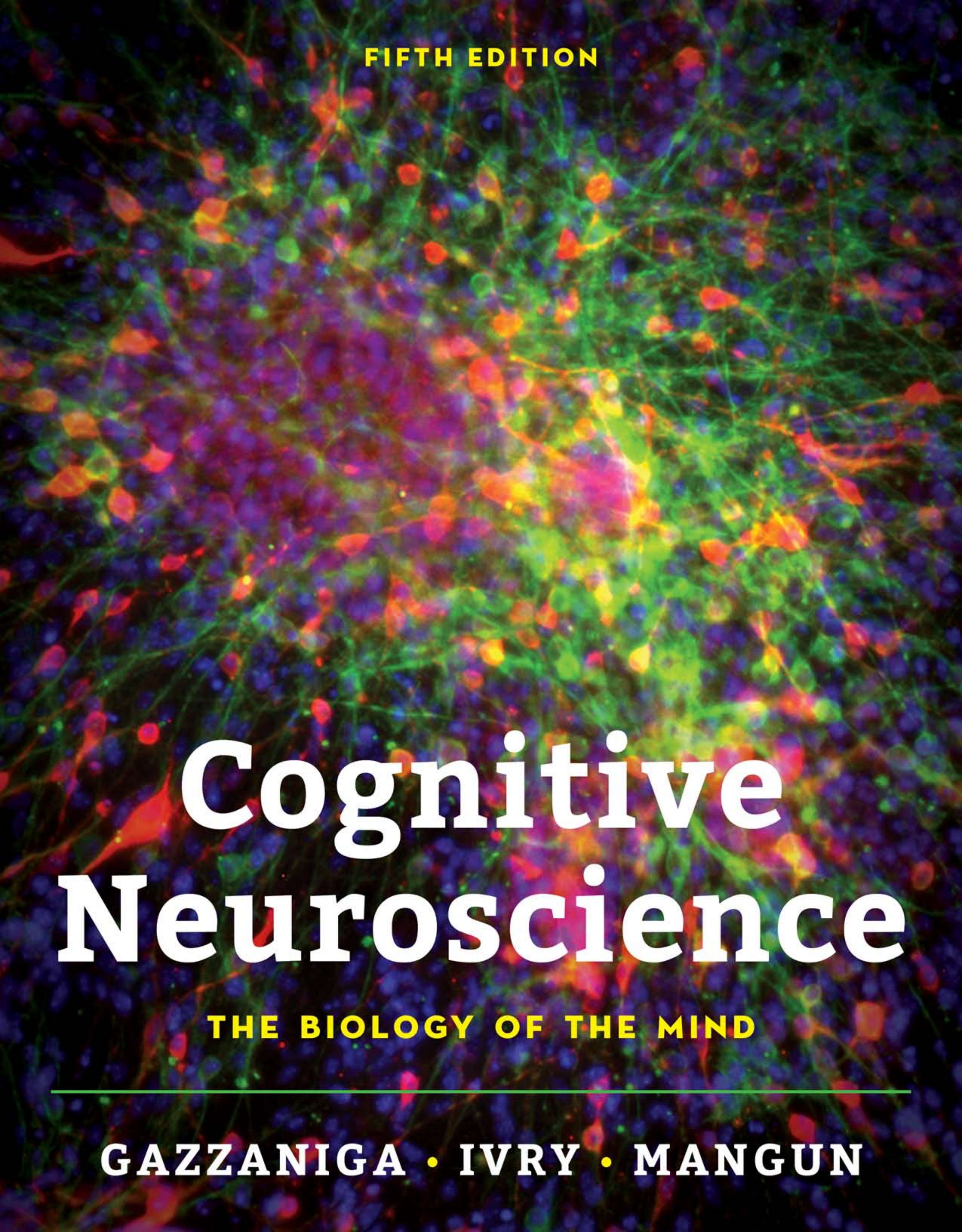

FIFTH EDITION

Cognitive Neuroscience

THE BIOLOGY OF THE MIND

GAZZANIGA · IVRY · MANGUN

FIFTH EDITION

Cognitive Neuroscience

The Biology of the Mind

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With special appreciation for the Fifth Edition to Rebecca A. Gazzaniga, MD

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For Lilly, Emmy, Garth, Dante,
Rebecca, and Leonardo
M.S.G.

For Henry and Sam
R.B.I.

For Nicholas and Alexander
G.R.M.

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Preface

Welcome to the Fifth Edition! When cognitive neuroscience emerged in the late 1970s, it remained to be seen whether this new field would have "legs." Today, the answer is clear: the field has blossomed in spectacular fashion. Cognitive neuroscience is well represented at all research universities, providing researchers and graduate students with the tools and opportunities to develop the interdisciplinary research programs that are the mainstay of the field. Multiple journals, some designed to cover the entire field, and others specialized for particular methodologies or research themes, have been launched to provide venues to report the latest findings. The number of papers increases at an exponential rate. The Cognitive Neuroscience Society has also flourished and just celebrated its 25th year.

The fundamental challenge we faced in laying the groundwork for our early editions was to determine the basic principles that make cognitive neuroscience distinct from physiological psychology, neuroscience, cognitive psychology, and neuropsychology. It is now obvious that cognitive neuroscience overlaps with, and synthesizes, these disciplinary approaches as researchers aim to understand the neural bases of cognition. In addition, cognitive neuroscience increasingly informs and is informed by disciplines outside the mind–brain sciences, such as systems science and physics, as exemplified by our new Chapter 14: "The Consciousness Problem."

As in previous editions of this book, we continue to seek a balance between psychological theory, with its focus on the mind, and the neuropsychological and neuroscientific evidence about the brain that informs this theory. We make liberal use of patient case studies to illustrate essential points and observations that provide keys to understanding the architecture of cognition, rather than providing an exhaustive description of brain disorders. In every section, we strive to include the most current information and theoretical views, supported by evidence from the cutting-edge technologies that are such a driving force in cognitive neuroscience. In contrast to purely cognitive or neuropsychological approaches, this text emphasizes the convergence of evidence that is a crucial aspect of any science, particularly studies of higher mental function. To complete the story, we also provide examples of research that uses computational techniques.

Teaching students to think and ask questions like cognitive neuroscientists is a major goal of our text. As cognitive neuroscientists, we examine mind–brain relationships using a wide range of techniques, such as functional and structural brain imaging, neurophysiological recording in animals, human EEG and MEG recording, brain stimulation methods, and analysis of syndromes resulting from brain damage. We highlight the strengths and weaknesses of these methods to demonstrate how these techniques must be used in a complementary manner.

We want our readers to learn what questions to ask, how to choose the tools and design experiments to answer these questions, and how to evaluate and interpret the results of those experiments. Despite the stunning progress of the neurosciences, the brain remains a great mystery, with each insight inspiring new questions. For this reason, we have not used a declarative style of writing throughout the book. Instead, we tend to present results that can be interpreted in more than one way, helping the reader to recognize that alternative interpretations are possible.

Since the first edition, there have been many major technological, methodological, and theoretical developments. There has been an explosion of brain-imaging studies; indeed, thousands of functional imaging studies are published each year. New technologies used for noninvasive brain stimulation, magnetic resonance spectroscopy, electrocorticography, and optogenetics have been added to the arsenal of the cognitive neuroscientist. Fascinating links to genetics, comparative anatomy, computation, and robotics have emerged. Parsing all of these studies and deciding which ones should be included has been a major challenge for us. We firmly believe that technology is a cornerstone of scientific advancement. Thus we have felt it essential to capture the cutting-edge trends in the field, while keeping in mind that this is an undergraduate survey text.

The first four editions provide compelling evidence that our efforts have led to a highly useful text for undergraduates taking their first course in cognitive neuroscience, as well as a concise reference volume for graduate students and researchers. Over 500 colleges and universities worldwide have adopted the text. Moreover, instructors tell us that in addition to our interdisciplinary approach, they like that our book has a strong narrative voice and offers a manageable number of chapters to teach in a one-semester survey course.

With every revised edition including this one, we have had to do some pruning and considerable updating to stay current with all of the developments in the field of cognitive neuroscience. We thought it essential to include new methods and, correspondingly, new insights that these tools have provided into the function of the brain, while being selective in the description of specific experimental results. The following table lists the major changes for each chapter.

Chapter	Changes in the Fifth Edition
1. A Brief History of Cognitive Neuroscience	Expanded discussion of the theoretical leap made by the early Greeks that enabled scientific endeavors. Added discussion of monism versus dualism and the mind–brain problem.
2. Structure and Function of the Nervous System	Added discussion of specific neurotransmitters. Added discussion of neural circuits, networks, and systems. Expanded discussion of the cortex from the viewpoint of functional subtypes. Added discussion of neurogenesis throughout the life span.
3. Methods of Cognitive Neuroscience	Updated discussion of direct and indirect stimulation methods used to probe brain function and as a tool for rehabilitation. Expanded discussion of electrocorticography. Added discussion of new methods to analyze fMRI data, including measures of connectivity. Added section on magnetic resonance spectroscopy.
4. Hemispheric Specialization	Expanded discussion of the problem of cross-cuing when evaluating the performance of split-brain patients. Added discussion of differing patterns of functional connectivity in the right and left hemispheres. Added discussion of atypical patterns of hemispheric lateralization. Expanded section on modularity.
5. Sensation and Perception	Added section on olfaction, tears, and sexual arousal. Added review of new concepts regarding gustatory maps in the cortex. Expanded section on perceptual and cortical reorganization after sensory loss. Added section on cochlear implants.
6. Object Recognition	Added section on decoding the perceptual content of dreams. Added discussion of deep neural networks as a model of the hierarchical organization of visual processing. Added section on feedback mechanisms in object recognition. Expanded section on category specificity.
7. Attention	Expanded discussion of neural oscillations and neural synchrony and attention. Updated discussion of pulvinar contributions to attentional modulation and control.
8. Action	Expanded discussion of the recovery from stroke. Updated with latest findings in research on brain–machine interface systems. Updated discussion of deep brain stimulation and Parkinson’s disease. Added discussion of the contributions of the cortex and subcortex to skilled motor movement.

Chapter	Changes in the Fifth Edition
9. Memory	Added brief section on dementias. Added discussion of the contribution of corticobasal ganglia loops to procedural memory. Expanded discussion of priming and amnesia. Updated discussion of frontal cortex activity and memory formation. Added brief section on learning while sleeping. Updated discussion of an unexpected finding concerning the cellular mechanisms of memory storage.
10. Emotion	Added section on the hypothalamic-pituitary-adrenal axis. Added discussion of theoretical disagreements between researchers of human emotion and nonhuman animal emotion. Added brief discussion of the role of the periaqueductal gray in emotion. Updated discussion of emotion and decision making.
11. Language	Added brief description of connectome-based lesion-symptom mapping for aphasic patients. Added section on feedback control and speech production. Updated discussion of language evolution in primates. Added investigation of how the brain represents semantic information.
12. Cognitive Control	Added section on cognitive control issues associated with neuropsychiatric disorders. Expanded discussion of decision making and reward signals in the brain. Added section on brain training to improve cognitive control.
13. Social Cognition	Added brief section on the development of social cognition. Added brief discussion of social isolation. Updated section on autism spectrum disorder. Updated discussion of the default network and social cognition. Added section on embodiment and visual body illusions, and body integrity identity disorder.
14. The Consciousness Problem	Added section on levels of arousal. Added section on the layered architecture of complex systems. Added discussion of sentience versus the content of conscious experience. Added discussion of the principle of complementarity in physics and how it may apply to the mind–brain problem.

Inspired by feedback from our adopters, we have also made the text even more user-friendly and focused on the takeaway points. Some ways in which we have made the Fifth Edition more accessible include the following:

- Each chapter now begins with a series of "Big Questions" to frame the key themes of the chapter.
- The introductory stories have been trimmed, and many of them feature patient case studies to engage students.
- "Anatomical Orientation" figures open Chapters 4 through 14 to highlight the brain anatomy that will be addressed in the pages that follow.
- Major section headings have been numbered for easy assigning. Each section ends with a set of bulleted "Take-Home Messages."
- Figure captions have been made more concise and more focused on the central teaching point.
- Two new types of boxes ("Lessons from the Clinic" and "Hot Science") feature clinical and research examples in cognitive neuroscience.

As with each edition, this book is the result of a dynamic yet laborious interactive effort among the three of us, along with extensive discussions with our colleagues, our students, and our reviewers. The product has benefited immeasurably from these interactions. Of course, we are ready to modify and improve any and all of our work. In our earlier editions, we asked readers to contact us with suggestions and questions, and we do so again. We live in an age where interaction is swift and easy. We are to be found as follows: gazzaniga@ucsb.edu; mangun@ucdavis.edu; ivry@berkeley.edu.

Good reading and learning!

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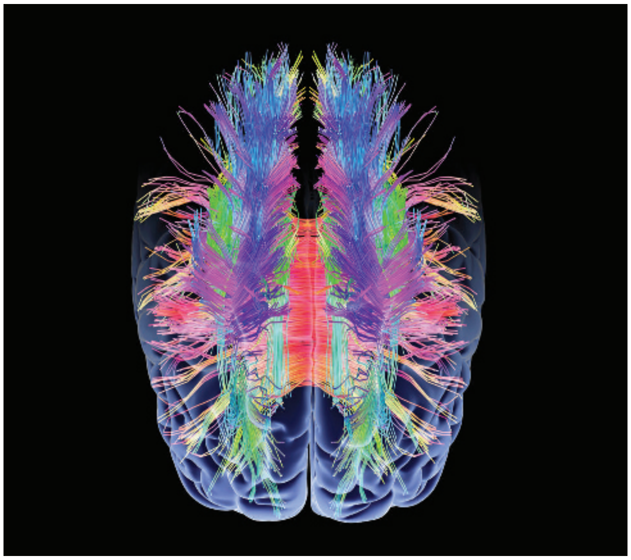

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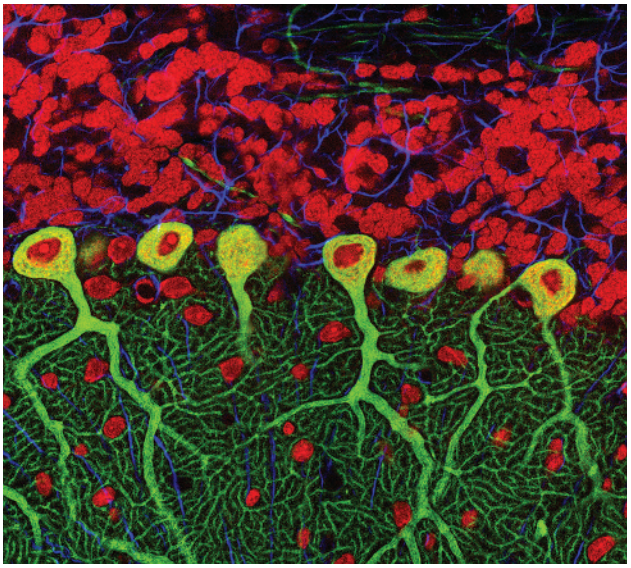

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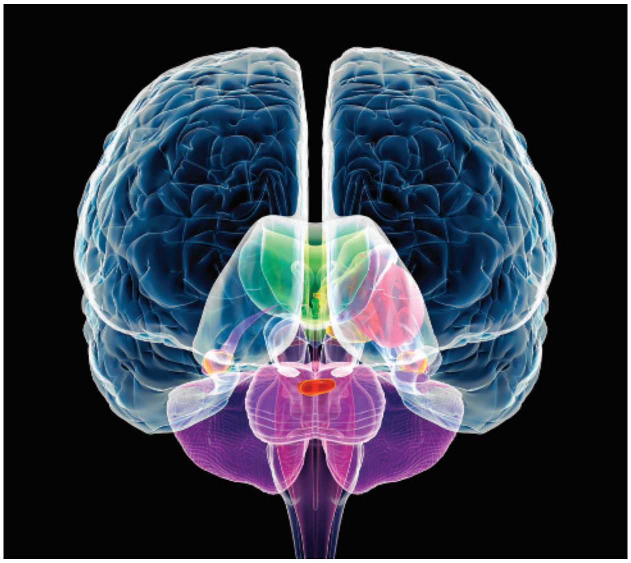

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FIFTH EDITION

Cognitive Neuroscience

The Biology of the Mind

> In science it often happens that scientists say, "You know that's a really good argument; my position is mistaken," and then they actually change their minds and you never hear that old view from them again. They really do it. It doesn't happen as often as it should, because scientists are human and change is sometimes painful. But it happens every day. I cannot recall the last time something like that happened in politics or religion.
>
> *Carl Sagan, 1987*

A Brief History of Cognitive Neuroscience

CHAPTER

1

ANNE GREEN WALKED to the gallows in the castle yard of Oxford, England, in 1650, about to be executed for a crime she had not committed: murdering her stillborn child. No doubt she felt scared, angry, and frustrated, and many thoughts raced through her head. However, "I am about to play a role in the founding of clinical neurology and neuroanatomy"—though accurate—certainly was not one of them. She proclaimed her innocence to the crowd, a psalm was read, and she was hanged. She hung there for a full half hour before she was taken down, pronounced dead, and placed in a coffin provided by Drs. Thomas Willis and William Petty. This was when her luck began to improve. Willis and Petty were physicians and had been given permission from King Charles I to dissect, for medical research, the bodies of any criminals killed within 21 miles of Oxford. So, instead of being buried, Green's body was carried to their office.

An autopsy, however, was not what took place. As if in a scene from Edgar Allan Poe, the coffin began to emit a grumbling sound. Green was alive! The doctors poured spirits in her mouth and rubbed a feather on her neck to make her cough. They rubbed her hands and feet for several minutes, bled 5 ounces of blood, swabbed her neck wounds with turpentine, and cared for her through the night. The next morning, feeling more chipper, she asked for a beer. Five days later, she was out of bed and eating normally (Molnar, 2004; Zimmer, 2004).

After her ordeal, the authorities wanted to hang Green again. But Willis and Petty fought in her defense, arguing that her baby had been stillborn and its death was not her fault. They declared that divine providence had stepped in and provided her miraculous escape from death, thus proving her innocence. Their arguments prevailed. Green was set free and went on to marry and have three more children.

This miraculous incident was well publicized in England (**Figure 1.1**). Thomas Willis (**Figure 1.2**) owed much to Anne Green and the fame brought to him by the events of her resurrection. With it came money he desperately needed and the

BIG Questions

- Why were the ancient Greeks important to science?
- What historical evidence suggested that the brain's activities produce the mind?
- What can we learn about the mind and brain from modern research methods?

FIGURE 1.1
An artistic rendition of the miraculous resurrection of Anne Green in 1650.

prestige to publish his work and disseminate his ideas, and he had some good ones. Willis became one of the best-known doctors of his time: He coined the term *neurology*, and he was the first anatomist to link specific brain damage—that is, changes in brain structure—to specific behavioral deficits and to theorize how the brain transfers information. He drew these conclusions after treating patients throughout their lives and autopsying them after their deaths.

With his colleague and friend Christopher Wren (the architect who designed St. Paul's Cathedral in London), Willis created drawings of the human brain that remained the most accurate representations for 200 years (**Figure 1.3**). He also coined names for numerous brain regions (**Table 1.1**; Molnar, 2004; Zimmer, 2004). In short, Willis set in motion the ideas and knowledge base that took hundreds of years to develop into what we know today as the field of cognitive neuroscience.

FIGURE 1.2
Thomas Willis (1621–1675), a founder of clinical neuroscience.

In this chapter we discuss some of the scientists and physicians who have made important contributions to this field. You will discover the origins of cognitive neuroscience and how it has developed into what it is today: a discipline geared toward understanding how the brain works, how brain structure and function affect behavior, and ultimately how the brain enables the mind.

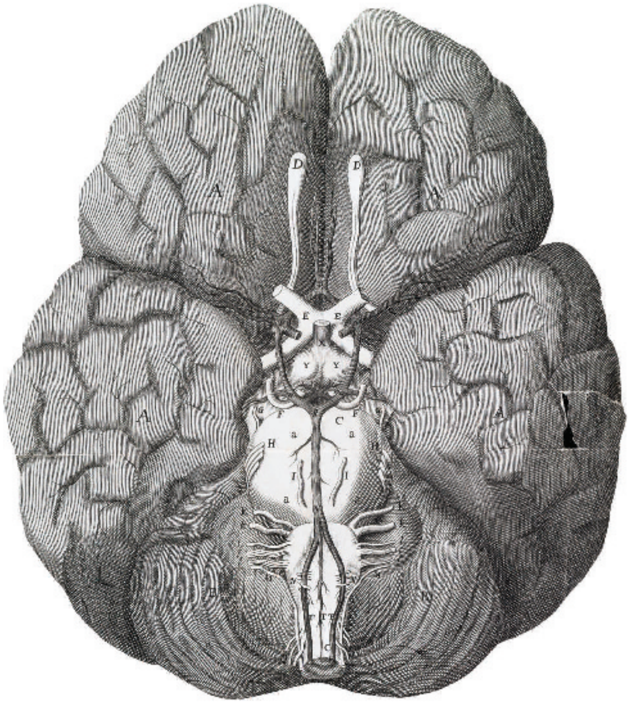


FIGURE 1.3 The human brain (ventral view) drawn by Christopher Wren.
Wren made drawings for Thomas Willis's *Anatomy of the Brain and Nerves*. The circle of dark vessels in the very center of the drawing was named the circle of Willis by one of Willis's students, Richard Lower.

1.1 A Historical Perspective

The scientific field of **cognitive neuroscience** received its name in the late 1970s in the back seat of a New York City taxi. One of us (M.S.G.) was riding with the great cognitive psychologist George A. Miller on the way to a dinner meeting at the Algonquin Hotel. The dinner was being held for scientists from Rockefeller and Cornell universities, who were joining forces to study how the brain enables the mind—a subject in need of a name. Out of that taxi ride came the term *cognitive neuroscience*—from *cognition*, or the process of knowing (i.e., what arises from awareness, perception, and reasoning), and *neuroscience* (the study of how the nervous system is organized and functions). This seemed the perfect term to describe the question of understanding how the functions of the physical brain can yield the thoughts, ideas, and beliefs of a seemingly intangible mind. And so the term took hold in the scientific community.

When considering the miraculous properties of brain function, bear in mind that Mother Nature built our brains through the process of evolution by natural selection. Unlike computers, our brains were designed not by a team of rational engineers, but through trial and error, and they are made of living cells, not inert substances.

TABLE 1.1 A Selection of Terms Coined by Thomas Willis

Term	Definition
Anterior commissure	Axonal fibers connecting the middle and inferior temporal gyri of the left and right hemispheres.
Cerebellar peduncles	Axonal fibers connecting the cerebellum and brainstem.
Claustrum	A thin sheath of gray matter located between two brain areas: the external capsule and the putamen.
Corpus striatum	A part of the basal ganglia consisting of the caudate nucleus and the lenticular nucleus.
Inferior olives	The part of the brainstem that modulates cerebellar processing.
Internal capsule	White matter pathways conveying information from the thalamus to the cortex.
Medullary pyramids	A part of the medulla that consists of corticospinal fibers.
Neurology	The study of the nervous system and its disorders.
Optic thalamus	The portion of the thalamus relating to visual processing.
Spinal accessory nerve	The 11th cranial nerve, which innervates the head and shoulders.
Stria terminalis	The white matter pathway that sends information from the amygdala to the basal forebrain.
Striatum	Gray matter structure of the basal ganglia.
Vagus nerve	The 10th cranial nerve, which, among other functions, has visceral motor control of the heart.

We must keep both these things in mind when we try to understand the brain's architecture and function.

Life first appeared on our 4.5-billion-year-old Earth approximately 3.8 billion years ago, but human brains, in their present form, have been around for only about 100,000 years, a mere drop in the bucket. The primate brain appeared between 34 million and 23 million years ago, during the Oligocene epoch. It evolved into the progressively larger brains of the great apes in the Miocene epoch between roughly 23 million and 7 million years ago. The human lineage diverged from the last common ancestor that we shared with the chimpanzee somewhere in the range of 5 million to 7 million years ago. Since that divergence, our brains have evolved into the present human brain, capable of all sorts of wondrous feats.

Throughout this book, we will be reminding you to take the evolutionary perspective: Why might this behavior have been selected for? How could it have promoted survival and reproduction? WWHGD? (What would a hunter-gatherer do?) The evolutionary perspective often helps us to ask more informed questions and provides insight into how and why the brain functions as it does.

During most of our history, life was given over to the practical matter of survival. Nonetheless, the brain mechanisms that enable us to generate theories about the characteristics of human nature thrived inside the heads of ancient humans. As civilization developed, our ancestors began to spend time looking for causes of and constructing complex theories about the motives of fellow humans. But in these early societies, people thought of the natural world just as they thought of themselves—having thoughts, desires, and emotions.

It was the ancient Greeks who made the theoretical leap to the view that we are separate from the world we occupy. This delineation allowed them to conceive of the natural world as an object, an "it" that could be studied objectively—that is, scientifically. Egyptologist Henri Frankfort called this leap "breath-taking": "These men proceeded, with preposterous boldness on an entirely unproved assumption. They held that the universe is an intelligible whole. In other words, they presumed that a single order underlies the chaos of our perceptions and, furthermore, that we are able to comprehend that order" (Frankfort et al., 1977). The pre-Socratic Greek philosopher Thales, presaging modern cognitive neuroscience, rejected supernatural explanations of phenomena and proclaimed that every event had a natural cause. But on the subject of cognition, the early Greeks were limited in what they could say: They did not have the methodology to systematically explore the brain and the thoughts it produces (the mind) through experimentation.

Over the past 2,500 years, there has been an underlying tension between two ideas concerning the brain and the conscious mind. Thales represents one perspective, which posits that the flesh-and-blood brain produces thoughts—a stance known as *monism*. René Descartes (**Figure 1.4**), the 17th-century French philosopher, mathematician, and scientist, is known for the other. He believed that the body (including the brain) had material properties and worked like a machine, whereas the mind was nonmaterial and thus did not follow the laws of nature (i.e., Newton's laws of physics). Even so,

FIGURE 1.4
René Descartes (1596–1650). Portrait by Frans Hals.

he thought that the two interacted: The mind could influence the body and, through "the passions," the body could influence the mind. He had a difficult time figuring out where this interaction occurred but decided it must have been inside a single brain structure (i.e., not one found bilaterally), and the pineal gland was all that he could find that fit this description, so he settled on it. Descartes's stance that the mind appears from elsewhere and is not the result of the machinations of the brain is known as *dualism.*

Cognitive neuroscience takes Thales's monistic perspective that the conscious mind is a product of the brain's physical activity and not separate from it. We will see that evidence for this view initially came from studying patients with brain lesions, and later from scientific investigations.

The modern tradition of observing, manipulating, and measuring became the norm in the 19th century as scientists started to determine how the brain gets its jobs done. To understand how biological systems work, we must make an observation, ask why it came about, form a hypothesis, design and perform an experiment that will either support or refute that hypothesis, and, finally, draw a conclusion. Then, ideally, a different researcher reads our work, replicates the experiment, and obtains the same findings. If not, then the topic needs to be revisited. This approach is known as the *scientific method*, and it is the only way that a topic can move along on sure footing. And in the case of cognitive neuroscience, there is no end of rich phenomena to study.

1.2 The Brain Story

Imagine that you are given a problem to solve. A hunk of biological tissue is known to think, remember, attend, solve problems, tell jokes, want sex, join clubs, write novels, exhibit bias, feel guilty, and do a zillion other things. You are supposed to figure out how it works. You might start by looking at the big picture and asking yourself a couple of questions. "Hmm, does the blob work as a unit, with each part contributing to a whole? Or is the blob full of individual processing parts, each carrying out specific functions, so the result is something that looks like it is acting as a whole unit?" From a distance, the city of New York (another type of blob) appears as an integrated whole, but it is actually composed of millions of individual processors—that is, people. Perhaps people, in turn, are made of smaller, more specialized units.

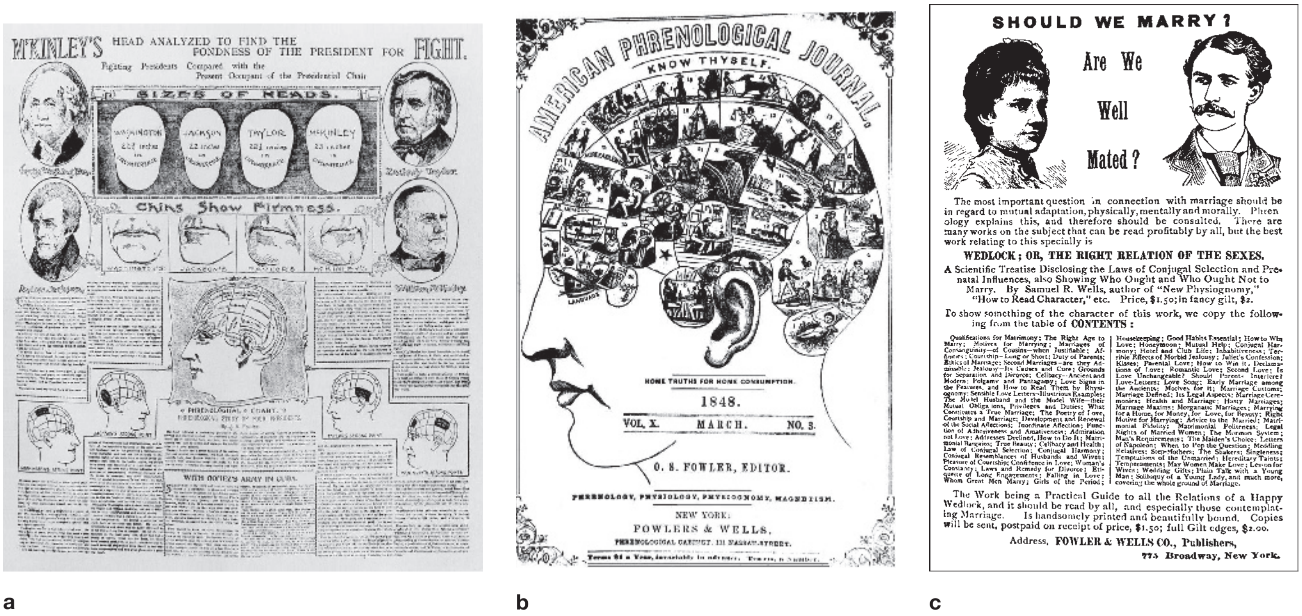
This central issue—whether the mind is enabled by the whole brain working in concert or by specialized parts of the brain working at least partly independently—is what fuels much of modern research in cognitive neuroscience. As we will see, the dominant view has changed back and forth over the years, and it continues to change today.

FIGURE 1.5 Franz Joseph Gall (1758–1828), one of the founders of phrenology.

Thomas Willis foreshadowed cognitive neuroscience with the notion that isolated brain damage (biology) could affect behavior (psychology), but his insights slipped from view. It took another century for Willis's ideas to resurface. They were expanded upon by a young Austrian physician and neuroanatomist, Franz Joseph Gall (**Figure 1.5**). After studying numerous patients, Gall became convinced that the brain was the organ of the mind and that innate faculties were localized in specific regions of the cerebral cortex. He thought that the brain was organized around some 35 or more specific functions, ranging from cognitive basics such as language and color perception to more ephemeral capacities such as affection and a moral sense, and that each was supported by specific brain regions. These ideas were well received, and Gall took his theory on the road, lecturing throughout Europe.

Gall and his disciple, Johann Spurzheim, hypothesized that if a person used one of the faculties with greater frequency than the others, the part of the brain representing that function would grow (Gall & Spurzheim, 1810–1819). This increase in local brain size would cause a bump in the overlying skull. Logically, then, Gall and his colleagues believed that a careful analysis of the skull could go a long way in describing the personality of the person inside the skull. Gall called this technique *anatomical personology.* The idea that character could be divined through palpating the skull was dubbed **phrenology** by Spurzheim and, as you may well imagine, soon fell into the hands of charlatans (**Figure 1.6**). Some employers even required job applicants to have their skulls "read" before they were hired.

Gall, apparently, was not politically astute. When asked to read the skull of Napoleon Bonaparte, he did not ascribe to it the noble characteristics that the future emperor was sure he possessed. When Gall later applied to the Academy of Sciences of Paris, Napoleon decided that phrenology needed closer scrutiny and ordered the academy to obtain some scientific evidence of its validity. Although Gall was a physician and neuroanatomist, he was not a scientist. He observed correlations and sought only to confirm, not disprove, them. The academy asked physiologist Marie-Jean-Pierre Flourens (**Figure 1.7**) to see whether he could come up with any concrete findings that could back up this theory.



SHOULD WE MARRY?

Are We Well Mated?

The most important question in connection with marriage should be in regard to mutual adaptation, physically, mentally and morally. Phrenology explains this, and therefore should be consulted. There are many works on the subject that can be read profitably by all, but the best work relating to this specially is

WEDLOCK; OR, THE RIGHT RELATION OF THE SEXES.

A Scientific Treatise Disclosing the Laws of Conjugal Selection and Prenatal Influences, also Showing Who Ought and Who Ought Not to Marry. By Samuel R. Wells, author of "New Physiognomy," "How to Read Character," etc. Price, $1.50; in fancy gilt, $2.

To show something of the character of this work, we copy the following from the table of CONTENTS:

Qualifications for Matrimony; The Right Age to Marry; Motives for Marrying; Marriages of Consanguinity—of Cousins—when Justifiable; Affinities; Courtship—Long or Short; Duty of Parents; Ethics of Marriage; Second Marriages—are they Admissible; Jealousy—Its Causes and Cure; Grounds for Separation and Divorce; Celibacy—Ancient and Modern; Polgamy and Pantagamy; Love Signs in the Features, and How to Read Them by Physiognomy; Sensible Love Letters—Illustrious Examples; The Model Husband and the Model Wife—their Mutual Obligations, Privileges and Duties; What Constitutes a True Marriage; The Poetry of Love, Courtship and Marriage; Development and Renewal of the Social Affections; Inordinate Affection; Function of Adhesiveness and Amativeness; Admiration not Love; Addresses Declined, How to Do It; Matrimonial Bargains; True Beauty; Celibacy and Health; Law of Conjugal Selection; Conjugal Harmony; Conjugal Resemblances of Husbands and Wives; Pleasure of Courtship; Confidence in Love; Woman's Constancy; Laws and Remedy for Divorce; Etiquette of Long Engagements; Falling in Love; Whom Great Men Marry; Girls of the Period; Housekeeping; Good Habits Essential; How to Win Love; Honeymoon; Mutual Help; Conjugal Harmony; Hotel and Club Life; Inhabitiveness; Terrible Effects of Morbid Jealousy; Juliet's Confession; Kisses; Parental Love; How to Win it, Declamations of Love; Romantic Love; Second Love; Is Love Unchangeable? Should Parents Interfere? Love-Letters; Love Song; Early Marriage among the Ancients; Motives for it; Marriage Customs; Marriage Defined; Its Legal Aspects; Marriage Ceremonies; Health and Marriage; Hasty Marriages; Marriage Maxims; Morganatic Marriages; Marrying for a Home, for Money, for Love, for Beauty; Right Motive for Marrying; Advice to the Married; Matrimonial Fidelity; Matrimonial Politeness; Legal Rights of Married Women; The Mormon System; Man's Requirements; The Maiden's Choice; Letters of Napoleon; When to Pop the Question; Meddling Relatives; Step-Mothers; The Shakers; Singleness; Temptations of the Unmarried; Hereditary Taints; Temperaments; May Women Make Love; Lesson for Wives; Wedding Gifts; Plain Talk with a Young Man; Soliloquy of a Young Lady, and much more, covering the whole ground of Marriage.

The Work being a Practical Guide to all the Relations of a Happy Wedlock, and it should be read by all, and especially those contemplating Marriage. Is handsomely printed and beautifully bound. Copies will be sent, postpaid on receipt of price, $1.50; full Gilt edges, $2.00.

Address, FOWLER & WELLS CO., Publishers,
775 Broadway, New York.

FIGURE 1.6 Phrenology goes mainstream.
(a) An analysis of Presidents Washington, Jackson, Taylor, and McKinley by Jessie A. Fowler, from the *Phrenological Journal*, June 1898. **(b)** The phrenological map of personal characteristics on the skull, from the *American Phrenological Journal*, March 1848. **(c)** Fowler & Wells Co. publication on marriage compatibility based on phrenology, 1888.

Flourens set to work. He destroyed parts of the brains of pigeons and rabbits and observed what happened. He was the first to show that, indeed, certain parts of the brain were responsible for certain functions. For instance, when he removed the cerebral hemispheres, the animal no longer had perception, motor ability, and judgment. Without the cerebellum, the animals became uncoordinated and lost their equilibrium. He could not, however, find any areas for advanced abilities such as memory or cognition, and he concluded that these were more diffusely scattered throughout the brain.

Flourens developed the notion that the whole brain participated in behavior—a view later known as the **aggregate field theory**. In 1824 Flourens wrote, "All sensations, all perceptions, and all volitions occupy the same seat in these (cerebral) organs. The faculty of sensation, percept and volition is then essentially one faculty." The theory of localized brain functions, known as localizationism, fell out of favor.

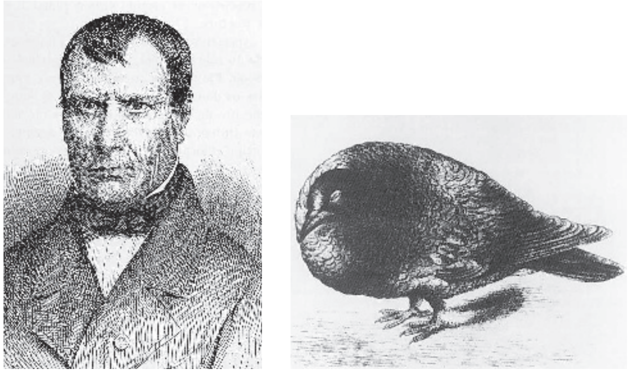


FIGURE 1.7
(a) Marie-Jean-Pierre Flourens (1794–1867), who supported the idea later termed the *aggregate field theory.* **(b)** The posture of a pigeon deprived of its cerebral hemispheres, as described by Flourens.

That state of affairs didn't last long, however. New evidence started trickling in from across Europe, and the pendulum slowly swung back to the localizationist view. In 1836 a neurologist from Montpellier, Marc Dax, provided one of the first bits. He sent a report to the French Academy of Sciences about three patients, noting that each had similar speech disturbances and similar left-hemisphere lesions found at autopsy. At the time, a report from the provinces got short shrift in Paris, and it would be another 30 years before anyone took much notice of this observation that speech could be disrupted by a specific lesion in the left hemisphere.

Meanwhile, in England, the neurologist John Hughlings Jackson (**Figure 1.8**) began to publish his observations on the behavior of persons with brain damage. A key feature of Jackson's

FIGURE 1.8
John Hughlings Jackson (1835–1911), an English neurologist who was one of the first to recognize the localizationist view.

writings was the incorporation of suggestions for experiments to test his observations. He noticed, for example, that during the start of their seizures, some epileptic patients moved in such characteristic ways that the seizure appeared to be stimulating a set map of the body in the brain; that is, the abnormal firings of neurons in the brain produced clonic and tonic jerks in muscles that progressed in the same orderly pattern from one body part to another. This phenomenon led Jackson to propose a *topographic* organization in the cerebral cortex: A map of the body was represented across a particular cortical area, where one part would represent the foot, another the lower leg, and so on (see **Box 1.1**). As we will see, this proposal was verified over a half century later by Wilder Penfield.

Although Jackson was also the first to observe that lesions on the right side of the brain affect visuospatial processes more than do lesions on the left side, he did not maintain that specific parts of the right side of the brain were solely committed to this important human cognitive function. Being an observant clinical neurologist, Jackson noticed that it was rare for a patient to lose a function completely. For example, most people who lost their capacity to speak following a cerebral stroke could still say some words. Patients unable to move their hands voluntarily to specific places on their bodies could still easily scratch those places if they itched. When Jackson made these observations, he concluded that many regions of the brain contribute to a given behavior.

Back in Paris, the well-known and respected physician Paul Broca (**Figure 1.9a**) published, in 1861, the results of his autopsy on a patient who had been nicknamed Tan (his real name was Leborgne)—perhaps the most

BOX 1.1 | LESSONS FROM THE CLINIC

Fits and Starts

If you were unlucky enough to have a neurological ailment before 1860, physicians had no organized way of thinking to make heads or tails of your problem. But that was about to change.

In 1867 John Hughlings Jackson wrote, "One of the most important questions we can ask an epileptic patient is, 'How does the fit begin?'" Before Jackson started shaking things up in the world of neurology, it was generally believed that the cerebral cortex was not excitable, and experimental physiologists had been convinced by Pierre Flourens that the cortex was equipotential, with no localized functions. But Jackson was armed with lessons he had learned from the clinic that disputed these theories. He had observed the progression of some of his patients' seizures and found consistent patterns to them: "I think the mode of beginning makes a great difference as to the march of the fit. When the fit begins in the face, the convulsion involving the arm may go down the limb. . . . When the fit begins in the leg, the convulsion marches up; when the leg is affected after the arm, the convulsion marches down the leg" (J. H. Jackson, 1868).

These observations led to Jackson's many conclusions: The cortex is excitable; seizures begin in a localized region of the cortex, and that particular region defines where the seizure manifests in the body; excitability of the cortex spreads to neighboring regions of the brain and, because the convulsion gradually progresses from one part of the body to the part immediately adjacent, the regions in the brain that correspond to the body parts must also be next to each other. From his clinical observations, Jackson created the conceptual framework for clinical neurophysiology and provided a systematic way to go about diagnosing diseases of the nervous system (York & Steinberg, 2006), which were later backed by experimentation. Throughout this book, we will follow in Jackson's footsteps and provide observations from clinical practice that must be taken into account when forming hypotheses about brain function.

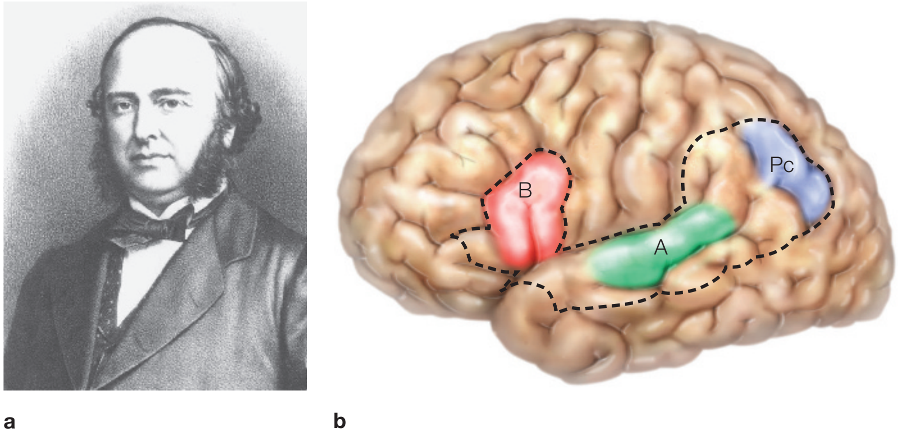


FIGURE 1.9
(a) Paul Broca (1824–1880). (b) The connections between the speech centers, from Carl Wernicke's 1876 article on aphasia. A = Wernicke's sensory speech center; B = Broca's area for speech; Pc = Wernicke's area concerned with language comprehension and meaning.

famous neurological case in history. Tan had developed aphasia: He could understand language, but "tan" was the only word he could utter. Broca found that Tan had a syphilitic lesion in his left-hemisphere inferior frontal lobe. This region is now called *Broca's area*. The impact of this finding was huge. Here was a specific aspect of language that was impaired by a specific lesion. Soon Broca had a series of such patients.

This theme was picked up by the German neurologist Carl Wernicke. In 1876 Wernicke reported on a stroke victim who (unlike Broca's patient) could talk quite freely but made little sense when he spoke. Wernicke's patient also could not understand spoken or written language. He had a lesion in a more posterior region of the left hemisphere, an area in and around where the temporal and parietal lobes meet, now referred to as *Wernicke's area* (**Figure 1.9b**).

Today, differences in how the brain responds to focal disease are well known (H. Damasio et al., 2004; Wise, 2003), but over 100 years ago Broca's and Wernicke's discoveries were earth-shattering. (Note that people had largely forgotten Willis's observations that isolated brain damage could affect behavior. Throughout the history of brain science, an unfortunate and oft-repeated trend is that we fail to consider crucial observations made by our predecessors.) With the discoveries of Broca and Wernicke, attention was again paid to this startling point: Focal brain damage causes specific behavioral deficits.

As is so often the case, the study of humans leads to questions for those who work on animal models. Shortly after Broca's discovery, the German physiologists Gustav Fritsch and Eduard Hitzig electrically stimulated discrete parts of a dog brain and observed that this stimulation produced characteristic movements in the dog. This discovery led neuroanatomists to more closely analyze the cerebral cortex and its cellular organization; they wanted support for their ideas about the importance of local regions. Because these regions performed different functions, it followed that they ought to look different at the cellular level.

Going by this logic, German neuroanatomists began to analyze the brain by using microscopic methods to view the cell types in different brain regions. Perhaps the most famous of the group was Korbinian Brodmann, who analyzed the cellular organization of the cortex and characterized 52 distinct regions (**Figure 1.10**). He published his cortical maps in 1909.

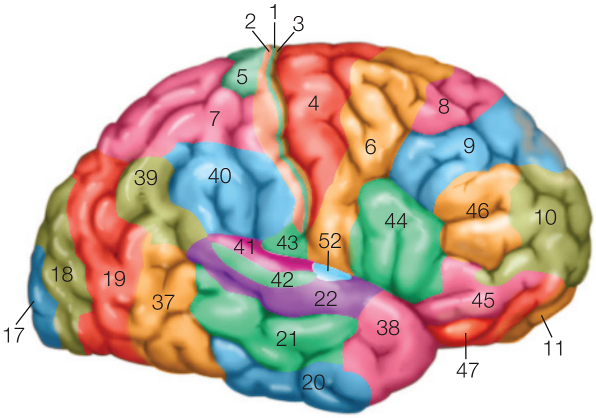
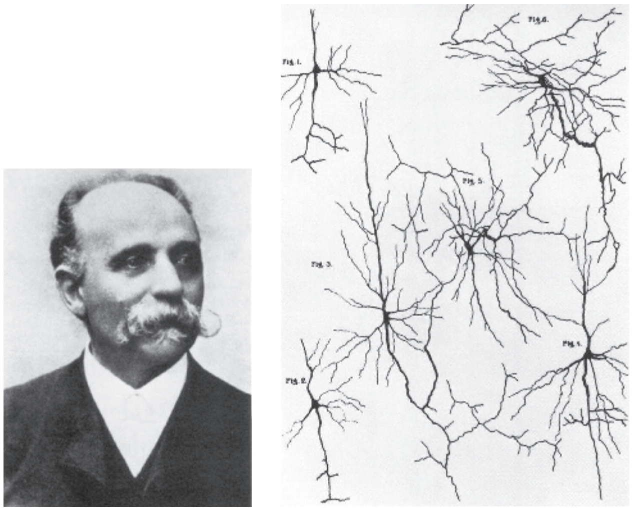


FIGURE 1.10 Brodmann's areas.
Sampling of the 52 distinct areas described by Brodmann on the basis of cell structure and arrangement.

Brodmann used tissue stains, such as the one developed by the German neuropathologist Franz Nissl, that permitted him to visualize the different cell types in different brain regions. How cells differ between brain regions is called **cytoarchitectonics**, or *cellular architecture*. Soon, many now famous anatomists—including Oskar Vogt, Vladimir Betz, Theodor Meynert, Constantin von Economo, Gerhardt von Bonin, and Percival Bailey—contributed to this work, and several subdivided the cortex even further than Brodmann had. To a large extent, these investigators discovered that various cytoarchitectonically described brain areas do indeed represent functionally distinct brain regions.

Despite all of this groundbreaking work in cytoarchitectonics, the truly huge revolution in our understanding of the nervous system was taking place elsewhere. In Italy and Spain, an intense struggle was going on between two brilliant neuroanatomists. Oddly, it was the work of one that led to the insights of the other. Camillo Golgi (**Figure 1.11**), an Italian physician, developed one of the most famous cell stains in the history of the world: the silver method for staining neurons—*la reazione nera*, "the black reaction"—which impregnated individual neurons with silver chromate. This stain permits visualization of individual neurons in their entirety.



a

b

FIGURE 1.11
(a) Camillo Golgi (1843–1926), cowinner of the 1906 Nobel Prize in Physiology or Medicine. **(b)** Golgi's drawings of different types of ganglion cells in dog and cat.