsifiable hypotheses (i.e., stating the hypothesis prior to performing the experiment), and the design of controlled laboratory experiments that could be replicated in other laboratories. An important advance for studies of the brain, in particular, was the careful analysis of the behavioral consequences resulting from damage to a particular brain structure. This method has come to be known as **neuropsychology** (*Tip 1.2*). Armed with this approach, specific localizationist claims of phrenologists began to be disproven. Perhaps most influential were the studies of French scientist Pierre Flourens (1794–1867). A tireless critic of phrenology, Flourens did much of his experimental work with pigeons and with dogs. This research was influential on two levels. First, particular experiments of Flourens disproved specific phrenological claims, such as his demonstration that damage to the **cerebellum** disrupted locomotor coordination, but had no effect on amateness (i.e., sexual arousal), as Gall's model would have predicted (see *Figure 1.2*; and *Tip 1.3*). Secondly, and at a broader level, Flourens' studies of the cerebral cortex largely failed to find evidence for localization of function. Thus, although damage to

**Tip 1.3**

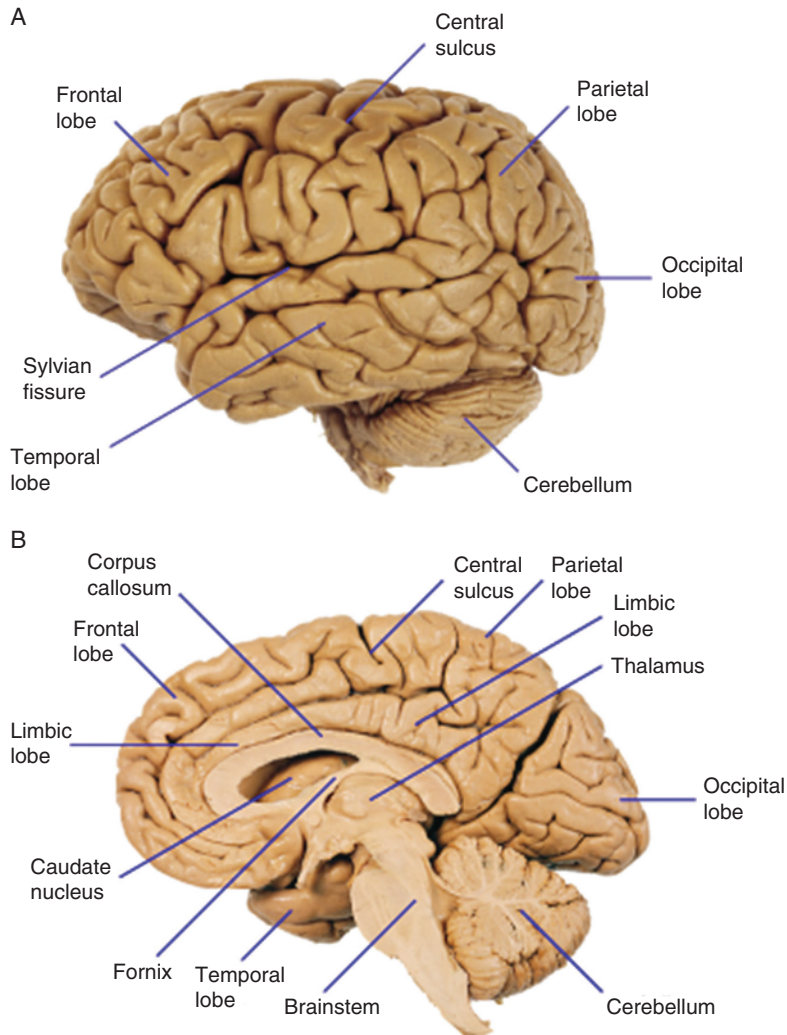
Gall's formal study of localization of function was not only controversial in scientific circles, but also had political implications. As the historian of science Stanley Finger puts it, "Authorities of the Austrian Catholic church viewed this work as championing materialism, atheism, and fatalism bordering on heresy." As a result, the Holy Roman Emperor (who ruled Vienna, where Gall had launched his career) sent to Gall a threatening letter that read, in part, "This doctrine concerning the head ... will perhaps cause a few to lose their heads" (Finger, 2000, pp. 124–125). Within a few years, Gall (and his head) left Vienna permanently, eventually settling in Paris.

the cortex invariably produced marked disruption of behaviors associated with judging, remembering, and perceiving, these impairments seemed to occur regardless of what part of the brain had been damaged. By inference, such results seemed to indicate that all regions of the cortex contributed equally to these behaviors. (Note that the same was not true of Flourens' studies of the brainstem, to which, for example, the cerebellum belongs (see *Figure 1.2* and *Web Link 1.1*).

Another important concept to come out of the work of Flourens was derived from the fact that, over time, animals with experimental damage to a part of cortex often recovered to presurgical levels of functioning. Because this occurred without evident repair of the damaged tissue itself, it was assumed that intact areas of the brain had taken over this function. This gave rise to the concept of **equipotentiality**, the idea that any given piece of cortical tissue had the potential to support any brain function.

Roughly 50 years prior to the writing of this textbook, and 130 years after the heyday of phrenology, neuroscientists Charles Gross and Lawrence Weiskrantz wrote that "The 'heroic age of our field' was opened by Gall (1835) ... [who] stimulated the search for centers and gave the mass action-localization pendulum its first major swing" (Gross and Weiskrantz, 1964). Implied in this





**FIGURE 1.2** The human brain (see *Chapter 2* and *Web Link 1.1*, a 3-D rotatable and “dissectable” human brain, for labels and terminology). **A.** Lateral view. **B.** Medial view. Source: Dr Colin Chumbley / Science Photo Library. Reproduced with permission.

quote was that understanding the localization–mass action dichotomy would provide insight into understanding key contemporary problems in neuroscience. Indeed, *Thought Box 1.2* elaborates further on this theme precisely because it retains its relevance today, and will prove to be useful for understanding many of the concepts and controversies that are prominent in contemporary cognitive neuroscience.

### **The first scientifically rigorous demonstrations of localization of function**

Although the concepts advocated by Gall, on the one hand, and Flourens, on the other, still resonate today, the same can not be said for most of the “facts” that their work produced. Rather, it was in the mid to late 1800s, during what can be seen as the first return of

## THOUGHT BOX

### 1.2 Localization vs. mass action down through the years

The core question in cognitive neuroscience is *How does the functioning of the brain give rise to cognition and behavior?* One way to approach the question of how a system works is to divide its overall behavior into logically discrete functions, and to determine whether different physical parts of the system might differentially support the different functions. To determine how an automobile works, for example, one might start by logically “decomposing” its overall behavior into two plausibly separable functions, accelerating and sustaining movement vs. decelerating and stopping. This approach naturally leads to a way of thinking about the system as being made up of discrete parts, each of which carries out a different function. However, not all systems are made up of discrete parts, each with a separate function, in the way that an automobile is. One example of such a system is a school of fish. It has properties (overall shape, smoothness of outside surfaces, changes of speed and direction) that cannot be localized to component parts. Each of these properties can be said to be an **emergent property**, in that they don’t exist in any of the constituent elements (i.e., in any one fish), but they “emerge” at the level of the school. (We shall see that many cognitive functions, including consciousness, are believed by many to be emergent.) When considering the school of fish, all parts perform the same function and are interchangeable (i.e., they display equipotentiality), and removing 20% of the fish from one region of the school vs. from a different region will have identical effects on the school (i.e., the principle of mass action applies). Localization of function is not possible with a school of fish. (Note, however, that localization of functions within an individual fish (e.g., moving the tail vs. extracting oxygen from water) *is* possible, and so specifying the grain of detail at which one is studying a system is very important.)

Because automobiles are manmade, we don’t actually have to perform experiments to determine how they work. And it is precisely because we know how they are designed and built that we know that a localization-of-function perspective is the correct way to think about how the different functions of the car are accomplished. Because a school of fish is fully observable (i.e., we know effectively everything that there is to know about what it’s made of), we know that the properties of emergence, equipotentiality, and mass action apply to it. (These are often summarized under the rubric **distributed systems**.) The brain is different from these two examples, however, in that we don’t know all there is to know about how it is “made.” To study it, therefore, cognitive neuroscientists devise models, then test these models with experiments. Although it is not always explicitly acknowledged, these models and/or the techniques used to test them often make an assumption that the brain system under investigation works on fundamentally localizationist or distributed principles. As we start to consider different contemporary problems in cognitive neuroscience, keep in mind that the choice of model and/or method can bias the extent to which one is likely to draw localizationist or mass-action/emergence conclusions from one’s experimental data.

the pendulum back toward localization, that we see the emergence of principles of brain function that, at least to a first order of approximation, have held up through to the present day. These involved the functions of motor control, vision, and language.

#### The localization of motor functions

Beginning in the 1860s, British neurologist John Hughlings Jackson (1835–1911) described the systematic trajectory of certain focal **seizures** that start in the fingers and spread along the arm toward the

trunk, sometimes ending with a loss of consciousness. From this distinctive pattern, which has since come to be known as the *Jacksonian march* (it's as though the seizure is marching along the body), Jackson proposed that the abnormal brain activity presumed to be the cause of the seizures begins in a part of the cortex that controls the fingers, then moves continuously along the surface of the cortex, progressively affecting brain areas that control the palm of the hand, the wrist, the forearm, and so forth. There were two important implications of Jackson's theory. The first was quite simply the proposal that the capacity for movement of the body (i.e., motor control) is a function that is localized within the brain. The second was what has come to be understood as a fundamental principle underlying the organization of function within many portions of the brain, which is that the organization of the brain can mirror the organization of the body (or, as we shall see, of a particular part of the body). Specifically in this case, the proposal was that the area of the brain that controls the muscles of the fingers is adjacent to the area of the brain that controls the muscles of the palm, which is adjacent to the area of the brain that controls the muscles of the wrist, and so forth. Thus, the functions of what came to be known as the *motor cortex* are physically laid out on the surface of the brain in a kind of map of the body (that is, in a **somatotopy**). In this way, the idea of a lawful, **topographic organization** of function was introduced in the void left by the (by-now-largely-discredited) arbitrary, willy-nilly scheme of the phrenologists. (The principle and characteristics of somatotopy will be considered in detail in *Chapter 4* and *Chapter 7*.)

Although the ideas that Jackson proposed were based on careful observation of patients, an idea such as the somatotopic organization of motor cortex couldn't be definitively evaluated without either direct observation or manipulation of the brain itself. The ability to undertake such definitive empirical investigation became possible because Age-of-Enlightenment advances in thinking about how science should be conducted, such as the importance of the scientific method, were being paralleled by technical advances that afforded improved experimental methods. Of particular importance was the development of methods for performing aseptic (i.e., sterile) surgery. These enabled experimenters to keep animals alive for weeks

or longer after performing the **craniotomy** that was necessary to create a lesion or to manipulate the functioning of the brain. Prior to this, infection would often limit postsurgical survival to a matter of hours or days. This technical advance had several important consequences, one of which was that it opened the way for direct stimulation of, and subsequently recording from, the brain of an intact animal (techniques that fall under the category of **neurophysiology**; see *Methodology Box 1.1*). Thus it was that German physicians Gustav Fritsch (1838–1927) and Eduard Hitzig (1838–1907) reported that electrical stimulation of **anterior** portions of the cerebral cortex of the dog, in the **frontal lobe**, produced movements on the opposite side of the body (Fritsch and Hitzig, 1870). Noteworthy were two facts. First, comparable stimulation of a more **posterior** brain region, the parietal lobe, did not produce body movements (*Figure 1.3*). Based on this demonstration of the **anatomical specificity** of their effect (see *Methodology Box 1.1*), Fritsch and Hitzig explicitly challenged the idea of equipotentiality that had been advocated by Flourens. Second, the part of the body affected by electrical stimulation (e.g., neck, forelimb, hindlimb) varied systematically with the positioning of the stimulating electrode. This very directly supported Jackson's idea of a somatotopic organization of motor functions in the brain.

### The localization of visual perception

A second function that was the focus of intense scientific investigation during this period was visual perception. Here, too, the work of Flourens had been influential. Although it had brought to light the principle of crossed lateralization of function – in that lesions of the left hemisphere produced visual impairments in the right visual field, and vice versa – it had found no evidence that this general pattern varied as a function of *where* in the hemisphere the lesion was made. That is, Flourens had failed to find evidence for localization of visual function within a **cerebral hemisphere**. As with other of his null findings, however, this one was overturned thanks to the advent of newer, better, empirical methods. In the case of vision research, the refinement of methods of experimental lesioning was the critical development that led to an important discovery. In particular, the development of aseptic surgical techniques resulted in longer and

## METHODOLOGY BOX

### 1.1 Neuropsychology and the importance of anatomical specificity

Neuropsychology relies on the logic that one way to understand the workings of a system is to systematically remove (or inactivate) parts of it and observe how the removal of each part affects the system's functioning. A neuropsychological study can address the question *Does region A make a necessary contribution to behavior X?*, but it cannot directly address how it is that *region A* may be doing so. That is, it cannot address questions of mechanism. Neurophysiological approaches, on the other hand, can study the manner in which the function of *region A* gives rise to *behavior X*. To give a concrete example, *Chapter 1* describes how neuropsychological experimentation was used to determine definitively that visual perception is localized to the occipital cortex. Not until *Chapter 3*, however (and, chronologically, not until roughly 80 years later), will we see that electrophysiological experiments revealed how it is that neurons in the occipital lobe process visual information. At another level, however, a carefully conducted neuropsychological experiment can support stronger inference about a region's contribution to behavior than can experiments that measure neurophysiological variables, because the former can tell us definitively about whether or not a region's contribution to a type of behavior is *necessary*. Neurophysiological measurement studies, in contrast, are inferentially limited to demonstrating correlations between activity in the brain and the behavior that is being studied. Neurophysiological stimulation studies, such as those of Fritsch and Hitzig that are considered in this chapter's section on *The localization of motor functions*, fall somewhere in between.

In both types of experiment, the strength of one's conclusions can depend on anatomical specificity. What made the Fritsch and Hitzig (1870) experiment so powerful, for example, was the specificity with which it demonstrated that stimulation of a particular portion of the frontal lobe in the left hemisphere produced movement of the right forelimb, and not the right hindlimb, nor the left forelimb. Further, stimulating a nearby area selectively produced movement of a different part of the body, the right hindlimb. Had the authors limited their report to the initial demonstration, two important questions would have been left unanswered. First, *might stimulation of other regions also produce movement of the right forelimb?* Hinging on the answer to this would be an understanding of how localized is the control of the right forelimb. Second, *does stimulation of this region of the brain produce movement of other parts of the body?* The answer to this would give an indication of how specific is the function of brain area in question. These considerations can be particularly important in neuropsychological studies of humans, such as those described in this chapter's section on *The localization of speech*, because such studies often rely on "accidents of nature," such as stroke, **neurodegenerative disease**, or head injury. In such studies, scientists have no control (other than patient selection) over the extent of damage in such patients, neither in terms of how many structures may be damaged, nor of the overall volume of tissue that is affected. When patient lesions are large, there is an inherent difficulty in determining which of the damaged structures is responsible for the observed behavioral deficit. One logical way to tackle this problem, the "double dissociation of function," will be introduced in *Chapter 5* (in *Research Spotlight 5.1*. and *Methodology Box 5.1*).



**FIGURE 1.3** Illustration of a top-down view of a dog's brain, with symbols indicating, from rostral to caudal, the areas whose stimulation produced muscle contractions on the right side of the body of the neck, forelimb, and hindlimb, respectively. Source: Fritsch and Hitzig, 1870.

healthier postsurgical survival of experimental animals than had previously been possible. This, in turn, afforded considerably more sophisticated and conclusive assessments of behavior. Indeed, for a time, it was not uncommon for a researcher to bring a lesioned animal to a scientific conference so as to demonstrate the behavioral alterations produced by a particular lesion. Perhaps for related reasons, this period also saw an increase in research with monkeys, whose brain and behavior are more comparable to those of humans than are those of, say, birds and carnivores. It is much more expensive to acquire and house monkeys relative to other species, such as birds, rodents, and carnivores. Thus, research with monkeys would not have been considered practical prior to nineteenth-century refinements of surgical techniques. (See *Thought Box 1.3* for a consideration of the role of nonhuman animals in neuroscience research.)

The discovery of a region specialized for motor control was quickly followed by intense research on the neural bases of visual perception. Using electrical stimulation techniques and surgical lesioning, initial research in dogs and in monkeys indicated a privileged role for posterior regions in supporting visual perception. That is, whereas it had been shown conclusively that motor control did *not* depend on posterior regions, the opposite was true for vision. The final decades of the nineteenth century witnessed vociferous debate about whether the “visual centres,” a characterization of British physiologist David Ferrier (1843–1928), were localized to a region of

the parietal cortex or to a region of the occipital cortex (*Figure 1.4*). This research, carried out primarily in monkeys and most prominently by Ferrier, by Berlin-based physiologist Hermann Munk (1839–1912), and by London-based physiologist Edward Schäfer (1850–1935), gradually converged on the conclusion that the region whose destruction produced frank and lasting blindness – as opposed to more nuanced and transient visual deficits – was the occipital cortex. This conclusion, reinforced by observations of human patients with head injuries, led to the universally accepted localization of **primary visual cortex** to the occipital lobe.

### The localization of speech

The last function of the brain that we will consider in this introductory chapter is language; more specifically, the ability to speak. The faculty of language had been localized by phrenologists to a region of the frontal lobe directly behind the eyes. (This idea is said to have derived from Gall's observation of a classmate who had a prodigious verbal memory and protruding eyes, the latter presumed by Gall to be the result of a bulging frontal lobe that pushed the eyes forward.) As was the case with motor control, the post-phrenology study of language began with clinical observations. In the decades prior to the 1860s, isolated reports indicated, in some cases, that damage to the left side of the brain was associated with impairments of speech, in others, that damage to anterior portions of the brain had this effect. As these cases accumulated, the more specific idea emerged that anterior portions of the left hemisphere were important for speech. During the 1860s, French surgeon Paul Broca (1824–1880) published a series of case studies that confirmed this idea. Most celebrated was the case of the **stroke** patient “Tan,” so nicknamed because this was the only sound that he could make with his mouth. (Phonetically, “tan” is pronounced in French as /tân/.) Importantly, Tan's impairment was specific to *speech production* (i.e., talking), because he could understand and follow verbal instructions that he was given. Additionally, there wasn't any obvious paralysis of the speech apparatus, in that, despite some right-side-of-the-body motor impairment, he could eat and drink and make his famous verbal utterance. Upon Tan's death, Broca examined the patient's brain and concluded from the prominent damage that he observed (*Figure 1.5*) that

## THOUGHT BOX

### 1.3 The role of nonhuman animals in neuroscience research

It is evident from this historical overview that modern cognitive neuroscience could not have been developed without research conducted on nonhuman animals. It is equally true that research performed on nonhuman animals continues to play a critical and necessary role in every branch of contemporary cognitive neuroscience. The reason for this, as you will see in each chapter, is that many questions about physiology and anatomy cannot be answered scientifically without carrying out experiments that are invasive. Reading this book will also make clear that, although we have learned an astounding amount of information about how the workings of the brain give rise to cognition, there remains an enormous amount that we still don't know. Despite recent and ongoing advances in a variety of noninvasive methods that can be used to study the brain (such as neuroimaging and computer modeling), there will continue, for the foreseeable future, to be questions that can be answered through no means other than invasive experimentation.

Because of these facts, another sociological factor with which the cognitive neuroscientist must be conversant (in addition to those raised in the second paragraph of this chapter) is the ethics of animal research. This is true even for researchers such as the author of this textbook, whose research is conducted exclusively on human subjects. This is because many ideas that motivate our experiments come from research that was performed with animals, and our ability to interpret our data often depends on what has been learned from animal research. For an informal index of this, consider the syllabus for my research group's lab meetings. During the academic semester that preceded the writing of this thought box, my group met on 14 occasions, and on each we discussed an article from a scientific journal that is relevant for our research. Of these 14 meetings, four (i.e., nearly 30%) were devoted to articles describing research performed with nonhuman animals.

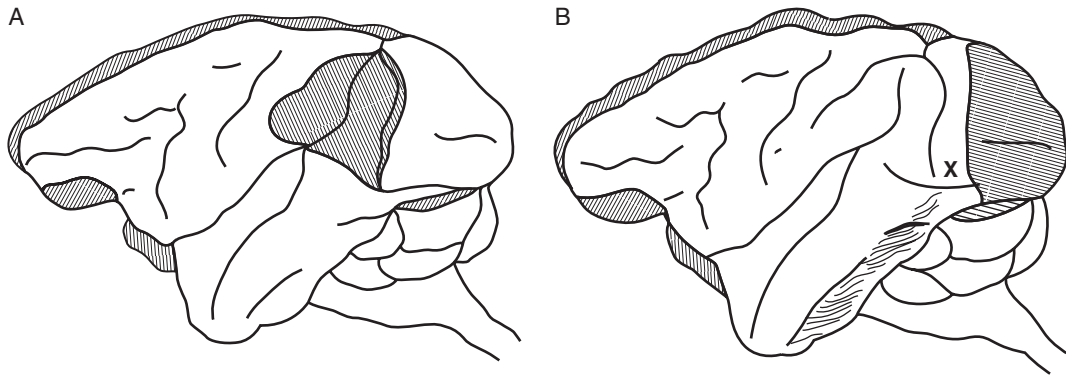
This brings up a stylistic point: throughout the book, when I refer to "primates" without any other context, I'm referring to all species within this taxonomic order (which includes humans). Typically this will be in the context of a structure/function/behavior that is shared by primates, but does not generalize to other mammals.

The ethics of animal research are complex, and the topic can arouse strong emotions. Debates are often framed in hypothetical terms for which there are no objectively "right" or "wrong" answers. One question that has been contemplated, for example, is *If one encounters a burning building and there's only time to save the human who is inside or the mouse that is inside (or the dog, or the monkey, ...), which does one save?* You can see how two people could devote an afternoon to debating whether or not this analogy is even appropriately relevant to the question of animal research. Although a more detailed consideration of this topic is outside the purview of this book, the *Further Reading* from neuroscientist Dario Ringach (2011) nicely summarizes many of the arguments in favor of and in opposition to animal research, and provides references to writings that represent both the pro and the con sides of the debate.

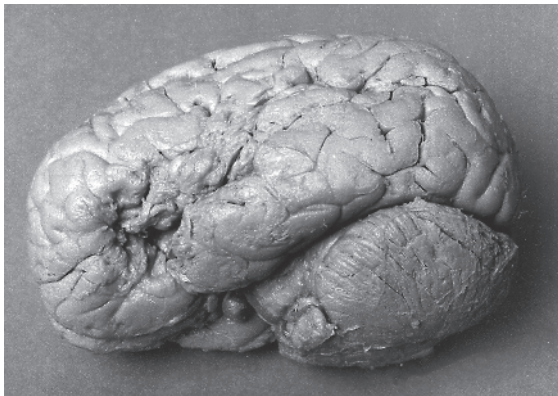
the ability to speak was localized to the "posterior third of the third convolution" (a portion of the left inferior frontal gyrus that today is known as Broca's area). It's worth taking a moment to consider why Broca, rather than some of his predecessors and contemporaries who had made similar observations

of patients, gets the credit for this discovery. One important factor is that Broca's reports were seen as confirming an idea that had been predicted ahead of time – a sequence of events that fit with the era's increasing emphasis on hypothesis testing as an important element of the scientific method.





**FIGURE 1.4** Two experimental lesions produced by Ferrier in experiments designed to localize the cortical locus of visual processing. Panel **A** illustrates a lesion of the parietal lobe that Ferrier interpreted in 1876 as producing lasting blindness, and, a decade later, as producing only temporary blindness. Panel **B** illustrates a lesion of the occipital lobe that he interpreted as producing no visual impairments. Neuroscientist Charles Gross (1998) has marked with an X the region that we now know to represent central (i.e., foveal) vision, a topic to be explored in depth in *Chapter 3*. These lesions, and their interpretation, illustrate how difficult it was for nineteenth-century neuroscientists to localize cognitive functions in the brain.



**FIGURE 1.5** The left external surface of the brain of Broca's patient Tan. Note the extensive damage in the posterior inferior frontal gyrus, a region that has come to be known as Broca's area. Source: Reproduced with permission from the Dupuytren Museum, Pierre and Marie Curie University, Paris. Reproduced in N. F. Dronkers, O. Plaisant, M. T. Iba-Zizen, and E. A. Cabanis. Paul Broca's historic cases: high resolution MR imaging of the brains of Leborgne and Lelong *Brain* (2007) 130 (5): 1432–1441, Figure 3A. Photograph by Bruno Delamain.

## WHAT IS A BRAIN AND WHAT DOES IT DO?

As we conclude this whirlwind review of the birth of modern brain science, it is interesting to consider why *motor control*, *vision*, and *language* were among the first three functions of the brain to yield to newly developed ways of thinking about and doing science. With particular relevance to the first two, let's pose the general questions of *What is a brain?* and *What does it do?* For example, what properties do animals with brains share that living organisms without brains (trees, for example) do not? One answer is that brains confer the ability to detect changes in the environment – let's say a falling rock – and to take an appropriate action: to get out of the way. The hapless tree, on the other hand, has no means of acquiring the information that something potentially dangerous is happening, nor the ability to do anything about it. So it gets crushed. Thus, the ability to see (i.e., vision) and the ability to move (i.e., motor control) are functions that are relatively easy to observe and measure. The same is not true for more nuanced examples of brain-mediated events that

occur in the world. Let's take the example of writing the textbook that you're reading right now. Certainly, vision and motor control were involved. (For example, when I received an emailed inquiry from the publisher about writing this textbook, I used vision to read the pattern of black and white characters on the computer screen that conveyed the inquiry from the publisher.) There were also, however, many additional steps. These included judgment and decision making (*Is it worth all the extra work to take this on? Are the terms of my contract with the publisher acceptable?*), retrieving long-term memories (*There's that great quote from Gross's chapter in the Warren & Akert book that I should use here*), making (and retrieving) new long-term memories (*Where did I put my copy of the MIT Encyclopedia of the Cognitive Sciences the last time I was working on this chapter?*), and much, much, more. These latter operations are "internal" or "mental," in the sense that they happened in my mind, without any obvious way of seeing or measuring them. Thus, although many aspects of so-called **high-level cognition** – including decision making and different aspects of memory – are the focus of intense research in contemporary cognitive neuroscience, we shall see that the ability to define what constitutes a distinct function (analogous to vision or motor control), as well as the ability to localize the brain region(s) on which these functions depend, become much more complicated propositions. The principles that explain how such functions work will be less accessible to direct observation and measurement than are brain functions that are more closely tied to either the "input" of information to the brain (in the example of vision), or the "output" of the brain that is expressed via movements of the body (i.e., the actions of the organism). (However, as we shall see, there are influential perspectives on brain function as a whole that construe it as a hierarchically organized series of **sensorimotor circuits**, with the more abstract ones (e.g., all the processes that went into writing a textbook) having been superimposed, over the course of evolution, onto more basic ones (e.g., reflexive avoidance of a threat).)

Okay, so the neural bases of vision and motor control may have been among the first to be studied "scientifically" because they are easy to observe. But the

same cannot be said about language. Although its production clearly has motoric components, we've already reviewed ways in which the language impairment experienced by Tan and other patients was fundamentally different than paralysis. Indeed, in ways, language can be construed as being at the opposite end of the concrete-to-abstract continuum of human faculties that spans from such "concrete" (that is, easily observable and relatively easily measurable) functions as vision and motor control to the most abstract aspects of conscious thought. Although language is readily observable, there is also a sense in which it epitomizes abstract, high-level cognition. One reason is that language entails the use of arbitrary, abstract codes (i.e., a **natural language**) to represent meaning. Intuitively, because many of us have the sense that we "think in words," language can be viewed as "the stuff of thought," and thus epitomizes an "internal," indeed, a *cognitive*, function. And so I'm reticent to conclude that language was among the first human faculties to be studied with modern neuroscientific techniques because it is easy to observe. Instead, what I'll offer is that it is language's intuitive "specialness," and its seeming uniqueness to humans, that has made it a focus of interest for millennia. The Age of Enlightenment, then, may simply be the epoch of human history when developments in the scientific method caught up with an aged-old focus of human curiosity.

## LOOKING AHEAD TO THE DEVELOPMENT OF COGNITIVE NEUROSCIENCE

To conclude this introductory chapter, we see that by the dawn of the twentieth century, brain scientists were beginning to investigate the brain from both ends of the continuum that captures its functions in relation to the outside world. In the process, we can think of modern brain science as developing along two paths. The first, pursued by physiologists and anatomists who studied brain structure and function in nonhuman animals, focused on neural *systems* that support various functions (e.g., visual perception and motor control), and has come to be known as systems neuroscience. The second took as its starting point a human behavior, such as language, and proceeded with the logic that careful



study of the way that the behavior in question is altered by insults to the brain can be informative, with respect both to how the behavior is organized, and to how the workings of the brain give rise to this organization. This latter approach has matured into the allied disciplines of behavioral neurology (when carried out by physicians) and neuropsychology (when carried out by non-physician scientists). Now of course, the notion of two categories of brain science developing in parallel at the dawn of modern brain science is an overly facile dichotomization imposed by this author, and many instances can be found that do not fit neatly into such a taxonomy (see *Tip 1.4*). Nonetheless, we will find this distinction to be useful as we proceed. It is these two scientific traditions summarized in this chapter, together with a third, experimental psychology (which also got its start in the second half of the nineteenth century, but which won't be covered in depth here (see *Further Reading* sections)), that provide the foundation from which modern cognitive neuroscience has emerged. Before we plunge full-on

### Tip 1.4

One example of the two major categories of neuroscience influencing the work of one investigator can be seen with Eduard Hitzig. His electrical stimulation experiments with Frisch are recognized as foundational in launching systems neuroscience. A formative influence that may have inspired these experiments, however, was the time earlier in his life when Hitzig served as a battlefield physician in the Prussian army. In this capacity, he encountered many soldiers who evinced various behavioral deficits as a result of injuries to the head acquired in battle.

into cognitive neuroscience itself, however, we need to review some facts about the brain – how it is put together (gross anatomy), and how it works (cellular physiology and network dynamics). These will be the focus of *Chapter 2*.

## END-OF-CHAPTER QUESTIONS

1. How does cognitive neuroscience differ from the related disciplines of cognitive psychology and systems neuroscience?
2. Although most of the specific claims arising from phrenology turned out to be factually incorrect, in what ways did they represent an important development in our thinking about the brain?
3. One of the major flaws of phrenology concerns the functions that it sought to relate to the brain: in some cases, they were not valid constructs; in others, they weren't amenable to neuroscientific explanation at the level that Gall was seeking to capture. From the phrenological bust in *Figure 1.1*, select at least one function to which each of these critiques applies, and explain your reasoning.
4. In the nineteenth century, what kind of scientific evidence was marshaled to support mass-action models of the brain? To support localizationist models of the brain?
5. Might it be possible that some tenets of mass-action and localization-of-function models could both be true? If yes, how might this be possible?
6. How does the concept of anatomical specificity relate to testing hypotheses of mass action and localization of function?
7. The neural bases of what domains of behavior were the first to be systematically explored in the second half of the nineteenth century? For each, what is a likely explanation?
8. What is the principle of topographic representation in the brain? Although this chapter emphasized the topographic organization of the motor system, according to what principles/dimensions might the topography of various sensory modalities (e.g., vision, somatosensation, audition) be organized?
9. Apart from one study that employed electrical stimulation, this chapter described experiments that relied on inferring the neural bases of a function from observation/measurement of the consequences of damage to different parts of the brain. Nonetheless, there are two fundamentally different ways in which one can pursue such research. Describe them, and name the disciplines of science and/or medicine that are associated with each. Which of the two requires the use of nonhuman experimental animals?

## REFERENCES

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- Finger, Stanley. 2000. *Minds Behind the Brain*. Oxford: Oxford University Press.
- Fritsch, Gustav, and Eduard Hitzig. 1870. "Über die elektrische Erregbarkeit des Grosshirns." *Archiv für Anatomie, Physiologie und wissenschaftliche Medicin* 37: 300–332. [Available in English translation as: Fritsch, Gustav, and Eduard Hitzig. 2009. "Electric excitability of the cerebrum (Über die elektrische Erregbarkeit des Grosshirns)." *Epilepsy and Behavior* 15 (2): 123–130. doi: 10.1016/j.yebeh.2009.03.001.]
- Gross, Charles G. 1998. *Brain, Vision, Memory*, Cambridge, MA: MIT Press.
- Gross, Charles G., and Lawrence Weiskrantz, L. 1964. "Some Changes in Behavior Produced by Lateral Frontal Lesions in the Macaque." In *The Frontal Granular Cortex and Behavior*, edited by John M. Warren and Konrad Akert, 74–98. New York: McGraw-Hill.
- Spurzheim, Johann C. 1834. *Phrenology or the Doctrine of the Mental Phenomenon*, 3rd ed. Boston: Marsh, Capen, and Lyon.

## OTHER SOURCES USED

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- Calvin, William H., and George A. Ojemann. 1994. *Conversations with Neil's Brain*. Reading, MA: Addison Wesley.
- Finger, Stanley. 1994. *Origins of Neuroscience*. Oxford: Oxford University Press.
- Gross, Charles G. 2007. "The Discovery of Motor Cortex and Its Background." *Journal of the History of the Neurosciences: Basic and Clinical Perspectives* 16 (3): 320–331. doi: 10.1080/09647040600630160.
- Holyoak, Keith J. 1999. "Psychology." In *The MIT Encyclopedia of the Cognitive Sciences*, edited by Robert A. Wilson and Frank C. Keil, xxxix–xlix. Cambridge, MA: MIT Press.
- Kolb, Bryan, and Ian Q. Whishaw. 2003. *Fundamentals of Human Neuropsychology*, 5th ed. New York: Worth Publishers.
- Whitaker, Harry, A. 1999. "Broca, Paul." In *The MIT Encyclopedia of the Cognitive Sciences*, edited by Robert A. Wilson and Frank C. Keil, 97–98. Cambridge, MA: MIT Press.

## FURTHER READING

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- Boring, Edwin G. 1929. "The Psychology of Controversy." *Psychological Review* 36 (2): 97–121.  
*A classic overview of key developments in nineteenth-century psychology and psychophysics, adapted from Boring's Presidential Address to the American Psychological Association, delivered on 28 December 1928. Boring was a professor at Harvard University.*
- Finger, Stanley. 2000. *Minds Behind the Brain*. Oxford: Oxford University Press.  
*A history, stretching from ancient Egypt to twentieth-century North America and Europe, of scientists who have made seminal contributions to the understanding of the structure and functions of the brain. It is longer and covers a broader scope of topics than Gross (1998). Finger has authored many authoritative books on the history of neuroscience, and is Editor-in-Chief of the Journal of the History of the Neurosciences.*
- Gross, Charles G. 1998. *Brain, Vision, Memory*. Cambridge, MA: MIT Press.  
*A highly engaging collection of "Tales in the history of neuroscience." It spans the same range of human history as does Finger (2000), but with fewer chapters and a narrower focus of the functions named in the title. The author is, himself, a highly respected visual neuroscientist, now Emeritus Professor at Princeton University.*
- Ringach, Dario L. 2011. "The Use of Nonhuman Animals in Biomedical Research." *American Journal of Medical Science* 342 (4): 305–313.  
*Ringach is a UCLA-based neuroscientist whose person, family, and house have been the targets of harassment and intimidation by animal rights activists. This fact, however, does not color this even-toned consideration of this debate. Among other things, he urges "civil discourse ... free of threats and intimidation," and concludes that "The public deserves an open and honest debate on this important topic." The article contains extensive references to original writings by individuals offering many different perspectives on this debate.*