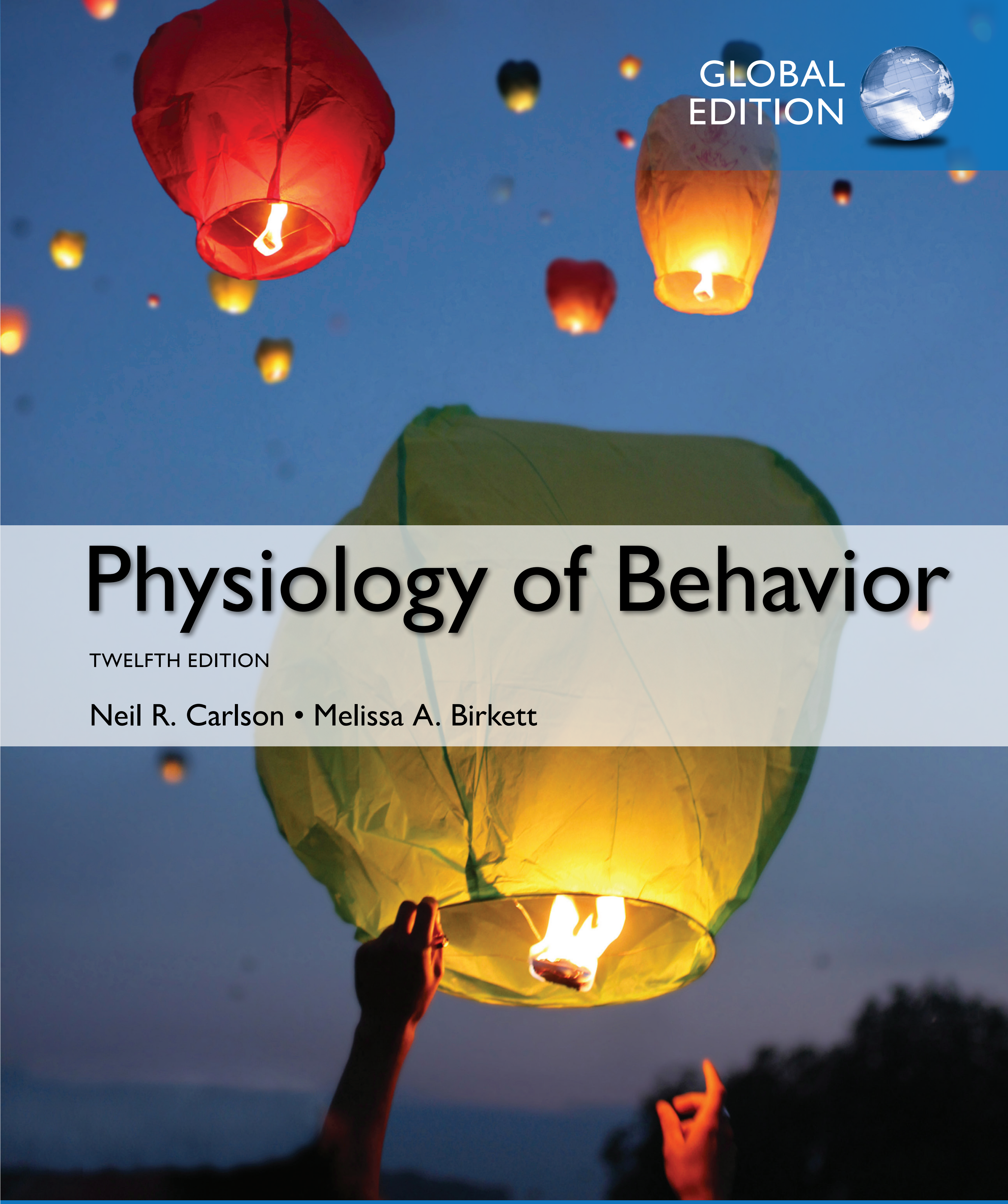

GLOBAL EDITION

Physiology of Behavior

TWELFTH EDITION

Neil R. Carlson • Melissa A. Birkett

ALWAYS LEARNING

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Physiology of Behavior

twelfth edition
global edition

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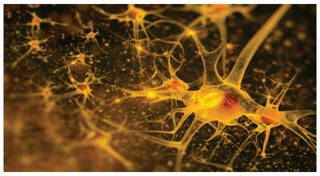

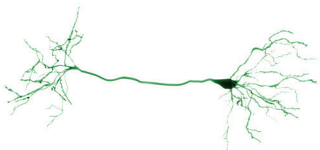

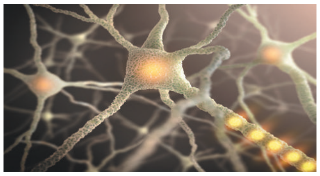

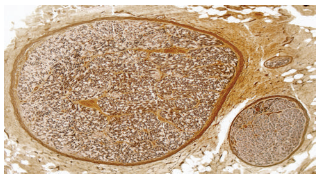

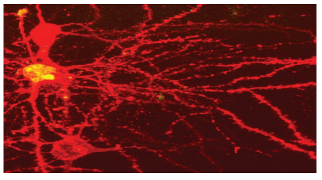

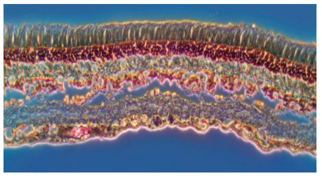

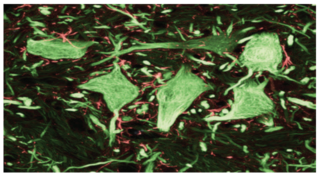

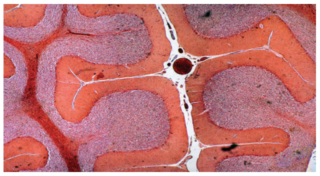

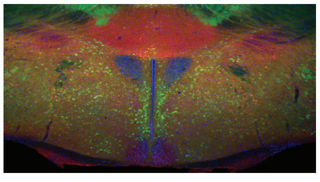

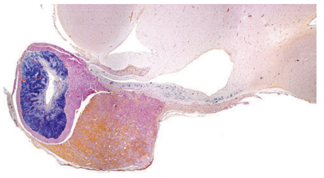

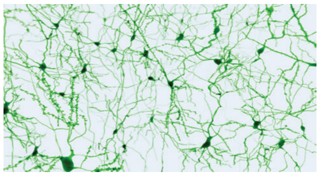

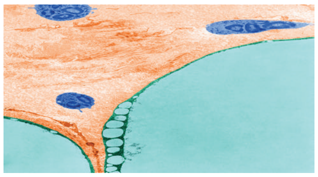

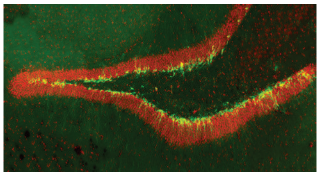

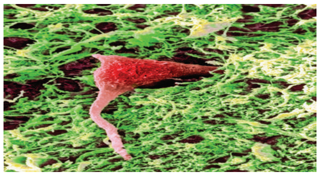

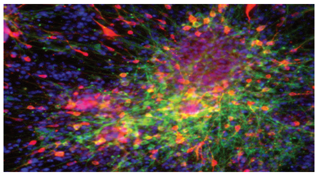

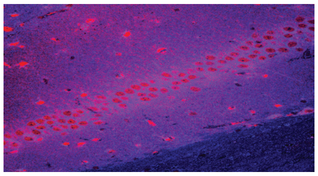

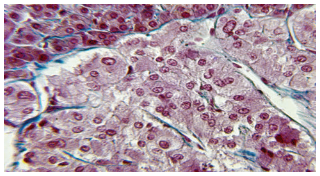

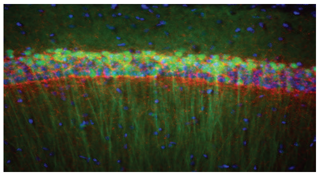

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Preface

I wrote the first edition of *Physiology of Behavior* over thirty years ago. When I did so, I had no idea I would someday be writing the twelfth edition. I'm still having fun, so I hope to do a few more. The interesting work coming out of my colleagues' laboratories—a result of their creativity and hard work—has given me something new to say with each edition. Because there was so much for me to learn, I enjoyed writing this edition just as much as the first one. That is what makes writing new editions interesting: learning something new and then trying to find a way to convey the information to the reader.

In this edition, Melissa Birkett joined the team and contributed to the review of the chapter structure and the addition of new pedagogical features, which include learning objectives and revised thought questions. Her work on this book helped to focus the content around critical concepts and provide ways for readers to more consistently self-assess their understanding of behavioral neuroscience. She also worked to implement the new online resources that complement the content of the text and contributed to the ongoing reassessment of research contained in this edition. Together, we drew upon our teaching and experience working with students to create a comprehensive and accessible guide for students of behavioral neuroscience.

The first part of the book is concerned with foundations of behavioral neuroscience: the history of the field, the structure and functions of neurons, neuroanatomy, psychopharmacology, and research methods. The second part is concerned with inputs and outputs that guide behavior: the sensory systems and the motor system. The third part deals with classes of species-typical behavior: sleep, reproduction, emotional behavior, and ingestion. The chapter on reproductive behavior includes parental behavior as well as courting and mating. The chapter on emotion includes a discussion of fear, anger and aggression, communication of emotions, and feelings of emotions. The chapter on ingestive behavior includes the neural and metabolic bases of drinking and eating. The fourth part of the book explores learning, including research on synaptic plasticity, the neural mechanisms that are responsible for perceptual learning and stimulus-response learning (including classical and operant conditioning), human amnesia, and the role of the hippocampal formation in relational learning. The final part of the book examines the neural basis of human communication and neurological, mental, and behavioral disorders. The latter topic is covered in three chapters; the first discusses schizophrenia and the affective disorders; the second discusses stress, anxiety, and neurodevelopmental disorders; and the third discusses substance abuse.

Each chapter begins with a *Case Study*, which describes the experience of people whose lives are impacted by an important issue in neuroscience. Other case studies are included within the text of the chapters. *Learning Objectives* to guide your reading are now found at the beginning of each major section of the text. The learning objectives can help you identify and understand the key points from each section and are also summarized at the end of each section. *Thought Questions* are also located at the end of each section and are designed to stimulate your thinking about what you have learned. *Chapter Review Questions* conclude each chapter. They provide useful reviews of each chapter and a more comprehensive opportunity to test your understanding. *Critical Concepts* features have been added to each chapter, with goals of highlighting important topics in neuroscience and providing opportunities to explore them in greater depth.

New to This Edition

The research reported in this edition reflects both the enormous advances made in research methods and the discoveries these methods have revealed. In neuroscience, as soon as a new method is developed in one laboratory, it is adopted by other laboratories and applied to a wide range of problems. Researchers are combining techniques that converge upon the solution to a problem and use many methods, often in collaboration with other laboratories.

The art in this book continues to evolve. For this twelfth edition, the art has been updated to give the book a fresh, modern, cohesive feel, as well as to keep up with the latest findings and studies in the field. We have always striven to be as up to date and as accurate as possible. We hope the new art in this edition reflects that ongoing effort.

Great effort was also put forth in this edition to make the content more accessible, engaging, and easier for students to understand. We made every attempt to create more scaffolding within each chapter, grouping and reorganizing material so that readers can better identify important concepts and also better see how those concepts relate to each other in more comprehensive patterns. In addition to those organizational revisions, we also, of course, tried to update the literature to stay atop the latest trends and findings in the field.

You'll notice that the chapters contain new headings and subheadings, as well as learning objectives. These are some of the most significant structural changes to the new edition. The subheadings in each chapter correspond with the newly developed learning objectives and are associated with a learning objective summary for each section. We believe that this approach will help the reader to more easily identify main themes and concepts.

The following list summarizes some of the updates new to this edition.

Chapter 1

A new case study reflecting an application of neuroscience research was added to open the chapter.

An emphasis on neuroplasticity as an important theme in neuroscience was added.

New content on contemporary developments in the field of neuroscience was added.

A new section including information about ethical considerations in research with human participants was added.

A summary of new research in support of strategies for learning (along with practical suggestions for readers) was added.

Chapter 4

A new case study was added to the beginning of the chapter, including information about bath salts.

Additional content addressing organization of the field of pharmacology was added.

Chapter 5

Information about deep brain stimulation techniques and application was added.

Chapter 6

The beginning of the chapter was reorganized to provide an introduction to sensation and perception.

The structure of this chapter was rearranged to better align with the format of subsequent chapters.

New content was added to provide an overview of the visual pathway.

The topic of blindsight was added to this chapter.

Chapter 7

A new case study was added to the beginning of the chapter, highlighting the experience of congenital lack of pain receptors.

Information about the application of mirror box therapy for phantom limb pain was added.

Chapter 9

Revised sleep stage scoring guideline information was added.

A description of hypnic jerks is now included.

Research on the experience of lucid dreaming was added.

Additional research on regional cerebral blood flow in slow wave sleep was added.

Information about interventions for insomnia is now included.

Chapter 10

This chapter now includes a discussion of the terms *sex, gender,* and *intersex.*

Additional research about prenatal environment and sexual orientation is now included.

New research about the relationship between testosterone and anticipation of sexual activity is now included.

Chapter 11

A new case study describing the effects of amygdala damage is included.

Additional information about serotonin, progesterone, and aggression has been added.

Details about the use of anabolic steroids have been added.

New information about research on thin slice assessment of emotion is now included.

Chapter 12

New case studies describing interventions for eating disorders have been added to the chapter.

Information about the risk of mortality in anorexia nervosa has been added.

New research on satiety signals has been added.

Additional information about the endocrine response to bariatric surgery has been added.

Research about brain changes associated with eating disorder interventions has been added.

New research about environmental factors related to eating is now included.

Chapter 13

New research on motor learning has been added.

Additional information about neurogenesis has been added.

New research on spatial memory and the hippocampus is now included.

Chapter 14

A new section describing brain regions involved in learning more than one language has been added.

New research on aphasia and American Sign Language is now included.

Chapter 15

A new case study describing interventions for traumatic brain injury has been added.

New information on chronic traumatic encephalopathy has been added.

New research on interventions in Down syndrome is now included.

Details about the prevalence of epilepsy and brain tumors are now included.

New information about the application of deep brain stimulation is included.

Chapter 16

The case study at the beginning of the chapter was revised to reflect the experience of schizophrenia in a young adult.

New research describing brain changes in schizophrenia has been added.

Details about symptom progression and prevalence of hallucination type in schizophrenia are now included.

New information about interventions for schizophrenia is included.

Risk and protective factors in schizophrenia are now included.

New research on the use of ketamine in treatment-resistant depression is included.

Chapter 17

A new case study describing the experience of a panic attack in a young adult is now included at the beginning of the chapter.

The chapter has been reorganized to reflect overlapping content in stress and anxiety disorders, and neurodevelopmental disorders.

The content of the chapter has been updated to reflect changes in *Diagnostic and Statistical Manual for Mental Disorders (5th ed.).*

New research on stress and immune suppression has been added.

New information about treatment for posttraumatic stress disorder has been added.

Research describing brain changes associated with ADHD is now included.

New information about interventions for autism spectrum disorder is now included.

Details about the prevalence for PTSD and comorbidity of PTSD and TBI are now included.

Information about stress resilience has been added.

Information about pharmacological intervention to treat and prevent PTSD has been added.

Information about a cross-cultural comparison of social anxiety has been added.

Chapter 18

The opening case study of this chapter has been updated to reflect trends in opiate abuse.

The content of the chapter has been updated to reflect changes in *Diagnostic and Statistical Manual for Mental Disorders (5th ed.).*

New information about interventions for substance abuse has been added.

Details about abstinence rates following substance abuse treatment have been added.

New research about adolescent THC exposure and risk of schizophrenia is now included.

Instructor's Manual Each chapter includes an Integrated Teaching Outline with teaching objectives, lecture material, demonstrations and activities, videos, suggested readings, web resources, and information about other supplements. An appendix contains a set of student handouts. The Instructor's Manual is available online at www.pearsonglobaleditions.com/carlson.

Test Bank Includes over 2,500 thoroughly reviewed multiple-choice, completion, short answer, and essay questions, each with answer justification, page references, difficulty rating, and skill type designation. The Test Bank is also available in Pearson *MyTest*, a powerful online assessment software program. Instructors can easily create and print quizzes and exams as well as author new questions online for maximum flexibility. Both the Test Bank and MyTest are available online at www.pearsonglobaleditions.com/carlson.

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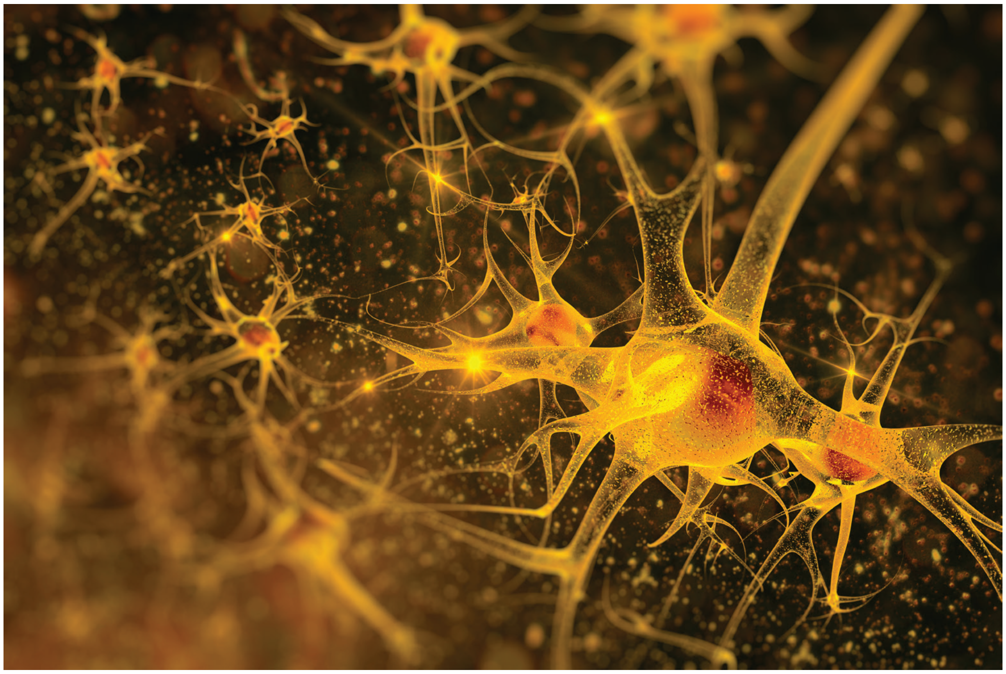
Chapter 1
Introduction



Chapter Outline

Learning Objectives

LO 1.1 Explain the importance of generalization and reduction in behavioral neuroscience research.

LO 1.2 Summarize contributions to the modern field of behavioral neuroscience made by individuals involved in philosophy, physiology, or other disciplines.

LO 1.3 Describe the role of natural selection in the evolution of behavioral traits.

LO 1.4 Identify factors involved in the evolution of large brains in humans.

LO 1.5 Outline reasons for the use of animals in behavioral neuroscience research.

LO 1.6 Discuss ethical considerations in research with human participants.

LO 1.7 Identify careers in behavioral neuroscience.

LO 1.8 Describe effective learning strategies for studying behavioral neuroscience.

Jeremiah is a 53-year-old lawyer. When he was just seven years old, he experienced a stroke while playing baseball. Although most strokes occur in older adults, unfortunately they can affect anyone, even children. A stroke occurs when a part of the brain is deprived of blood flow and oxygen (you will read more about strokes, cerebrovascular accidents, in Chapter 15). As a result of damage to the left side of his brain, Jeremiah lost all sensation on the right side of his body and had limited ability to use his right arm or leg. He received some rehabilitation immediately following the stroke and learned to walk with the assistance of a cane. He had to learn to write with his left hand because the fine motor movements proved too difficult for him to continue writing with his right hand.

He was never able to regain full movement of the right side of his body, however, and so despite the progress he made, Jeremiah fell frequently. More than forty years after his stroke, he still fell nearly 150 times a year, resulting in multiple injuries including bone fractures in his hand, foot, and hip. Jeremiah's ongoing struggles over a span of four decades prompted him to seek a new treatment to improve his balance, coordination, and fine motor skills. Remarkably, after only two weeks of training for his right hand, and three weeks for his right leg, Jeremiah's balance improved and he was once again able to write his name with his right hand. What happened in Jeremiah's brain that allowed this drastic improvement?

Jeremiah received a form of therapy called constraint-induced movement (CI) therapy. The therapy is based on the idea that stroke-induced paralysis is due to disuse of the limb and fewer cells in the brain being devoted to the limb's movement. To reteach the brain to engage in behaviors once again, the therapy involves intensive physical activity using the affected parts of the body. For example, Jeremiah spent hours each day working to move his affected limbs, doing things like picking up a pencil, stacking blocks, and clipping clothespins to a yardstick. To force Jeremiah to work with his weaker, right hand, therapists used mitts to cover his left hand. Such incremental training, or shaping, of the affected body part "rewires" the brain, allowing it to "relearn" basic functions and processes. This kind of "rewiring" of the brain is known to neuroscientists as plasticity, or the ability of the brain to change over time. Due to the plasticity of the brain, Jeremiah, after hours of intensive practice, was able to regain much of his motor control that had been lost decades before during the stroke he suffered as a child (Doidge, 2007).

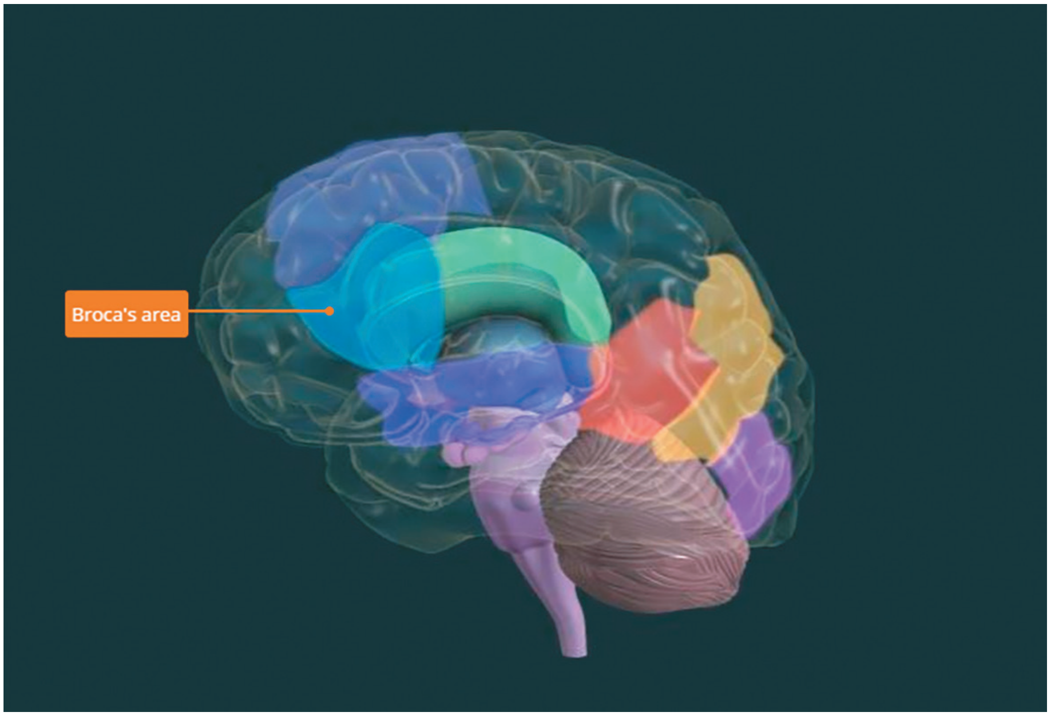
*****

Until nearly the beginning of the twenty-first century, most researchers believed that the brain was not capable of change in adulthood. Several pioneering neuroscientists suggested the cells and connections of the adult brain are in fact flexible, or plastic, and attempted to change beliefs about the brain that had been held for more than a century. It was not an easy process. Though equipped with revolutionary new data, the researchers were criticized for years, their data and methods questioned. Eventually, the data accumulated and even the strongest critics began to retract their statements and accept the data demonstrating neural changes in the adult brain, including the presence of new cells in some regions of the brain.

Today, we know the adult brain forms connections between the cells in the brain, called **neurons,** throughout a lifetime. This change in understanding about the brain has been met with optimism and excitement. Therapies for brain injury and mental illness have been developed based on understanding about lifelong brain changes. Dozens of researchers are also making new discoveries every year about **neurogenesis,** the generation of new neurons.

This story of the change in how we understand the brain, and the potential benefits of that understanding, illustrates many of the important principles you will encounter throughout this book. Behavioral neuroscience is a dynamic and ever-changing field. As you read this book, consider not only the facts it contains, but also the process of obtaining those facts, the numerous and dedicated scientists responsible for conducting the research, and the exciting possibility that there is still much to learn about the brain and the nervous system.

The last frontier in this world—and perhaps the greatest one—lies within us. The human nervous system makes possible all that we can do, all that we can know, and all that we can experience. Its complexity is immense, and the task of studying it and understanding it dwarfs all previous explorations our species has undertaken.

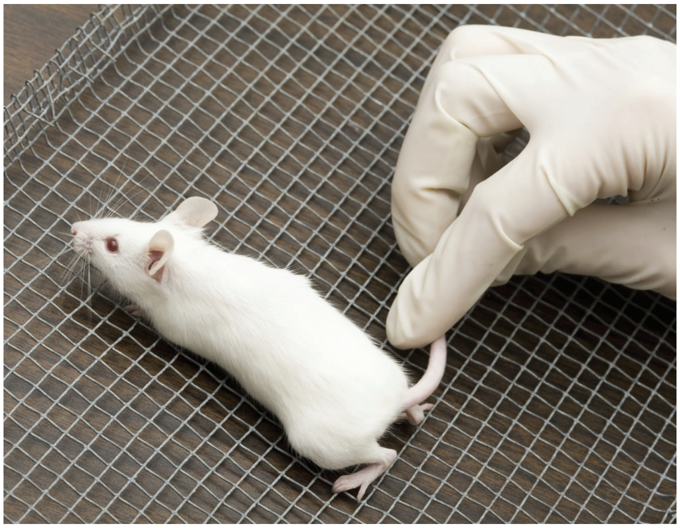


This figure depicts Broca's area, a region important in speech production that was discovered through pioneering studies of brain functions described in this chapter.

Foundations of Behavioral Neuroscience

Behavioral neuroscience was formerly known as *physiological psychology*, and it is still sometimes referred to by that name. In fact, the first psychology textbook, written by Wilhelm Wundt in the late nineteenth century, was titled *Principles of Physiological Psychology*. In recent years, the explosion of information from experimental biology, chemistry, animal behavior, psychology, computer science, and other fields has contributed to creating the diverse interdisciplinary field of behavioral neuroscience. This united effort is due to the realization that the ultimate function of the nervous system is behavior.

When we ask our students what they think the ultimate function of the brain is, they often say "thinking," or "logical reasoning," or "perceiving," or "remembering things." The nervous system does perform these functions, but they support the primary one: control of movement. (Note that movement includes speech and other forms of communication, an important category of human behavior.) The basic function of perception is to inform us of what is happening in our environment so that our behaviors will be adaptive and useful: Perception without the ability to act would be useless. Once perceptual abilities evolved, they could be used for purposes other than guiding behavior. For example, we can enjoy a beautiful sunset or a great work of art without our perception causing us to do anything in particular. And thinking can often take place without causing any overt behavior. However, the *ability to think* evolved because it permits us to perform complex behaviors that accomplish useful self-preserving goals. And whereas reminiscing about things that happened in our past can be an enjoyable pastime, the ability to learn and remember evolved—again—because it permitted our ancestors to profit from experience and perform behaviors that were useful to them.


Jaroslav74/Shutterstock

The study of nest-building behavior in mice shows that the same mechanisms can be activated by different parts of the brain.

The growing field of behavioral neuroscience has been formed by scientists who have combined the experimental methods of psychology with those of physiology and have applied them to the issues that concern researchers in many different fields. Research in neuroscience includes topics in perceptual processes, control of movement, sleep and waking, reproductive behaviors, ingestive behaviors, emotional behaviors, learning, and language. In recent years we have begun to study the neuroscience underlying human pathological conditions, such as substance abuse and neurological and mental disorders. These topics are discussed in subsequent chapters of this book.

The Goals of Research

LO 1.1 Explain the importance of generalization and reduction in behavioral neuroscience research.

The goal of all scientists is to explain the phenomena they study. But what do we mean by *explain?* Scientific explanation takes two forms: generalization and reduction. **Generalization** refers to explanations as examples of general laws, which are revealed through experiments. **Reduction** refers to explanations of complex phenomena in terms of simpler ones.

The task of the behavioral neuroscientist is to explain behavior by studying the physiological processes that control it. But behavioral neuroscientists cannot simply be reductionists. It is not enough to observe behaviors and correlate them with physiological events that occur at the same time. We must also understand the function of a given behavior. For example, mice, like many other mammals, often build nests. Behavioral observations show that mice will build nests under two conditions: when the air temperature is low and when the animal is pregnant. A nonpregnant mouse will build a nest only if the temperature is cool, whereas a pregnant mouse will build one regardless of the temperature. The same behavior occurs for different reasons. In fact, nest-building behavior is controlled by two different physiological mechanisms. Nest building can be studied as a behavior related to the process of temperature regulation, or it can be studied in the context of parental behavior. Although the same set of brain mechanisms will control the movements that a mouse makes in building a nest in both cases, these mechanisms will be activated by different parts of the brain. One part receives information from the body's temperature detectors, and the other part is influenced by hormones that are present in the body during pregnancy.

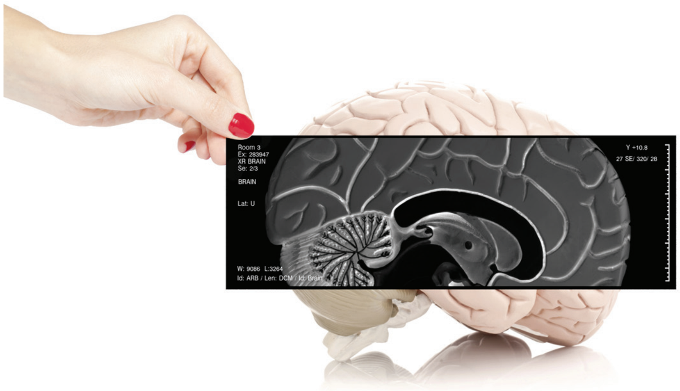
Sometimes, physiological mechanisms can tell us something about psychological processes such as language, memory or mood. For example, damage to a particular part of the brain can cause very specific impairments in a person's language abilities. The nature of these impairments suggests how these abilities are organized. When the damage involves a brain region that is important in analyzing speech sounds, it also produces deficits in spelling. This finding suggests that the ability to recognize a spoken word and the ability to spell it call on related brain mechanisms. Damage to another region of the brain can produce extreme difficulty in reading unfamiliar words by sounding them out, but it does not impair the person's ability to read words with which he or she is already familiar. This finding suggests that reading comprehension can take two routes: one that is related to speech sounds and another that is primarily a matter of visual recognition of whole words.

In practice, the research efforts of behavioral neuroscientists involve both forms of explanation: generalization and reduction. Ideas for experiments are stimulated by the investigator's knowledge both of psychological generalizations about behavior and of physiological mechanisms. A good behavioral neuroscientist must therefore be an expert in the study of behavior *and* the study of physiology.

Biological Roots of Behavioral Neuroscience

LO 1.2 Summarize contributions to the modern field of behavioral neuroscience made by individuals involved in philosophy, physiology, or other disciplines.

From the earliest historical times, human beings have believed that they possess something intangible that animates them: a mind, or a soul, or a spirit. We each also have a physical body, with muscles that move it and sensory organs



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Most neuroscientists believe that once we understand the workings of the human body, we will be able to explain how we perceive, how we think, how we remember, and how we behave.

such as eyes and ears that perceive information about the world around us. Within our bodies the nervous system plays a central role, receiving information from the sensory organs and controlling the movements of the muscles. But what role does the mind play? Does it *control* the nervous system? Is it a *part of* the nervous system? Is it physical and tangible, like the rest of the body, or is it a spirit that will always remain hidden?

This puzzle has historically been called the *mind–body question.* Philosophers have been trying to answer it for many centuries, and more recently scientists have taken up the task. Basically, people have followed two different approaches: dualism and monism. **Dualism** is a belief in the dual nature of reality. Mind and body are separate; the body is made of ordinary matter, but the mind is not. **Monism** is a belief that everything in the universe consists of matter and energy and that the mind is a phenomenon produced by the workings of the nervous system.

Mere speculation about the nature of the mind can get us only so far. If we could answer the mind–body question simply by thinking about it, philosophers would have done so long ago. Behavioral neuroscientists, on the other hand, take an empirical, monistic approach to the study of human nature. Most neuroscientists believe that once we understand the workings of the human body—and, in particular, the workings of the nervous system—the mind–body question will be resolved. We will be able to explain how we perceive, how we think, how we remember, and how we behave. We will even be able to explain the nature of our own self-awareness. This section explores some of the important discoveries of the past that contributed to today's field of behavioral neuroscience.

ANCIENT WORLD Study of (or speculations about) the physiology of behavior has its roots in antiquity. A papyrus scroll from approximately 1700 B.C.E. contains surgical records of head injuries and the oldest surviving descriptions of the brain, cerebrospinal fluid, meninges, and skull (Feldman and Goodrich, 1999).

Because its movement was necessary for life and because emotions caused it to beat more strongly, ancient Egyptian, Indian, and Chinese cultures considered the heart to be the seat of thought and emotions. The ancient Greeks did too, but Hippocrates (460–370 B.C.E.) concluded that this role should be assigned to the brain.

Not all ancient Greek scholars agreed with Hippocrates. Aristotle did not; he thought the brain served to cool the passions of the heart. But Galen (130–200 C.E.), who had the greatest respect for Aristotle, thought enough of the brain to dissect and study the brains of cattle, sheep, pigs, cats, dogs, weasels, monkeys, and apes (Finger, 1994), and concluded that Aristotle's theory about the brain's role was "utterly absurd, since in that case Nature would not have placed the encephalon [brain] so far from the heart, . . . and she would not have attached the sources of all the senses [the sensory nerves] to it" (Galen, 1968 translation, p. 387). (See Figure 1.1.)

SEVENTEENTH CENTURY Philosophers and physiologists in the 1600s contributed greatly to the foundations of today's behavioral neuroscience. The French philosopher René Descartes' speculations concerning the roles of the mind and brain in the control of behavior provide a good starting point in the modern history of behavioral neuroscience. To Descartes, animals were mechanical devices; their behavior was controlled by environmental stimuli. His view of the human body was much the same: It was a machine. As

Figure 1.1 Galen (130–200 C.E.)

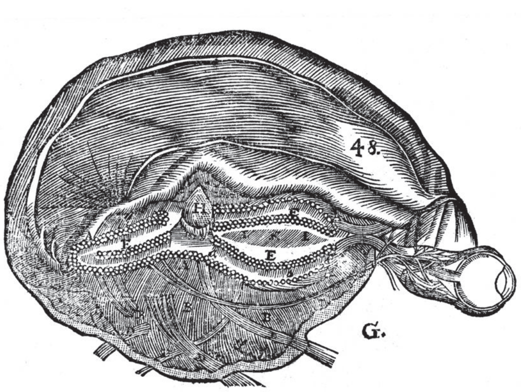
Descartes observed, some movements of the human body were automatic and involuntary. For example, if a person's finger touched a hot object, the arm would immediately withdraw from the source of stimulation. Reactions like this did not require participation of the mind; they occurred automatically. Descartes called these actions **reflexes.** (See Figure 1.2.)

Like most philosophers of his time, Descartes was a dualist and believed that each person possessed a mind—a uniquely human attribute that was not subject to the laws of the universe. But his thinking differed from that of his predecessors in one important way: He was the first to suggest that a link exists between the human mind and its purely physical housing, the brain. He believed that the mind controlled the movements of the body, while the body, through its sense organs, supplied the mind with information about what was happening in the environment. In particular, he hypothesized that this interaction took place in the pineal body, a small organ situated on top of the brain stem, buried beneath the cerebral hemispheres. He noted that the brain contained hollow chambers (the *ventricles*) that were filled with fluid, and he hypothesized that this fluid was under pressure. When the mind decided to perform an action, it tilted the pineal body in a particular direction like a little joystick, causing fluid to flow from the brain into the appropriate set of nerves. This flow of fluid caused muscles to inflate and move.

However, it did not take long for biologists to disprove Descartes' belief about the brain using pressurized fluid to control behavior. Luigi Galvani, a seventeenth-century Italian physiologist, found that electrical stimulation of a frog's nerve caused contraction of the muscle to which it was attached. Contraction occurred even when the nerve and muscle were detached from the rest of the body, so the ability of the muscle to contract and the ability of the nerve to send a message to the muscle were characteristics of these tissues themselves. Thus, the brain did not inflate muscles by directing pressurized fluid through the nerve. Galvani's experiment prompted others to study the nature of the message transmitted by the nerve and the means by which muscles contracted. The results of these efforts gave rise to an accumulation of knowledge about the physiology of behavior.

Figure 1.2 Descartes' Model

Descartes believed that the "soul" (what we now call the mind) controls the movements of the muscles through its influence on the pineal body. According to his theory, the eyes sent visual information to the brain, where it could be examined by the soul. When the soul decided to act, it would tilt the pineal body (labeled H in the diagram), which would divert pressurized fluid through nerves to the appropriate muscles.



NINETEENTH CENTURY One of the most important figures in the development of experimental physiology was Johannes Müller, a nineteenth-century German physiologist. Müller applied experimental techniques to physiology. Previously, most natural scientists had been limited to observation and classification. Although these activities are essential, Müller insisted that major advances in our understanding of the workings of the body would be achieved only by experimentally removing or isolating animals' organs, testing their responses to various chemicals, and otherwise altering the environment to see how the organs responded. His most important contribution to the study of the physiology of behavior was his **doctrine of specific nerve energies.** Müller observed that although all nerves carry the same basic message—an electrical impulse—we perceive the messages of different nerves in different ways. For example, messages carried by the optic nerves produce sensations of visual images, and those carried by the auditory nerves produce sensations of sounds. How can different sensations arise from the same basic message?

The answer is that the messages occur in different channels. The portion of the brain that receives messages from the optic nerves interprets the activity as visual stimulation, even if the nerves are actually stimulated mechanically. (For example, when we rub our eyes, we see flashes of light.) Because different parts of the brain receive messages from different nerves, the brain must be functionally divided: Some parts perform some functions, while other parts perform others.

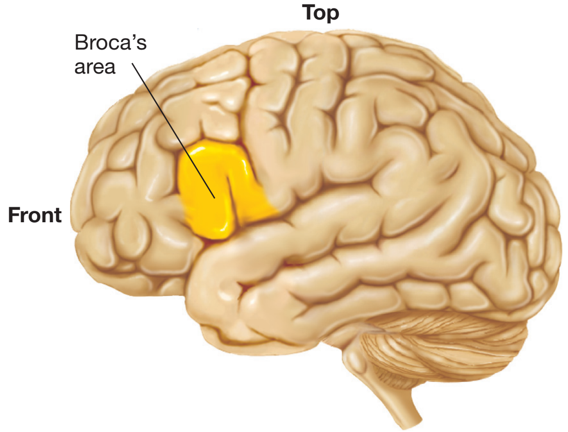
Müller's advocacy of experimentation and the logical deductions from his doctrine of specific nerve energies set the stage for performing experiments directly on the brain. Pierre Flourens, a nineteenth-century French physiologist, did just that. Flourens removed various parts of animals' brains and observed their behavior. By seeing what the animal could no longer do, he could infer the function of the missing portion of the brain. This method is called **experimental ablation.** Flourens claimed to have discovered the regions of the brain that control heart rate and breathing, purposeful movements, and visual and auditory reflexes.

Soon after Flourens performed his experiments, Paul Broca, a French surgeon, applied the principle of experimental ablation to the human brain. He did not intentionally remove parts of human brains to see how they worked but observed the behavior of people whose brains had been damaged by strokes. In 1861, he performed an autopsy on the brain of a man who had had a stroke that resulted in the loss of the ability to speak. Broca's observations led him to conclude that a portion of the cerebral cortex on the front part of the left side of the brain performs functions that are necessary for speech. This came to be known as Broca's area (see Figure 1.3). Other physicians soon obtained evidence supporting his conclusions. As you will learn in Chapter 14, the control of speech is not localized to only one particular region of the brain. Speech requires many different functions, which are organized throughout the brain. Nonetheless, the method of experimental ablation remains important to our understanding of the brains of both humans and laboratory animals.

As mentioned earlier, Luigi Galvani used electricity to demonstrate that muscles contain the source of the energy that powers their contractions. In 1870, German physiologists Gustav Fritsch and Eduard Hitzig used electrical stimulation as a tool for understanding the physiology of the brain. They applied weak electrical current to the exposed surface of a dog's brain and observed the effects of the stimulation. They found that stimulation of different portions of a specific region of the brain caused contraction of specific muscles on the opposite side of the body. We now refer to this region as the *primary motor cortex,* and we know that nerve cells there communicate directly with those that cause muscular contractions. We also know that other regions of the brain communicate with the primary motor cortex and thus control behaviors. For example, the region that Broca found necessary for speech communicates with, and controls, the portion of the primary motor cortex that controls the muscles of the lips, tongue, and throat, which we use to speak.

Figure 1.3 Broca's Area

This region of the brain is named for French surgeon Paul Broca, who discovered that damage to a part of the left side of the brain disrupted a person's ability to speak.



German physicist and physiologist Hermann von Helmholtz devised a mathematical formulation of the law of conservation of energy; invented the ophthalmoscope (used to examine the retina of the eye); devised an important and influential theory of color vision and color blindness; and studied audition, music, and many physiological processes. Helmholtz was the first scientist to attempt to measure the speed of conduction through nerves. Scientists had previously believed that such conduction was identical to the conduction that occurs in wires, traveling at approximately the speed of light. But Helmholtz found that neural conduction was much slower—only about 90 feet per second. This measurement proved that neural conduction was more than a simple electrical message, as we will see in Chapter 2.

Jan Purkinje, a Czech physiologist, studied both the central and peripheral nervous systems. He discovered Purkinje fibers—neurons terminating on cardiac cells responsible for controlling contractions of the heart. He also investigated neurons in the brain, describing Purkinje cells in the cerebellum and conducting studies of the visual system. Interestingly, he was also the first to describe the individuality of fingerprints (Bhattacharyya, 2011).

Late in the nineteenth century, Spanish anatomist Ramon Santiago y Cajal used the Golgi staining technique (described in Chapter 5) to examine individual neurons of the brain. His drawings of neurons (made under magnification from a microscope) from the brain, spinal cord, and retina depicted the detailed structures of these cells for the first time. Santiago y Cajal proposed that the nervous system consisted of billions of discrete, individual neurons, in opposition to the predominant idea of the time that the nervous system was a continuous network. In 1906, he was awarded the Nobel Prize for his work describing the structure of the nervous system.

CONTEMPORARY RESEARCH Twentieth-century developments in experimental physiology included many important inventions, such as sensitive amplifiers to detect weak electrical signals, neurochemical techniques to analyze chemical changes within and between cells, and histological techniques to visualize cells and their constituents. These and many other important developments are discussed in detail in subsequent chapters.

Briefly, highlights in contributions to neuroscience during the twentieth century include discoveries ranging from the electrical and chemical messages used by neurons, to the circuits and brain structures involved in a wide variety of behaviors, such as the mirror neuron system for coordinating social behavior (described in Chapter 8). Other developments contributed to new brain-based treatments for disorders such as depression and schizophrenia.

The twenty-first century has already witnessed several important advances and discoveries. As researchers continue to refine their understanding of the structures and functions of the brain, new discoveries about pathways and circuits abound. For example, the 2014 Nobel Prize was awarded to John O'Keefe, May-Britt Moser, and Edvard Moser for work on spatial positioning systems in the brain (often called the brain's global positioning system, or GPS). New advances in technology enabled treatments for severe depression and Parkinson's disease using deep brain stimulation techniques (see Chapters 15 and 16). The development of optogenetics provided researchers with the ability to selectively activate single neurons and observe changes in behavior—using light! (See Chapter 5.)

As behavioral neuroscience continues to progress as an interdisciplinary field, efforts such as the European Human Brain Project, which is working to develop a computer simulation of the brain, and the Brain Research through Advancing Innovative Neurotechnologies (BRAIN) initiative in the United States will continue to bring together groups of researchers from biology, chemistry, engineering, psychology, physiology, and other fields. Behavioral neuroscience, after all, has its roots—and its future—in interdisciplinary research.

DIVERSITY IN NEUROSCIENCE Neuroscience is a diverse, interdisciplinary field whose researchers work around the globe. The *Society for Neuroscience* was founded in 1969, with 500 members committed to developing a professional organization for scientists and physicians devoted to understanding the brain and nervous system. This international organization now has approximately 40,000 members from over 90 different countries. Reviewing the list of Nobel Prizes related to neuroscience research in Table 1.1, you'll notice the names of men and women from several different countries. The field is striving to increase diversity through inclusivity of women and underrepresented groups in the sciences.

Table 1.1 Selected Nobel Prizes for Research Related to Neuroscience

Year	Recipients (Country)	Field of Study
1906	Camillo Golgi (Italy) and Santiago Ramon y Cajal (Spain)	Structure of the nervous system
1963	Sir John Carew Eccles (Australia), Sir Alan Lloyd Hodgkin (U.K.), and Sir Andrew Fielding Huxley (U.K.)	Ionic mechanisms of nerve cell membrane
1970	Julius Axelrod (U.S.), Sir Bernard Katz (Germany, U.S.), and Ulf Svante von Euler (Sweden)	Neurotransmitters
1979	David Hubel (Canada, U.S.), Torsten Wiesel (Sweden, U.S.), and Roger Sperry (U.S.)	Functions of the nervous system
2000	Arvid Carlsson (Sweden), Paul Greengard (U.S.), and Eric Kandel (U.S.)	Neural communication
2014	John O'Keefe (U.S. U.K.), Edvard I. Moser (Norway), and May-Britt Moser (Norway)	Spatial positioning system in the brain

Section Review

Foundations of Behavioral Neuroscience

LO 1.1 Explain the importance of generalization and reduction in behavioral neuroscience research.

To explain the results of behavioral neuroscience research, generalization can be used to reveal general laws of behavior. Reduction can be used to explain complex phenomena in terms of simpler ones.

LO 1.2 Summarize contributions to the modern field of behavioral neuroscience made by individuals involved in philosophy, physiology, or other disciplines.

Ancient scholars disagreed on the importance of the brain in behavior. French philosopher Descartes described reflexes but believed that behavior was the product of pressurized fluid causing muscles to contract. Müller proposed the doctrine of specific nerve energies while Flourens and Broca studied brain region functions using ablation. Galvani discovered that nerves convey electrical messages and von Helmholtz refined that understanding to begin to account for chemical communication between cells. Purkinje and Santiago y Cajal studied the structures and functions of specific sets of neurons.

Thought Question

Recent advances such as the Brain Activity Map Project and the Human Brain Project have been considered by some as stepping stones toward artificial intelligence. There is a possibility that future machines may mimic some functions of the human brain. What do you think of the possible implications of such developments with respect to the advancement of human race? Can computers have self-awareness and consciousness?

Natural Selection and Evolution

Following the tradition of Müller and von Helmholtz, other biologists continued to observe, classify, and think about what they saw, and some of them arrived at valuable conclusions. The most important of these scientists was Charles Darwin. (See Figure 1.4.) Darwin formulated the principles of *natural selection* and *evolution,* which revolutionized biology.

Functionalism and the Inheritance of Traits

LO 1.3 Describe the role of natural selection in the evolution of behavioral traits.

Darwin's theory emphasized that all of an organism's characteristics—its structure, its coloration, its behavior—have functional significance. For example, the strong talons and sharp beaks that eagles possess permit the birds to catch and eat prey. Caterpillars that eat green leaves are themselves green, and their color makes it difficult for birds to see them against their usual background. Mother mice construct nests, which keep their offspring warm and out of harm's way. The behavior itself is not inherited. What *is* inherited is a structure—the brain—that causes the behavior to occur. Thus, Darwin's theory gave rise to **functionalism,** a belief that characteristics of living organisms perform useful functions. So, to understand the physiological basis of various behaviors, we must first understand what these behaviors accomplish. We must therefore understand something about the natural history of the species being studied so that the behaviors can be seen in context.

Figure 1.4 Charles Darwin (1809–1882)

Darwin's theory of evolution revolutionized biology and strongly influenced early psychologists.

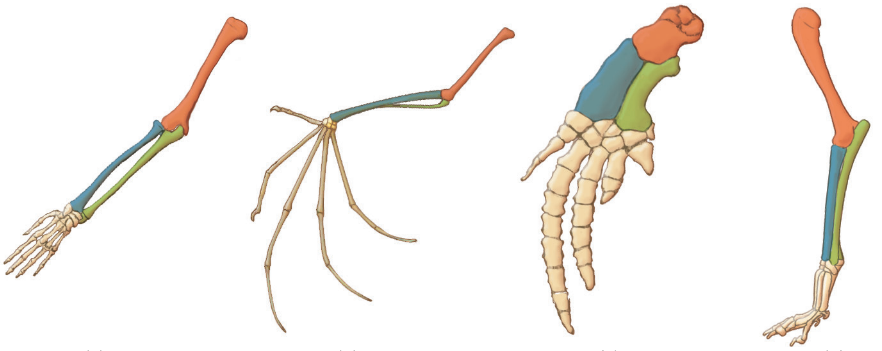
(North Wind Picture Archives.)

To understand the workings of something as complex as a nervous system, we should know what its functions are. Organisms of today are the result of a long series of changes due to genetic variability. Strictly speaking, we cannot say that any physiological mechanisms of living organisms have a *purpose.* But they do have *functions,* and these we can try to determine. For example, the forelimb structures shown in Figure 1.5 are adapted for different functions in different species of mammals. Adaptations also occur in brain structures. For example, male songbirds such as the white crowned sparrow possess highly developed brain structures (the *robust nucleus of the archistriatum*, *high vocal center,* and *Area X)* that differ from some of their close, nonsongbird relatives. The songbirds' unique structures allow them to learn and produce songs in response to complex social and environmental stimuli. The function of male song behavior in these species is to attract a mate and deter rivals. The nonsongbirds lack these brain structures and their associated functions (Beecher and Brenowitz, 2005). Among the various songbirds, in species in which only the males sing, males have larger song brain structures compared to females. In species in which both sexes sing duets, there is no difference between the size of the structures in males and females (Brenowitz, 1997).

Darwin formulated his theory of evolution to explain the means by which species acquired their adaptive characteristics.

Figure 1.5 Bones of the Forelimb

The figure shows the bones of (a) human, (b) bat, (c) whale, (d) dog. Through the process of natural selection, these bones have been adapted to suit many different functions.



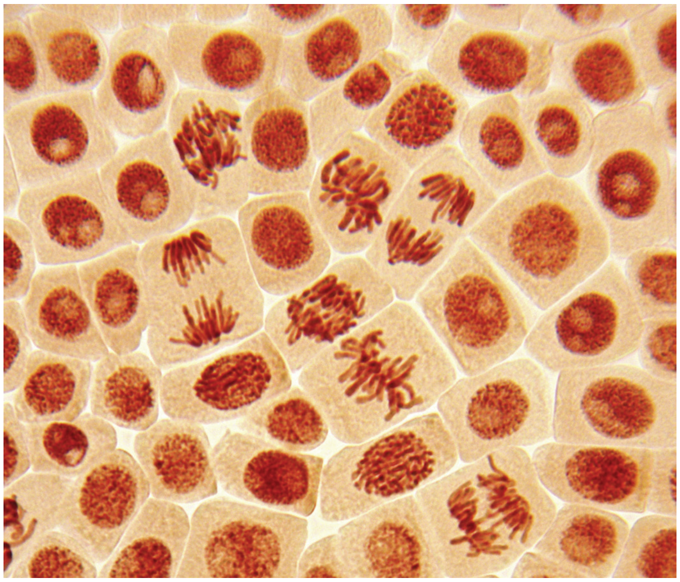
The cornerstone of this theory is the principle of **natural selection.** Darwin noted that members of a species were not all identical and that some of the differences they exhibited were inherited by their offspring. If an individual's characteristics permit it to reproduce more successfully, some of the individual's offspring will inherit the favorable characteristics and will themselves produce more offspring. As a result, the characteristics will become more prevalent in that species. He observed that animal breeders were able to develop strains that possessed particular traits by mating together only animals that possessed the desired traits. If *artificial selection,* controlled by animal breeders, could produce so many varieties of dogs, cats, and livestock, perhaps *natural selection* could be responsible for the development of species. In natural selection, it was the natural environment, not the hand of the animal breeder, that shaped the process of evolution.

Darwin and his fellow scientists knew nothing about the mechanism by which the principle of natural selection works. In fact, the principles of molecular genetics were not discovered until the middle of the twentieth century. Briefly, here is how the process works: Every sexually reproducing multicellular organism consists of a large number of cells, each of which contains chromosomes. Chromosomes are large, complex molecules that contain the recipes for producing the proteins that cells need to grow and to perform their functions. In essence, the chromosomes contain the blueprints for the construction (that is, the embryological development) of a particular member of a particular species. If the plans are altered, a different organism is produced.

The plans do get altered from time to time; mutations occur. **Mutations** are accidental changes in the chromosomes of sperm or eggs that join together and develop into new organisms. For example, a random mutation of a chromosome in a cell of an animal's testis or ovary could produce a mutation that affects that animal's offspring. Most mutations are deleterious; the offspring either fails to survive or survives with some sort of defect. However, a small percentage of mutations are beneficial and confer a **selective advantage** to the organism that possesses them. That is, the animal is more likely than other members of its species to live long enough to reproduce and hence to pass on its chromosomes to its own offspring. Many different kinds of traits can confer a selective advantage: resistance to a particular disease, the ability to digest new kinds of food, more effective weapons for defense or for procurement of prey, and even a more attractive appearance to members of the other sex (after all, one must reproduce to pass on one's chromosomes).

The traits that can be altered by mutations are physical ones; chromosomes make proteins, which affect the structure and chemistry of cells. But the *effects* of these physical alterations can be seen in an animal's behavior. Thus, the process of natural selection can act on behavior indirectly. For example, if a particular mutation results in changes in the brain that cause a small animal to change its behavior and freeze when it perceives a novel stimulus, that animal is more likely to escape undetected when a predator passes nearby. This tendency makes the animal more likely to survive and produce offspring, thus passing on its genes to future generations.

Other mutations are not immediately favorable, but because they do not put their possessors at a disadvantage, they are inherited by at least some members of the species. As a result of thousands of such mutations, the members of a particular species possess a variety of genes and are all at least somewhat different from one another. Variety is a definite advantage for a species. Different environments provide optimal habitats for different kinds of organisms. When the environment changes, species must adapt or run



Dimarion/Shutterstock

Mutations are accidental changes in the chromosomes of sperm or eggs that join together and develop into new organisms.

the risk of becoming extinct. If some members of the species possess assortments of genes that provide characteristics permitting them to adapt to the new environment, their offspring will survive, and the species will continue.

An understanding of the principle of natural selection plays some role in the thinking of every scientist who undertakes research in behavioral neuroscience. Some researchers explicitly consider the genetic mechanisms of various behaviors and the physiological processes on which these behaviors depend. Others are concerned with comparative aspects of behavior and its physiological basis; they compare the nervous systems of animals from a variety of species to make hypotheses about the evolution of brain structure and the behavioral capacities that correspond to this evolutionary development. But even though many researchers are not directly involved with the problem of evolution, the principle of natural selection guides the thinking of behavioral neuroscientists. We ask ourselves what the selective advantage of a particular trait might be. We think about how nature might have used a physiological mechanism that already existed to perform more complex functions in more complex organisms. When we entertain hypotheses, we ask ourselves whether a particular explanation makes sense in an evolutionary perspective.

Evolution of Large Brains

LO 1.4 Identify factors involved in the evolution of large brains in humans.

To *evolve* means to develop gradually. The process of **evolution** is a gradual change in the structure and physiology of plant and animal species as a result of natural selection. New species evolve when organisms develop novel characteristics that can take advantage of unexploited opportunities in the environment.

Appearance of the earliest humans can be traced back to the Cenozoic period when tropical forests covered much of the land areas. In these forests our most direct ancestors, the primates, evolved. The first primates were small and preyed on insects and small cold-blooded vertebrates such as lizards and frogs. They had grasping hands that permitted them to climb about in small branches of the forest. Over time, larger species developed, with larger, forward-facing eyes (and the brains to analyze what the eyes saw), which facilitated moving among the trees and the capture of prey.

The evolution of fruit-bearing trees provided an opportunity for fruit-eating primates. In fact, the original advantage of color vision (and the associated sensory regions of the brain) was probably the ability to discriminate ripe fruit from green leaves and eat the fruit before it spoiled—or some other animals got to it first. And because fruit is such a nutritious form of food, its availability provided an opportunity that could be exploited by larger primates, which were able to travel farther in quest of food.

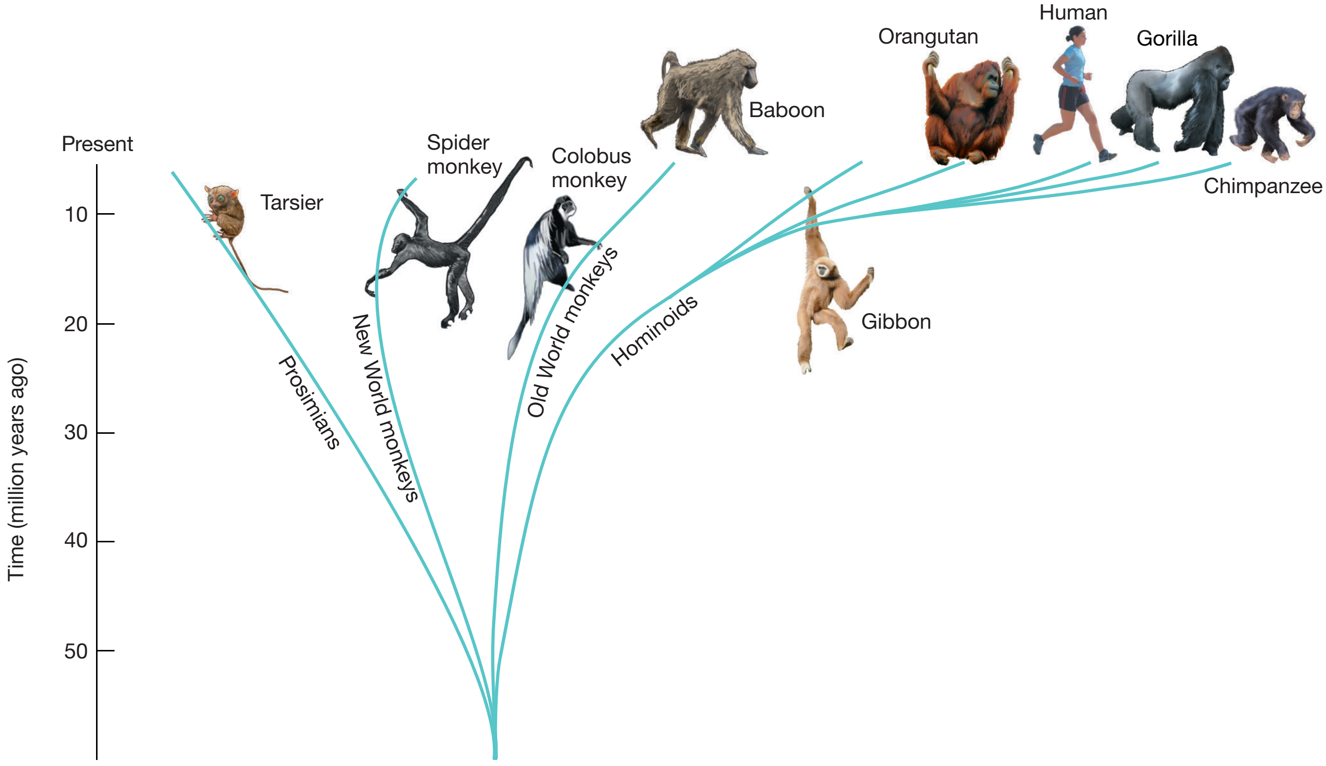
The first *hominids* (humanlike apes) appeared in Africa. They appeared not in dense tropical forests but in drier woodlands and in the savanna. Our fruit-eating ancestors continued to eat fruit, but they evolved characteristics that enabled them to gather roots and tubers as well, to hunt and kill game, and to defend themselves against other predators. They made tools that could be used to hunt, produce clothing, and construct dwellings; they discovered the many uses of fire; they domesticated dogs, which greatly increased their ability to hunt and helped warn of attacks by predators; and they developed the ability to communicate symbolically, by means of spoken words.

Figure 1.6 shows the primate family tree. Our closest living relatives—the only hominids besides ourselves who have survived—are the chimpanzees, gorillas, and orangutans. DNA analysis shows that genetically, there is very little difference between these four species. For example, humans and chimpanzees share almost 99 percent of their DNA.

The first hominid to leave Africa did so around 1.7 million years ago. This species, *Homo erectus* ("upright man"), scattered across Europe and Asia. One branch of *Homo erectus* appears to have been the ancestor of *Homo neanderthalis,* which inhabited Western Europe between 120,000 and 30,000 years ago. Neanderthals resembled modern humans. They made tools out of stone and wood and discovered the use of fire. Our own species, *Homo sapiens,* evolved in East Africa around 100,000 years ago. Some of our ancestors migrated to other parts of Africa and out of Africa to Asia, Polynesia, Australia, Europe, and the Americas (see Figure 1.7).

Figure 1.6 Evolution of Primate Species

(Redrawn from Lewin, R. *Human Evolution: An Illustrated Introduction,* 3rd ed. Boston: Blackwell Scientific Publications, 1993. Reprinted with permission by Blackwell Science Ltd.)

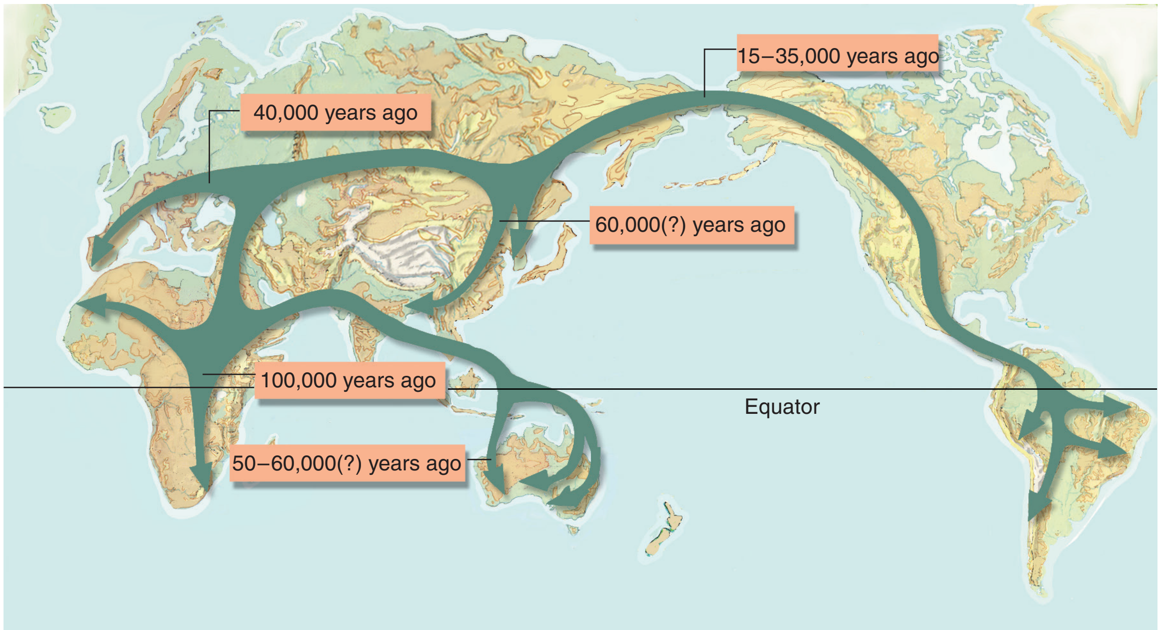


Humans possessed several characteristics that enabled them to compete with other species. Their agile hands enabled them to make and use tools. Their excellent color vision helped them to spot ripe fruit, game animals, and dangerous predators. Their mastery of fire enabled them to cook food, provide warmth, and frighten nocturnal

Figure 1.7 Migration of *Homo sapiens*

The figure shows proposed migration routes of *Homo sapiens* after evolution of the species in East Africa.

(Redrawn with permission from Cavalli-Sforza, L. L. Genes, peoples and languages. *Scientific American,* Nov. 1991, p. 75.)



predators. Their upright posture and bipedalism (ability to walk using two rear limbs) made it possible for them to walk long distances efficiently, with their eyes far enough from the ground to see long distances across the plains. Bipedalism also permitted them to carry tools and food with them, which meant that they could bring fruit, roots, and pieces of meat back to their tribe. Their linguistic abilities enabled them to combine the collective knowledge of all the members of the tribe, to make plans, to pass information on to subsequent generations, and to form complex civilizations that established their status as the dominant species. All of these characteristics required a larger brain.

A large brain requires a large skull, and an upright posture limits the size of a woman's birth canal. A newborn baby's head is about as large as it can safely be. As it is, the birth of a baby is much more arduous than the birth of mammals with proportionally smaller heads, including those of our closest primate relatives. Because a baby's brain is not large or complex enough to perform the physical and intellectual abilities of an adult, the brain must continue to grow after the baby is born. In fact, all mammals (and all birds, for that matter) require parental care for a period of time while the nervous system develops. The fact that young mammals (particularly young humans) are guaranteed to be exposed to the adults who care for them means that a period of apprenticeship is possible. Consequently, the evolutionary process did not have to produce a brain that consisted solely of specialized circuits of neurons that performed specialized tasks. Instead, it could simply produce a larger brain with an abundance of neural circuits that could be modified by experience. Adults would nourish and protect their offspring and provide them with the skills they would need as adults. Some specialized circuits were necessary, of course (for example, those involved in analyzing the complex sounds we use for speech), but, by and large, the brain is a general-purpose, programmable computer.

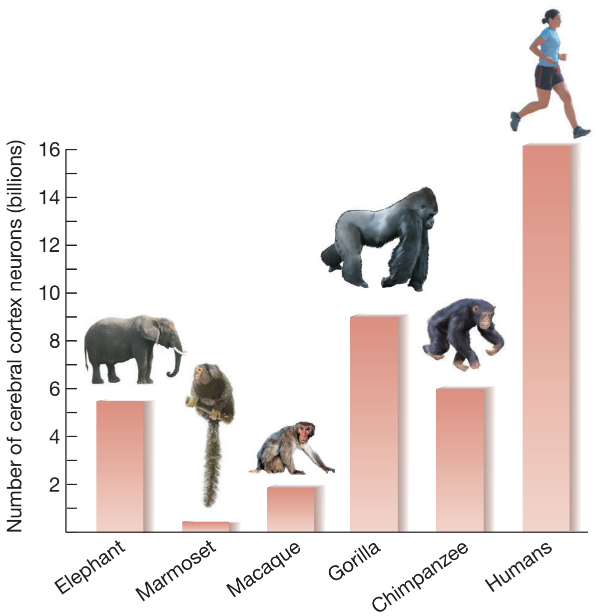
How does the human brain compare with the brains of other animals? In absolute size, our brains are dwarfed by those of elephants or whales. However, we might expect such large animals to have large brains to match their large bodies. Indeed, the human brain makes up 2.3 percent of our total body weight, while the elephant brain makes up only 0.2 percent of the animal's total body weight, which makes our brains seem very large in comparison. However, the shrew, which weighs only 7.5 grams (g), has a brain that weighs 0.25 g, or 3.3 percent of its total body weight. The shrew brain is much less complex than the human brain, so something is wrong with this comparison.

The answer is that although bigger bodies require bigger brains, the size of the brain does not have to go up proportionally with that of the body. For example, larger muscles do not require more nerve cells to control them. What counts, as far as intellectual ability goes, is having a brain with plenty of neurons that are not committed to moving muscles or analyzing sensory information—neurons that are available for behavior, learning, remembering, reasoning, and making plans. Besides varying in size, brains also vary in the number of neurons found in each gram of tissue. Herculano-Houzel et al. (2007) compared the weight of the brains of several species of rodents and primates with the number of neurons that each brain contained. They found that primate brains—especially large ones—contain many more neurons per gram than rodent brains do (see Figure 1.8).

What types of genetic changes were responsible for the evolution of the human brain? This question will be addressed in more detail in Chapter 3, but evidence suggests that the most important principle is a slowing of the process of brain development, allowing more time for growth. As we will see, the prenatal period of cell division in the brain is prolonged in humans, which results in a brain that weighs an average of 350 g and contains approximately 100 billion neurons. After birth the brain continues to grow. Production of new neurons almost ceases, but those that are already present grow and establish connections with each other, and other brain cells, which protect and support neurons, begin to proliferate. Not until late adolescence does the human brain reach its adult size of approximately 1,400 g—about four times the weight of a newborn's brain. This prolongation of maturation is known as **neoteny** (roughly translated as "extended youth"). The mature human head and brain retain some infantile characteristics, including their disproportionate size relative to the rest of the body.

Figure 1.8 Comparison of Mammalian Brains

Species with more complex behaviors have brains with more neurons that are available for behavior, learning, remembering, reasoning, and making plans. Primate brains—especially large ones—contain many more neurons per gram than rodent brains and many more neurons in the cortex. Source: Herculano-Houzet, S., Marino, L. Brain Behav Evol 1998;51 230–238.



Section Review

Natural Selection and Evolution

LO 1.3 Describe the role of natural selection in the evolution of behavioral traits.

Natural selection is the process responsible for evolution of structures with specific functions. Members of a species possess a variety of structures. If the structures permit an individual to reproduce more successfully, its offspring will also have these structures and they will become more prevalent in the population. An example of inherited structures responsible for behavior is the set of brain structures responsible for male song behavior in some species of songbirds.

LO 1.4 Identify factors involved in the evolution of large brains in humans.

The evolution of specialized structures responsible for functions such as color vision, fine motor control, complex vision, and language required a larger brain. The size of a human brain at birth is limited by the size of the birth canal. Additional brain development occurs after birth and throughout an extended period of development and parental care in humans. Primate brains contain many more neurons per gram than other species. These additional cells are responsible for behavior, learning, remembering, reasoning, and making plans.

Thought Question

A recent paper by Kavoi & Jameela (2011) reported that a part of the brain responsible for olfaction, the olfactory bulb, is larger in dogs than humans, even after accounting for differences in overall brain size. Using the principles of natural or artificial selection, hypothesize how dogs came to have this larger structure in their brain and predict how it might impact their behavior.

Ethical Issues in Research with Humans and Other Animals

This book contains many facts about what is currently known about the structure and function of the nervous system. Where do these facts come from? They are the result of carefully designed experiments that can include computer simulations, individual cells, and often humans and other animals. Neuroscience research involving humans and animals is subject to important ethical considerations. This section addresses these issues in more detail.

Research with Animals

LO 1.5 Outline reasons for the use of animals in behavioral neuroscience research.

Most of the research described in this book involves experimentation on living animals. Any time we use another species of animals for our own purposes, we should be sure that what we are doing is both humane and worthwhile. It is important that a good case can be made that research in behavioral neuroscience qualifies on both counts. Humane treatment is a matter of procedure. We know how to maintain laboratory animals in good health in comfortable, sanitary conditions. We know how to administer anesthetics and analgesics so that animals do not suffer during or after surgery, and we know how to prevent infections with proper surgical procedures and the use of antibiotics. Most industrially developed societies have very strict regulations about the care of animals and require approval of the experimental procedures that are used on them. There is no excuse for mistreating animals in our care. In fact, the vast majority of laboratory animals *are* treated humanely.

Whether an experiment is *worthwhile* can be difficult to say. We use animals for many purposes. We eat their meat and eggs, and we drink their milk; we turn their hides into leather; we extract insulin and other hormones from their organs to treat people's diseases; we train them to do useful work on farms or to entertain us. Even having a pet is a form of exploitation; it is we—not they—who decide that they will live in our homes. The fact is we have been using other animals throughout the history of our species.

Pet owning has the potential to cause much more suffering among animals than scientific research does. Pet owners are not required to receive permission from a board of experts that includes a veterinarian to house their pets, nor are they subject to periodic inspections to be sure that their home is clean and sanitary, that their pets have enough space to exercise properly, or that their pets' diets are appropriate. Scientific researchers are.

In the United States, any institution that receives federal research funding to use animals in research is required to have an *Institutional Animal Care and Use Committee* (IACUC). The IACUC is typically composed of a veterinarian, scientists who work with animals, nonscientist members, and community members not affiliated with the institution. This group reviews all proposals for research involving animals, with the

Everett Collection/Shutterstock

Research with laboratory animals has produced important discoveries about the possible causes or potential treatments of neurological and mental disorders.

intent of ensuring humane and ethical treatment of all animals involved. Even noninvasive research with animals (such as field work or observational studies) must pass review and be approved by the IACUC. This approval process ensures not only the welfare of the animals, but also that the research is compliant with local, state, and federal regulations.

The disproportionate amount of concern that animal rights activists show toward the use of animals in research and education is puzzling, particularly because this is the one *indispensable* use of animals. We *can* survive without eating animals, we *can* live without hunting, we *can* do without furs; but without using animals for research and for training future researchers, we *cannot* make progress in understanding and treating diseases. In not too many years scientists will probably have developed a vaccine that will prevent the further spread of diseases such as ebola, malaria, or AIDS. Even diseases that we have already conquered would take new victims if drug companies could no longer use animals to develop and test new treatments. If they were deprived of animals, these companies could no longer extract hormones used to treat human diseases, and they could not prepare many of the vaccines we now use to prevent disease.

Our species is beset by medical, psychological, and behavioral problems, many of which can be solved only through biological research. Let us consider some of the major neurological disorders. Strokes, such as the one experienced by Jeremiah at the beginning of this chapter, are caused by bleeding or obstruction of a blood vessel within the brain, and often leave people partly paralyzed, unable to read, write, or converse with their friends and family. Basic research on the means by which nerve cells communicate with each other has led to important discoveries about the causes of the death of brain cells. This research was not directed toward a specific practical goal; the potential benefits actually came as a surprise to the investigators.

Experiments based on these results have shown that if a blood vessel leading to the brain is blocked for a few minutes, the part of the brain that is nourished by that vessel will die. However, the brain damage can be prevented by first administering a drug that interferes with a particular kind of neural communication. This research is important, because it may lead to medical treatments that can help to reduce the brain damage caused by strokes. But it involves operating on a laboratory animal, such as a rat, and pinching off a blood vessel. (The animals are anesthetized.) Some of the animals will sustain brain damage, and all will be euthanized so that their brains can be examined. However, you will probably agree that research like this is just as legitimate as using animals for food.

As you will learn later in this book, research with laboratory animals has produced important discoveries about the possible causes or potential treatments of neurological and mental disorders, including Parkinson's disease, schizophrenia, bipolar disorder, anxiety disorders, obsessive-compulsive disorder, anorexia nervosa, obesity, and substance abuse. Although much progress has been made, these problems persist, and they cause much human suffering. Unless we continue our research with laboratory animals, they will not be solved.

Some people have suggested that instead of using laboratory animals in our research, we could use tissue cultures or computers. While these techniques can be used to pursue some research questions, unfortunately, tissue cultures or computers are not substitutes for complex, living organisms. We have no way to study behavioral problems such as substance abuse in tissue cultures, nor can we program a computer to simulate the workings of an animal's nervous system. (If we could, that would mean we already had all the answers.)

Research with Humans

LO 1.6 Discuss ethical considerations in research with human participants.

Not all neuroscience research is conducted with animal models. Much of what we currently understand about the brain and behavior is the result of research with human participants. Much like animal research, research with human volunteers is essential to advancing our knowledge of the brain in health and disease. Also similar to animal research, work with human participants is subject to strict regulation and must be reviewed and approved by a board of experts and lay people. The *Institutional Review Board* (IRB)

Figure 1.9 Behavioral Neuroscience Research with Human Participants

Researchers work with volunteers to learn more about the brain mechanisms responsible for functions such as emotion, learning, memory, and behavior.

functions similarly to the IACUC to ensure ethical treatment of volunteers in research (see Figure 1.9).

In addition to humane research conditions, research with human participants must also include informed consent and precautions to protect the identity of the participants. **Informed consent** describes the process in which researchers must inform any potential participant about the nature of the study, how any data will be collected and stored, and what the anticipated benefits and costs of participating will be. Only after obtaining this information can the participant make an informed decision about whether to participate in a study. Violating the informed consent process can have ethical, legal, and financial consequences. In 2010, the case of *Havasupai Tribe v. Arizona Board of Regents* was settled, including the return of biological samples and a payment of $700,000 to the Havasupai tribe after six years of dispute. The settlement was issued in response to a vague and incomplete informed consent process that resulted in the use of blood samples originally intended for research on diabetes being used in contested research involving factors related to schizophrenia (Van Assche et al., 2013). Protecting the identity of participants is crucial for all research with human participants, and particularly important in behavioral neuroscience research investigating potentially sensitive topics (for example, the use of illicit drugs in studies of brain changes in substance abuse and treatment development).

An emerging interdisciplinary field, **neuroethics,** is devoted to better understanding implications of and developing best practices in ethics for neuroscience research with human participants. A 2014 report from a panel of national experts explored the ethical challenges of neuroscience research by investigating (1) neuroimaging and brain privacy; (2) dementia, personality, and changed preferences; (3) cognitive enhancement and justice; and (4) deep brain stimulation research and the ethically difficult history of psychosurgery (Presidential Commission for the Study of Bioethical Issues, 2014). The panel recommendations included integrating ethics and science through education at all levels.

Section Review

Ethical Issues in Research with Humans and Other Animals

LO 1.5 Outline reasons for the use of animals in behavioral neuroscience research.

Animals are used in behavioral neuroscience research to improve understanding of the nervous system and develop treatments for disease and injury. Animal models are used when it is not possible or it is inappropriate to conduct research with human participants and when cell models or computer programs cannot simulate the complexity of the nervous system.

LO 1.6 Discuss ethical considerations in research with human participants.

Ethical considerations for research involving human participants include protections such as informed consent and confidentiality. The field of neuroethics is devoted to better understanding implications of and developing best practices in ethics for neuroscience research with human participants.

Thought Question

Behavioral neuroscience research presents unique ethical considerations. For example, the development of drugs to enhance attention and learning, the refinement of imaging techniques to reveal a person's mood or beliefs, or new tests to reveal the likelihood of a person to engage in aggressive behavior all present challenging ethical dilemmas. Select one of the examples above and identify the ethical challenge and suggest whether this research should be conducted and why. If it is conducted, what precautions should be in place to protect the rights of participants?

The Future of Neuroscience: Careers and Strategies for Learning

What is behavioral neuroscience, and what do behavioral neuroscientists do? What are the best ways to learn more about this diverse and exciting field? By the time you finish this book, you will have a much richer answer to these questions. The next section will describe the field—and careers open to those who specialize in it. Likewise we want to provide you with some strategies to help you learn as you read and study this fascinating discipline.

Careers in Neuroscience

LO 1.7 Identify careers in behavioral neuroscience.

Behavioral neuroscience belongs to a larger field that is simply called *neuroscience.* Neuroscientists concern themselves with all aspects of the nervous system: its anatomy, chemistry, physiology, development, and functioning. The research of neuroscientists ranges from the study of molecular genetics to the study of social behavior. **Behavioral neuroscientists** study all behavioral phenomena that can be observed in humans and animals. They attempt to understand the physiology of behavior: the role of the nervous system, interacting with the rest of the body (especially the endocrine system, which secretes hormones), in controlling behavior. They study such topics as sensory processes, sleep, emotional behavior, ingestive behavior, aggressive behavior, sexual behavior, parental behavior, and learning and memory. They also study animal models of disorders that afflict humans, such as anxiety, depression, obsessions and compulsions, phobias, and schizophrenia. Although the original name for the field described in this book was *physiological psychology,* several other terms are now in general use, such as *biological psychology, biopsychology, psychobiology,* and—the most common one—*behavioral neuroscience.*

Two other fields often overlap with that of behavioral neuroscience: *neurology* and *cognitive neuroscience.* Neurologists are physicians who diagnose and treat diseases of the nervous system. Most neurologists are solely involved in the practice of medicine, but some engage in research. They study the behavior of people whose brains have been damaged by natural causes, using advanced brain-imaging techniques to study the activity of various regions of the brain as a person participates in various behaviors. This research is also carried out by cognitive neuroscientists—researchers with a Ph.D. (usually in psychology) and specialized training in the principles and procedures of neurology.

Most professional behavioral neuroscientists have received a Ph.D. from a graduate program in psychology or from an interdisciplinary program. Programs can include faculty members from departments such as psychology, biology, chemistry, biochemistry, or computer science. Most professional behavioral neuroscientists are employed by colleges and universities, where they are engaged in teaching and research. Others are employed by institutions devoted to research—for example, in laboratories owned and operated by national governments or by private philanthropic organizations. A few work in industry, usually for pharmaceutical companies that are interested in assessing the effects of drugs on behavior.

To become a professor or independent researcher, one must receive a doctorate—usually a Ph.D., although some people turn to research after receiving an M.D. Most behavioral neuroscientists spend two years or more in a postdoctoral position after completing their graduate degree, working in the laboratory of a senior scientist to gain more research experience. During this time they write articles describing their research findings and submit them for publication in scientific journals. These publications are an important factor in obtaining an independent position.

Not all people who are engaged in neuroscience research have doctoral degrees. Research technicians with bachelor's or master's level degrees perform essential—and intellectually rewarding—services working with senior scientists. Technicians can continue to gain experience and education on the job, enabling them to assume responsibility for managing and completing projects independently. (See Figure 1.10.)

Strategies for Learning

LO 1.8 Describe effective learning strategies for studying behavioral neuroscience.

The brain is a complicated organ. After all, it is responsible for all our abilities and all our complexities. Scientists have been studying this organ for many years and (especially in recent years) have been learning a lot about how it works. It is impossible to summarize this progress in a few simple sentences; therefore, this book contains a lot of information. We have tried to organize this information logically, telling you what you need to know in the order in which you need to know it. (To understand some things, you sometimes need to understand other things first.) We have also tried to write as clearly as possible, making examples as simple and as vivid as we can. Still, you cannot expect to master the information in this book by simply giving it a passive read; you will have to do some work.

Learning about behavioral neuroscience involves much more than memorizing facts. Of course, there *are* facts to be memorized: names of parts of the nervous system, names of chemicals and drugs, scientific terms for particular phenomena and procedures used to investigate them, and so

Figure 1.10 Pursuing a Research Career in Neuroscience

What kinds of training are required for a career in neuroscience? Where do neuroscientists work? Explore this timeline to learn more.

Time Period	Description
High school	Students interested in neuroscience may take courses in biology, chemistry, psychology, or other sciences in high school. 
College	Students interested in neuroscience may study biology, chemistry, psychology, neuroscience, or other related areas. Some students work as research assistants in laboratories and develop mentored relationships with researchers. College graduates interested in neuroscience can work as research technicians or assistants. 
Graduate Training	Students can pursue advanced graduate training for one or more years after college. Graduate training typically involves advanced course work and more independent research. Graduate students are expected to conduct research (with the guidance of a research mentor) and disseminate the results of their work. After completing a graduate program, individuals may teach in a secondary or postsecondary institution, conduct research, or work in industry. 
Postgraduate Training	Postgraduate positions are more independent and often involve additional training in specialized research areas or with specialized research techniques. After completing postgraduate training, individuals may teach in a secondary or postsecondary institution, conduct research, or work in industry. 

on. But the quest for information is nowhere near completed; we know only a small fraction of what we have to learn. And almost certainly, many of the "facts" that we now accept will someday be shown to be incorrect. If all you do is learn facts, where will you be when these facts are revised?

Our goal is to offer some practical advice about studying. You have been studying throughout your academic career, and you have undoubtedly learned some useful strategies along the way. Even if you have developed efficient and effective study skills, at least consider the possibility that there might be some ways to improve them. This section is intended to provide you with suggestions to maximize your learning about behavioral neuroscience. These suggestions are supported by empirical research on learning.

- Take notes that organize information into meaningful groups. Linking new information to prior knowledge is an important means for learning. To do this will require actively thinking about the new information at hand and finding ways to link it to your current understanding. This is an active and involved process that will take some time and effort. Highlighting or underlining without combining the information into your own notes is passive and does not facilitate learning and retention the way that writing or typing your own notes does. Previous research has demonstrated the highlighting and underlining alone do not improve test scores, and in some cases may be detrimental to learning (Dunlosky et al., 2013).
- Teach yourself by teaching someone else. After reading a section or chapter, consider how you would teach the information to someone else—a classmate, a friend, or maybe a curious family member. This activity will help you to think about the most important aspects of the section. Nestojko et al. (2014) found that students who prepared to teach others about the content of a complex reading assignment performed better on a later test than students who had prepared themselves for a test on the reading.
- Study in the environment you will be tested in. State dependent learning theory says that information learned in one environment is most readily recalled in the same environment. The rationale behind this performance boosting effect of environment is that the context (e.g., the color of the walls, the seat, the people around you) provides important cues that help you recall what was previously learned in that environment. If you're *not* able to study in the same environment as you will be tested, you can try to incorporate as many of the same elements as possible (e.g., use the same computer, pens, procedure for note taking, etc.) *or* you can study in many different environments (e.g., at home, in the student union, in your residence hall) so that you will not become dependent on any one single cue or set of cues when you are tested. In an interesting test of state dependent learning, Godden & Baddeley (1975) tested college student scuba divers on information they read while underwater or on land. Students recalled information learned underwater the best in an underwater test. The students performed most poorly on the tests of information in a different context (for example, information learned underwater but tested on land).
- Study with the absolute minimum of distractions. Your brain works best when it focuses on one challenging task (like learning about neuroscience!) at a time (Hattie & Yates, 2014). Turn off televisions, social media, and phones whenever possible, and try to study in a quiet environment. Lee et al. (2012) assigned college students learning about science, history, and politics to three groups: reading in silence, reading with a TV show playing in the background that students could ignore, and reading with a TV show playing in the background that students would later be tested on so that they would be sure to pay attention to both the TV show and their assigned study material. Students were instructed to read and answer multiple choice questions. As you might expect, students who tried to read and pay attention to the TV show performed the worst on the test.
- Spread out your study sessions. Studying new information in two shorter but separated sessions leads to more effective recall than studying in one long session. Don't cram. Instead, plan to study something new once, then study it again a different day before being asked to recall or apply it on a final test or assignment. Though you should plan your own study sessions around your schedule and based on assignment or test due dates in your class, some cognitive spacing has already been built into this book for you. While there is no "one size fits all" time period for spacing out reading and study sessions, one to several days is a good rule of thumb (Carpenter et al., 2012).
- Study the most challenging topic first or last. Classic studies in psychology revealed that when people were asked to learn long lists of words, the first words learned (the *primacy effect*) and the last words learned (the *recency effect*) were the most likely to be recalled. The same principles can hold true for learning about behavioral neuroscience. For example, if you are reading about the cortex, the thalamus, and the meninges in Chapter 3, and you already know most of the parts of the meninges, but are not feeling confident about your understanding of the cortex and thalamus, plan to study the cortex first, then the meninges and finally the thalamus information.

- Use mnemonics. Mnemonics are short-cuts for helping retain new information. For example, you could try *story chaining* by inventing a short story to link together discrepant items; *method of loci* to use images of physical locations enabling you to position items along an imaginary walk; and *acrostics* to use a word to represent a list (such as FPOT for the lobes of the cortex: **f**rontal, **p**arietal, **o**ccipital, **t**emporal) (Hattie and Yates, 2014).

How this book is organized.

- The text, animations, interactives, and illustrations are integrated as closely as possible. In our experience, one of the most frustrating aspects of reading some books is not knowing when to look at an illustration. Here everything is presented to you as you need it.
- Each chapter begins with a case study that profiles a person's real-life experience, a list of learning objectives, and a figure of the brain. The case studies are meant to personalize and make more relatable the concepts we will discuss in the chapter. The learning objectives are there to help you focus on the key ideas included in the chapter, and the figure of the brain will help orient you in the regions of the brain relevant in that particular chapter.
- You will notice that some words in the text are *italicized*, and others are printed in **boldface.** *Italics* mean that either the word is being stressed for emphasis or it is a new term. Terms in **bold** are key terms that are part of the vocabulary of the behavioral neuroscientist and you will see many of these terms used again in later chapters.
- At the end of each section, you will find two different types of review activities: section reviews and thought questions. The section reviews will remind you of key points from the chapter and the thought questions will challenge you to apply what you have learned to a new context or to expand your thinking on a relevant topic. Finally, there are Chapter Review Questions at the end of each chapter to help you assess your understanding of the concepts.

Now that you have a sense of what the field of behavioral neuroscience entails, welcome to the rest of this book! The next chapter starts with the structure and functions of neurons, the most important elements of the nervous system.

Section Review

The Future of Neuroscience: Careers and Strategies for Learning

LO 1.7 Identify careers in behavioral neuroscience.

Researchers work in the fields of general neuroscience, behavioral neuroscience, and cognitive neuroscience. Neurologists are physicians who specialize in the nervous system. Individuals pursuing careers in neuroscience work in academia and industry and often pursue graduate education.

LO 1.8 Describe effective learning strategies for studying behavioral neuroscience.

Active strategies for learning are most effective. Taking notes, practicing teaching or sharing information with another person, making sure your study and test-taking environment share some common features, studying with as few distractions as possible, spacing out your study sessions, carefully planning when to study challenging material, and using mnemonics whenever possible can enhance your learning.

Thought Question

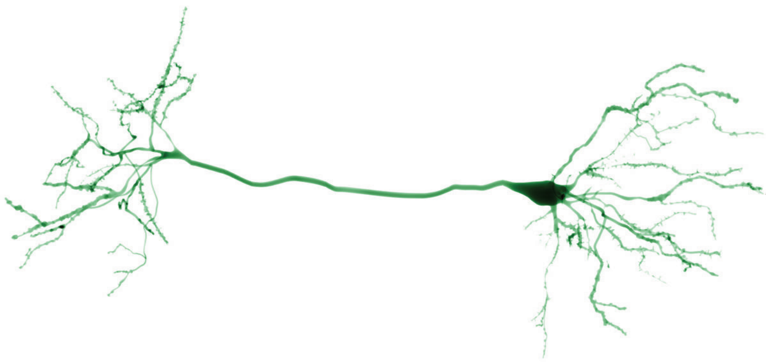
What is it like to work as a neuroscientist today? What kinds of training do careers in neuroscience require? What kinds of activities do neuroscientists engage in on the job? Conduct an online search and locate a job advertisement for a position in neuroscience. Read the job description and qualifications carefully. What qualifications are required for the job? Why do you think these experiences or this training is required? What kinds of responsibilities and activities will the person in this position engage in?

Chapter Review Questions

1. Explain the goals of behavioral neuroscience research.
2. Describe the biological roots of behavioral neuroscience.
3. Describe the role of natural selection in the evolution of behavioral traits.
4. Explain the evolution of the human species and a large brain.
5. What measures may be adopted for preventing ethical misconduct in neuroscience research involving human participants?
6. Describe the scope and various disciplines and fields under the umbrella of behavioral neuroscience research.
7. Describe the various types of learning strategies and styles and their importance in maximizing your learning about behavioral neuroscience.

Chapter 2

Structure and Functions of Cells of the Nervous System



Chapter Outline

Learning Objectives

LO 2.1 Contrast the location of the central and peripheral nervous systems.

LO 2.2 Describe the structures of a neuron, including their general function.

LO 2.3 Differentiate functions of supporting cells of the central and peripheral nervous systems.

LO 2.4 Discuss the features and importance of the blood–brain barrier.

LO 2.5 Compare neural communication in a withdrawal reflex with and without inhibition of the reflex.

LO 2.6 Contrast the changes in electrical potential within a neuron when it is experiencing resting potential, hyperpolarization, depolarization, and an action potential.

LO 2.7 Summarize the contributions of diffusion, electrostatic pressure, and the sodium–potassium pump to establishing membrane potential.

LO 2.8 Summarize the series of ion movements during the action potential.

LO 2.9 Describe the propagation of an action potential.

LO 2.10 Describe the structures and functions of presynaptic cells that are involved in synaptic communication.

LO 2.11 Describe the process of neurotransmitter release.

LO 2.12 Contrast ionotropic and metabotropic receptors.

LO 2.13 Compare the functions of EPSPs and IPSPs in postsynaptic cells.

LO 2.14 Explain the roles of reuptake and enzymatic deactivation in terminating postsynaptic potentials.

LO 2.15 Summarize the process of neural integration of EPSPs and IPSPs.

LO 2.16 Differentiate between the locations and functions of autoreceptors and postsynaptic receptors.

LO 2.17 Identify synapses other than those involved in neural integration.

LO 2.18 Describe examples of nonsynaptic communication.

Kathryn was getting desperate. She had always been healthy and active, eating wisely and keeping fit with sports and regular exercise. She went to the gym almost every day for cardio classes and swimming. But several months prior she began having trouble keeping up with her usual schedule. At first, she found herself getting tired toward the end of her exercise classes. Her arms, particularly, seemed to get heavy. Then when she entered the pool and started swimming, she found that it was hard to lift her arms over her head. She did not have any other symptoms, so she told herself that she needed more sleep.

Over the next few weeks, however, things only got worse. Her exercise classes were more and more difficult to complete. Her instructor became concerned and suggested that Kathryn see her doctor. She made an appointment, but her doctor could find nothing wrong with her. She was not sick, showed no signs of an infection, and seemed to be generally healthy. Her doctor asked how things were going at work. Kathryn explained that she had been experiencing a particularly stressful month at her job. Kathryn and her physician agreed that increased stress could be the cause of her problem. The doctor did not prescribe any medication, but asked Kathryn to make another appointment if she did not feel better soon.

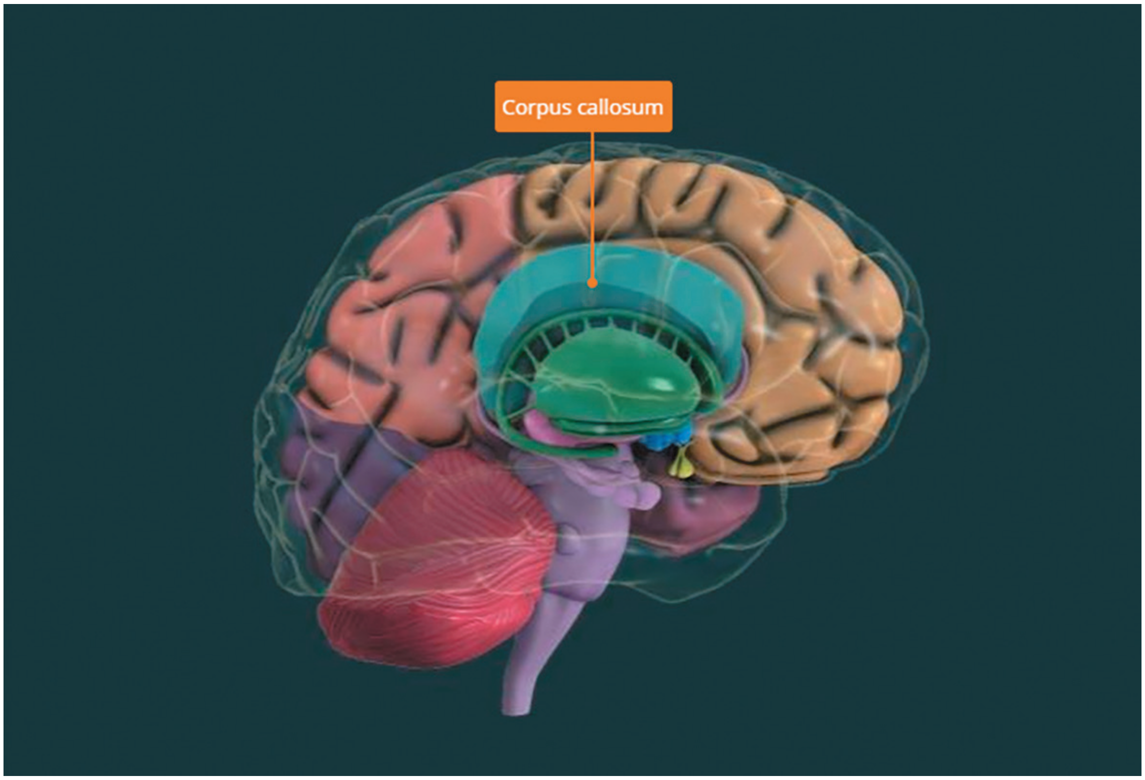
She did feel better for a while, but then all of a sudden her symptoms got worse. She quit going to the gym and found that she even had difficulty finishing a day's work. One afternoon she tried to look up at the clock on the wall and realized that she could hardly see—her eyelids were drooping, and her head felt as if it weighed a hundred pounds. Just then, one of her supervisors came over to her and asked her to fill him in on the progress she had been making on a new project. As she talked, she found herself getting weaker and weaker. It even felt as if breathing seemed to take a lot of effort. She managed to finish the interview, but immediately afterward she went home.

She called her physician, who arranged for her to go to the hospital to be seen by a neurologist. The neurologist listened to a description of Kathryn's symptoms and examined her briefly. The *neurologist thought she might know what was wrong. She prepared an injection and gave it to Kathryn. She started questioning Kathryn about her job. Kathryn answered slowly, her voice almost a whisper. As the questions continued, she realized that it was getting easier and easier to talk. She straightened her back and took a deep breath. She stood up and raised her arms above her head. "Look," she said, her excitement growing. "I can do this again. I've got my strength back! What did you give me? Am I cured?"*

*****

All we are capable of doing—perceive, think, learn, remember, act—is made possible by the integrated activity of the cells of the nervous system. To understand how the nervous system controls behavior, we must first understand its parts—the cells that compose it. In Kathryn's case, the cells of her nervous system were not functioning appropriately, leading to her symptoms of fatigue. Kathryn was diagnosed with *myasthenia gravis*. The term literally means "grave muscle weakness." It is an uncommon disorder, but most experts believe that many mild cases go undiagnosed. Although there are drug treatments, unfortunately no cure has yet been found for it.

Myasthenia gravis is an autoimmune disease. For unknown reasons the immune system breaks down proteins in the nervous system that allow cells to receive messages. Understanding the structure and function of the cells of the nervous system allowed the neurologist to diagnose and treat Kathryn. Kathryn's case highlights many of the key aspects you will learn about in this chapter, including communication within and between cells of the nervous system. To learn more about the specific cells involved in myasthenia gravis, look ahead to the section on acetylcholine in *Termination of Postsynaptic Potentials*.



This figure depicts the corpus callosum, a band of white matter composed of many axons crossing between the right and left hemisphere of the brain. In this chapter you'll learn about the importance of axons in neural communication.

Cells of the Nervous System

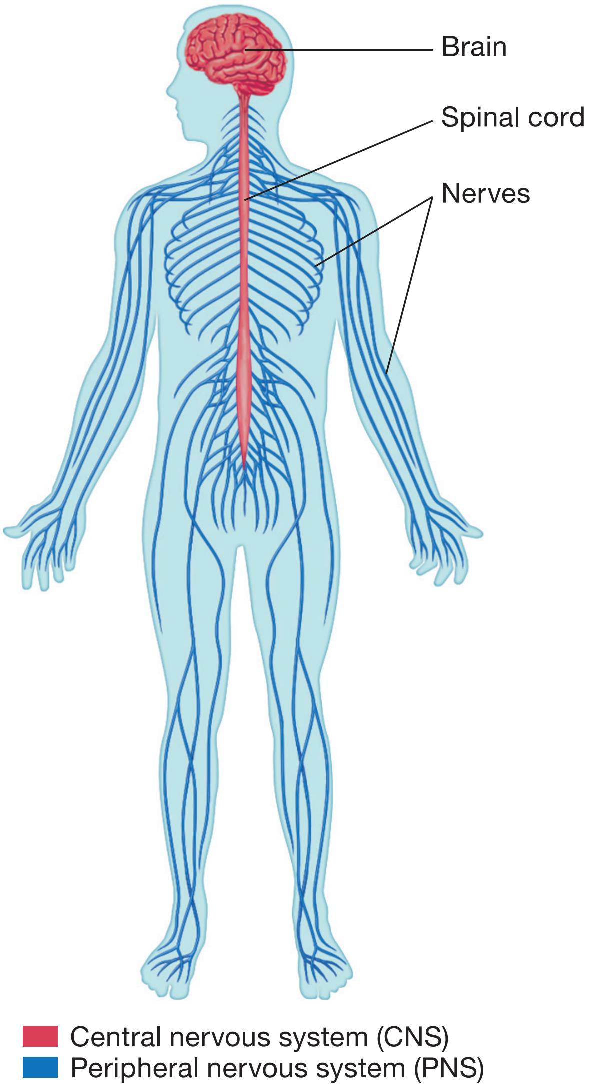
There are billions of nerve cells, or *neurons*, in the human nervous system. Because this chapter deals with cells, you need not be familiar with the structure of the entire nervous system, which is presented in Chapter 3. However, you do need to know that the nervous system consists of two basic divisions: the central nervous system and the peripheral nervous system.

The Nervous System: An Overview

LO 2.1 Contrast the location of the central and peripheral nervous systems.

The **central nervous system (CNS)** consists of the parts that are encased by the bones of the skull and spinal column: the brain and the spinal cord. The **peripheral nervous system (PNS)** is found outside these bones and consists of the nerves and most of the sensory organs. (See Figure 2.1.)

Figure 2.1 The Central and Peripheral Nervous Systems
The central nervous system includes the brain and spinal cord. The peripheral nervous system includes all of the nerves that relay information between the central nervous system and the rest of the body.



The CNS communicates with the rest of the body through **nerves** attached to the brain and to the spinal cord. Nerves are bundles of thousands of individual neurons, all wrapped in a tough, protective membrane. Under a microscope, nerves look something like telephone cables, with their bundles of wires. Like the individual wires in a telephone cable, nerve fibers transmit messages through the nerve, from a sense organ to the brain or from the brain to a muscle or gland.

Information, in the form of light, sound waves, odors, tastes, or contact with objects, is gathered from the environment by specialized cells of the PNS called **sensory neurons.** Movements are accomplished by the contraction of muscles, which are controlled by **motor neurons** in the PNS. And in between sensory neurons and motor neurons are the **interneurons—**neurons that lie entirely within the CNS. *Local interneurons* form circuits with nearby neurons and analyze small pieces of information. *Relay interneurons* connect circuits of local interneurons in one region of the brain with those in other regions. Through these connections, circuits of neurons throughout the brain perform functions essential to tasks such as perceiving, learning, remembering, deciding, and controlling complex behaviors. (See Figure 2.2.)

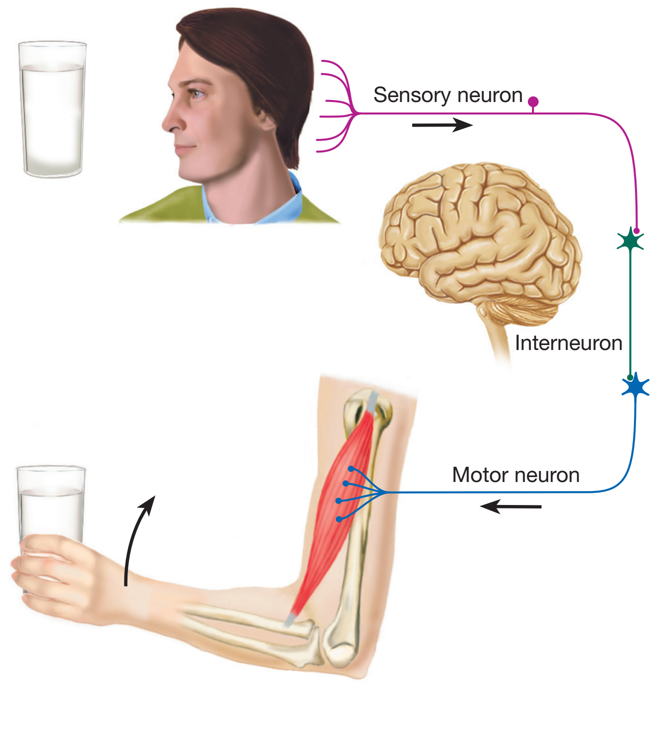
This section is devoted to a description of the most important cells of the nervous system—neurons and their supporting cells—and to the blood–brain barrier, which provides neurons in the CNS with chemical isolation from the rest of the body.

Neurons

LO 2.2 Describe the structures of a neuron, including their general function.

The neuron is the information-processing and information-transmitting element of the nervous system. Neurons come in many shapes and varieties, according to the specialized jobs they perform. Most neurons have, in one form or another, the

Figure 2.2 Sensory, Motor, and Interneurons
These three types of neurons relay information between the central and peripheral nervous systems. In this example, the person sees the glass of water and sensory nerves relay the sensory information toward the central nervous system. The motor output from the central nervous system allows the person to lift the glass to take a drink.



following four structures or regions: (1) cell body, or soma; (2) dendrites; (3) axon; and (4) terminal buttons.

SOMA The **soma** (cell body) contains the nucleus and much of the machinery that provides for the life processes of the cell. (See Figure 2.3.) Its shape varies considerably in different kinds of neurons.

DENDRITES *Dendron* is the Greek word for tree, and the branched **dendrites** of the neuron look very much like trees (look again at Figure 2.3). Neurons communicate with one another and dendrites serve as important receivers of these messages. Dendrites function much like antennas to receive messages from other neurons. Just like an antenna can receive a message over a distance (think of an antenna that detects radio or Wi-Fi signals) dendrites receive neural messages that are transmitted across the **synapse,** a small space between the terminal buttons (described later) of the sending cell and a portion of the somatic or dendritic membrane of the receiving cell. Communication at a synapse proceeds in one direction: from the terminal button to the membrane of the other cell. (Like many general rules, this one has some exceptions. As we will see in Chapter 4, some synapses pass information in both directions.)

AXON The **axon** is a long, slender tube, often covered by a *myelin sheath.* (The myelin sheath is described later.) The outer surface of the axon carries information from the cell body to the terminal buttons and functions much like an electrical cord carrying an electrical message from an outlet to an appliance (look again at Figure 2.3). However, the basic message the axon carries is called an *action potential.* This function of an action potential is an important one and will be described in more detail later in the chapter. For now, know that an action potential is a brief electrical event that starts at the end of the axon next to the cell body and travels toward the terminal buttons. The action potential is like a brief pulse; in any given axon the action potential is always of the same size and duration. When it reaches a point where the axon branches, it splits but does not diminish in size. Each branch receives a *full-strength* action potential. Like dendrites, axons and their branches come in different shapes.

TERMINAL BUTTONS Most axons divide and branch many times. At the ends of the branches are little knobs called **terminal buttons.** Terminal buttons have a very special function: When an action potential traveling down the axon reaches them, they secrete a chemical called a **neurotransmitter.** This chemical (there are many different ones in the CNS) either excites or inhibits the receiving cell and thus helps to determine whether an action potential occurs in its axon. In this way, terminal buttons function like spray bottles by releasing chemicals into the synapse. Details of this process will be described later in this chapter.

An individual neuron receives information from the terminal buttons of axons of other neurons—and the terminal buttons of its axons form synapses with other neurons. A neuron may receive information from dozens or even hundreds of other neurons, each of which can form a large number of synaptic connections with it. Figure 2.4 illustrates the nature of these connections. As you can see, terminal buttons can form synapses on the membrane of the dendrites or the soma.

Axons can be extremely long relative to their diameter and the size of the soma. For example, the longest axon in a human stretches from the foot to a region located in the base of the brain. Because terminal buttons need some items that can be produced only in the soma; there must be a system that can transport these items rapidly and efficiently *within* the axon (like a subway system). This process is separate from the movement of the action potential along the surface of the axon. Instead, **axoplasmic transport** is an active process that propels substances along microtubule "tracks" that run inside the length of the axon. Movement from the soma to the terminal buttons is called **anterograde** axoplasmic transport. (*Antero-* means "toward the front.") This form of transport is accomplished by molecules of a protein called *kinesin.* In the cell body, kinesin molecules, which resemble a pair of legs and feet, attach to the item being transported down the axon. The kinesin molecule then walks down a microtubule, carrying the cargo to its destination (Yildiz et al., 2004). Energy is supplied by ATP molecules produced by the mitochondria. (See Figure 2.5.) Another protein, *dynein*, carries substances from the terminal buttons to the soma, a process known as **retrograde** axoplasmic transport. Anterograde axoplasmic transport is remarkably fast: up to 500 millimeters (mm) per day. Retrograde axoplasmic transport is about half as fast as anterograde transport.

Figure 2.3 Parts of a Neuron

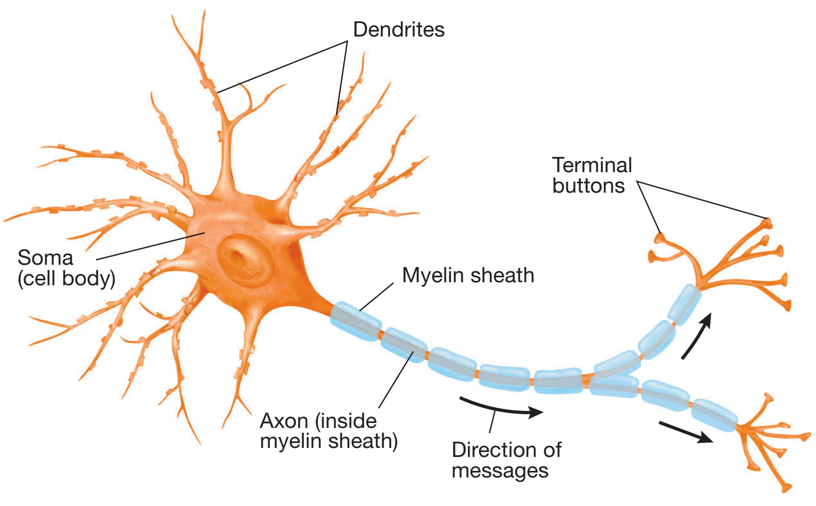


Figure 2.4 Overview of Structure and Synaptic Connections Between Neurons

The arrows represent the directions of the flow of information.

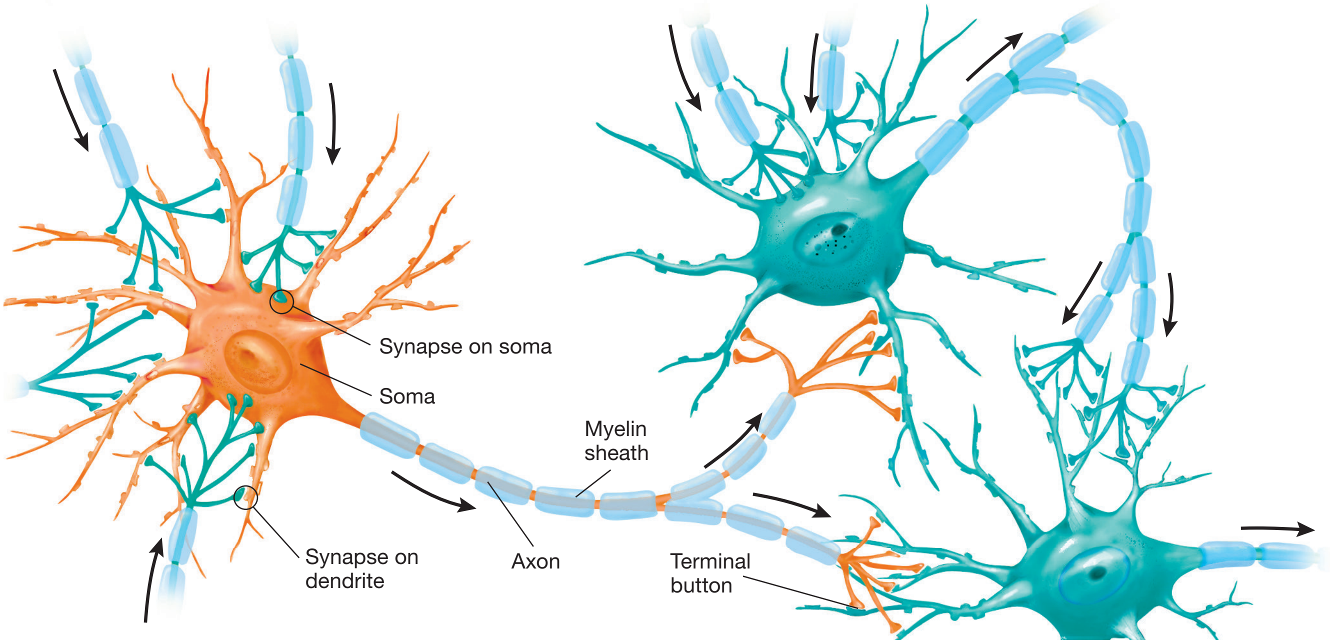


Figure 2.5 Axoplasmic Transport

This figure shows how kinesin molecules transport cargo along the cytoskeleton from the soma to the terminal button. Another protein, dynein, carries cargo from the terminal buttons to the soma.

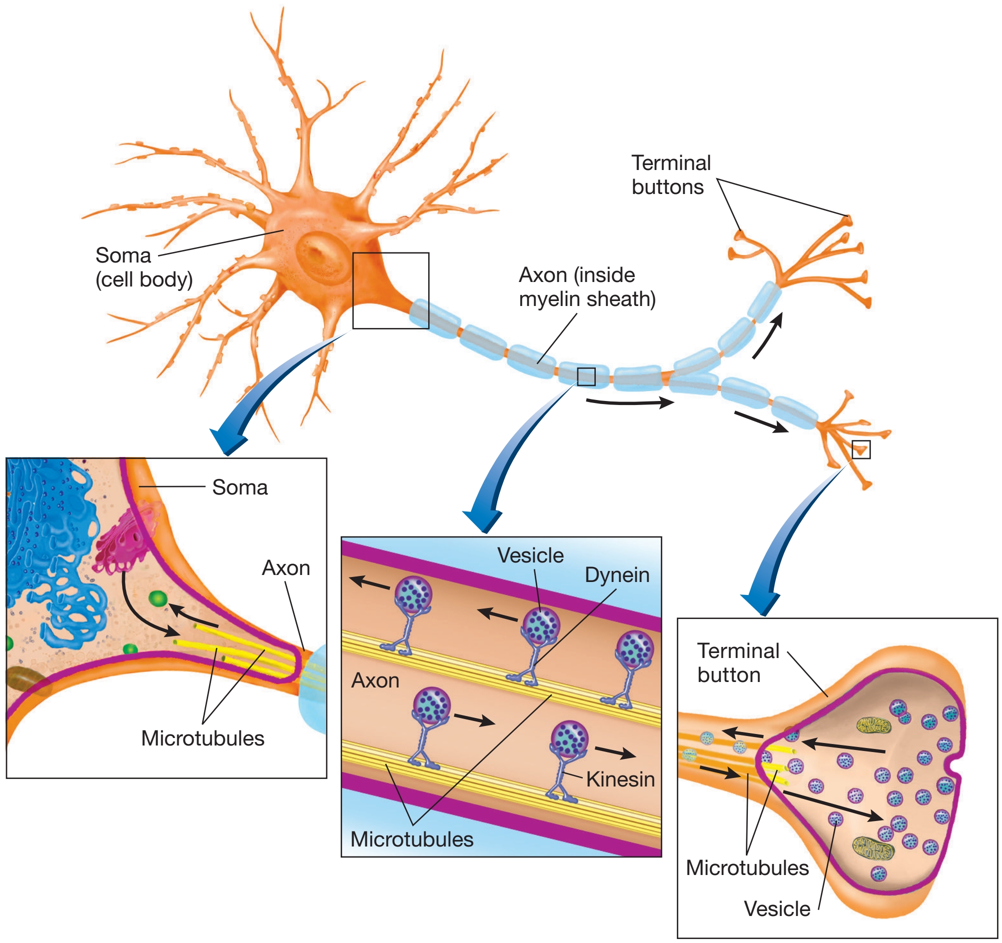
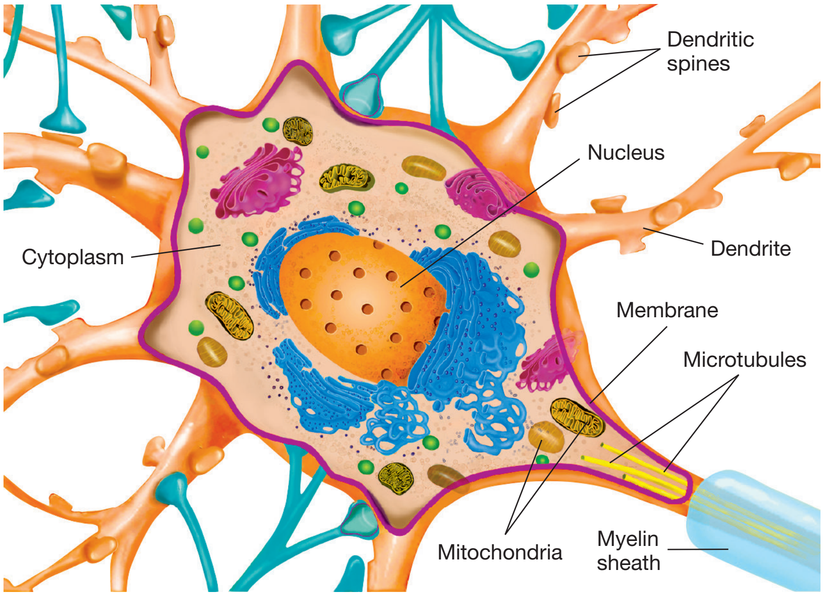


Figure 2.6 Internal Structures of a Neuron



OTHER CELL STRUCTURES Figure 2.6 illustrates the internal structure of a typical neuron.

Much like your skin, the cell **membrane** defines the boundary of the neuron. It consists of a double layer of lipid (fatlike) molecules. Embedded in the membrane are a variety of protein molecules that have special functions. Some proteins detect substances outside the cell (such as hormones) and pass information about the presence of these substances to the interior of the cell. Other proteins control access to the interior of the cell, permitting some substances to enter but barring others. Still other proteins act as transporters, actively carrying certain molecules into or out of the cell. Because the proteins that are found in the membrane of the neuron are especially important in the transmission of information, their characteristics will be discussed in more detail later in this chapter.

The interior of the neuron contains a matrix of strands of protein. Much like the bones of your skeletal system, this matrix, called the **cytoskeleton,** gives the neuron its shape. The cytoskeleton is made of three kinds of protein strands, linked to each other and forming a cohesive mass. The thickest of these strands, **microtubules,** are bundles of thirteen protein filaments arranged around a hollow core.

Cytoplasm is complex and varies considerably across types of cells, but it can most easily be characterized as a jellylike, semiliquid substance that fills the space outlined by the membrane. It contains small, specialized structures, just as the human body contains specialized organs. The generic term for these structures is *organelle,* "little organ." The most important organelles are described next.

The **nucleus** of the cell is a round or oval structure found in the soma. The nucleus is enclosed by the nuclear membrane. The nucleolus and the chromosomes reside inside the nucleus. The **nucleolus** is responsible for the production of **ribosomes,** small structures that are involved in protein synthesis. The **chromosomes,** which consist of long strands of **deoxyribonucleic acid (DNA),** contain the organism's genetic information. When they are active, portions of the chromosomes **(genes)** cause production of another complex molecule, **messenger ribonucleic acid (mRNA),** which receives a copy of the information stored at that location. The mRNA leaves the nuclear membrane and attaches to ribosomes. (See Figure 2.7.)

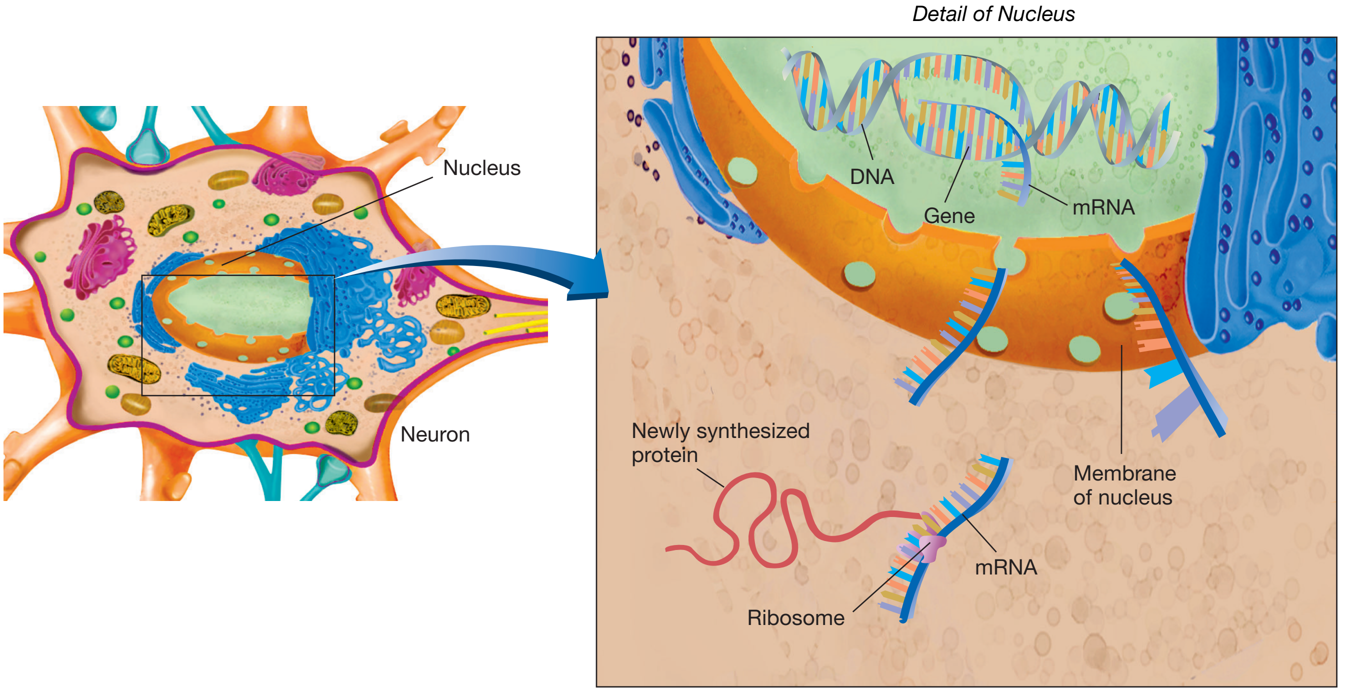
Proteins are produced through a two-step process. In the first step of the process, *transcription*, information from DNA (which cannot leave the nucleus) is transcribed into a portable form: mRNA. mRNA takes this information to the ribosomes for the second step of the process: *translation*. During translation, the ribosomes use the information from the mRNA and create proteins.

To help you remember the complicated process of protein production, compare it to making a cake from a top-secret recipe. Imagine that the recipe for the cake is found in a rare cookbook in a library and you cannot remove the cookbook from the library. You can go into the library and take a picture of the recipe with the camera on your cell phone. Now you have the information in a new, more portable form. Next, you take the picture of the recipe home with you to your kitchen. There, you use the recipe information to assemble raw ingredients like flour, eggs, and milk into the cake. In this example, the cookbook locked in the library is like the DNA stored in the nucleus. The process of photographing the cookbook and removing the recipe information from the library represents transcription of information from DNA locked in the nucleus to a new, more portable form of information, mRNA. Taking the photo home and using the information it contains to assemble raw materials into a final product represents translation as the mRNA leave the nucleus and take information to the ribosomes, which the ribosomes then use to create proteins.

Proteins are important in cell functions. In addition to providing structure, proteins serve as **enzymes,** which direct the chemical processes of a cell by controlling chemical reactions. Enzymes are special protein molecules that act as catalysts; that is, they cause a chemical reaction to take place without becoming a part of the final product themselves. Because cells contain the ingredients needed to synthesize an enormous variety of compounds, the ones that cells actually do produce depend primarily on the particular enzymes that are present. Furthermore, there are enzymes that break molecules apart as well as enzymes that put them

Figure 2.7 Protein Synthesis

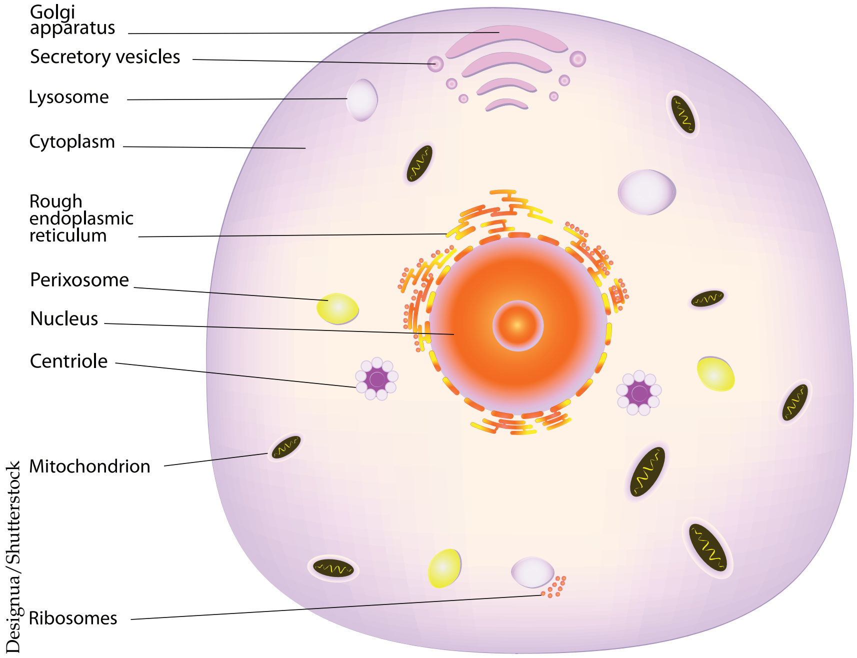
When a gene is active, a copy of the information is made onto a molecule of messenger RNA. The mRNA leaves the nucleus and attaches to a ribosome, where the protein is produced.



together; the enzymes that are present in a particular region of a cell thus determine which molecules remain intact.

Cells also contain an endomembrane system (a network of internal membranes) comprised of endoplasmic reticulum, Golgi apparatus, and lysosomes. The **endoplasmic reticulum** appears in two forms: rough and smooth. Both types consist of parallel layers of the same membrane that encloses the cell. Rough endoplasmic reticulum contains ribosomes. The protein produced by the ribosomes that are attached to the rough endoplasmic reticulum is destined to be transported out of the cell or used in the membrane. Unattached ribosomes are also distributed around the cytoplasm; the unattached variety appears to produce protein for use within the neuron. Smooth endoplasmic reticulum provides channels for the segregation of molecules involved in various cellular processes. Lipid (fatlike) molecules are also produced here. The **Golgi apparatus** is a special form of smooth endoplasmic reticulum. Some complex molecules, made up of simpler individual molecules, are assembled here. The Golgi apparatus also serves as a wrapping or packaging agent. For example, secretory cells (such as those that release hormones) wrap their product in a membrane produced by the Golgi apparatus. When the cell secretes its product, it uses a process called **exocytosis.** In exocytosis, the membrane-wrapped product migrates to the inside of the outer membrane of the cell, fuses with the membrane, and bursts, spilling its contents into the fluid surrounding the cell. As we will see, neurons communicate with one another by secreting chemicals by this means. We will describe the process of exocytosis in more detail later in this chapter. The Golgi apparatus also produces **lysosomes,** small sacs that contain enzymes that break down substances no longer needed by the cell. These products are then recycled or excreted from the cell.

Mitochondria (singular: mitochondrion) are shaped like oval beads and are formed from a double membrane. The inner membrane is wrinkled, and the wrinkles make up a set of shelves *(cristae)* that fill the inside of the bead. Mitochondria perform a vital role in the economy of the cell; many of the biochemical steps that are involved in the extraction of energy from the breakdown of nutrients take place on the cristae, controlled by enzymes located there. Most cell biologists believe that many eons ago, mitochondria were free-living organisms that came to "infect" larger cells. Because the mitochondria could extract energy more efficiently than the cells they infected, the mitochondria became useful to the cells and eventually became a permanent part of them. Cells provide mitochondria with nutrients, and mitochondria provide cells with a special molecule—**adenosine triphosphate (ATP)**—that cells use as their immediate source of energy. Because of their role in generating usable energy, mitochondria can be considered the "power plants" of neurons.



Structure of a typical animal cell.

Supporting Cells

LO 2.3 Differentiate functions of supporting cells of the central and peripheral nervous systems.

Neurons constitute only about half the volume of the CNS. The rest consists of a variety of supporting cells. Because neurons have a very high rate of metabolism but have no means of storing nutrients, they must constantly be supplied with nutrients and oxygen or they will quickly die. Thus, the role played by the cells that support and protect neurons is very important to our existence.

SUPPORTING CELLS OF THE CENTRAL NERVOUS SYSTEM The most important supporting cells of the central nervous system are the *neuroglia,* or "nerve glue." **Glia** (also called *glial cells*) do indeed glue the CNS together, but they do much more than that. Neurons lead a very sheltered existence; they are buffered physically and chemically from the rest of the body by the glial cells. Glial cells surround neurons and hold them in place, controlling their supply of nutrients and some of the chemicals they need to exchange messages with other neurons; they insulate neurons from one another so that neural messages do not get scrambled; and they even act as housekeepers, destroying and removing the carcasses of neurons that are killed by disease or injury.

There are several types of glial cells, each of which plays a special role in the CNS. The three most important types are *astrocytes, oligodendrocytes,* and *microglia.*

Astrocytes **Astrocyte** means "star cell," and this name accurately describes the shape of these cells. Astrocytes provide physical support to neurons and clean up debris within the brain. They produce some chemicals that neurons need to fulfill their functions. They help to control the chemical composition of the fluid surrounding neurons by actively taking up or releasing substances whose concentrations must be kept within critical levels. Finally, astrocytes are involved in providing nourishment to neurons.

Some of the astrocyte's processes (the arms of the star) are wrapped around blood vessels; other processes are wrapped around parts of neurons, so the somatic and dendritic membranes of neurons are largely surrounded by astrocytes. This arrangement suggested to the Italian histologist Camillo Golgi (1844–1926) that astrocytes supplied neurons with nutrients from the capillaries and disposed of their waste products (Golgi, 1903). He thought that nutrients passed from capillaries to the cytoplasm of the astrocytes and then through the cytoplasm to the neurons.

Recent evidence suggests that Golgi was right: Although neurons receive some glucose directly from capillaries, they receive most of their nutrients from astrocytes. Astrocytes receive glucose from capillaries and break it down to *lactate,* the chemical produced during the first step of glucose metabolism. They then release lactate into the extracellular fluid that surrounds neurons, and neurons take up the lactate, transport it to their mitochondria, and use it for energy (Tsacopoulos & Magistretti, 1996; Brown et al., 2004; Pellerin et al., 2007). Apparently, this process provides neurons with a fuel that they can metabolize even more rapidly than glucose. In addition, astrocytes store a small amount of a carbohydrate called *glycogen* that can be broken down to glucose and then to lactate when the metabolic rate of neurons in their vicinity is especially high. (See Figure 2.8.)

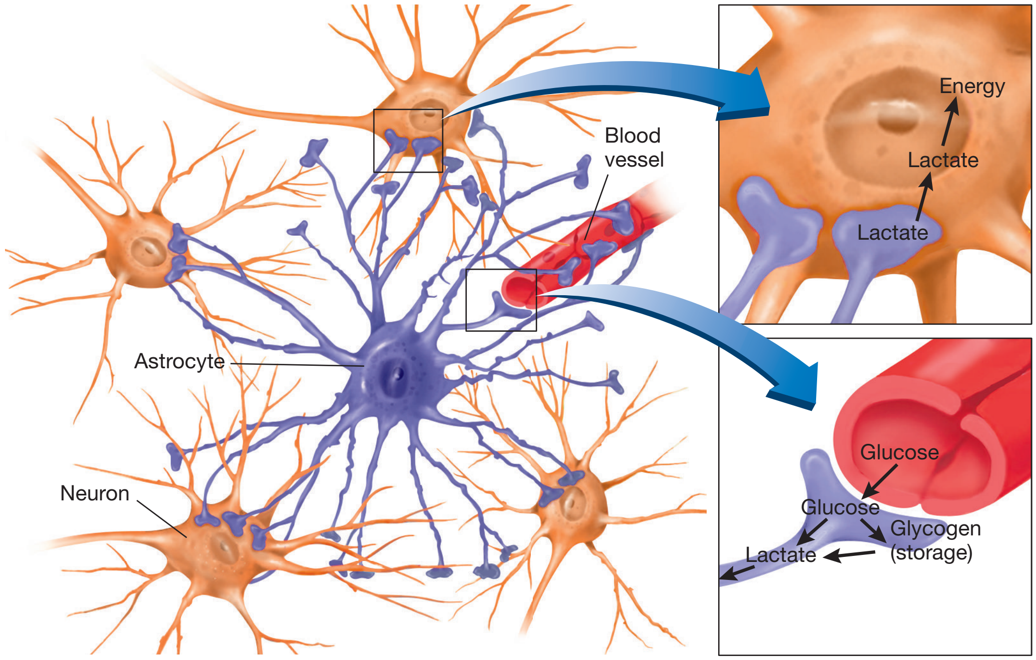
Besides transporting chemicals to neurons, astrocytes serve as the matrix that holds neurons in place—the "nerve glue," so to speak. These cells also surround and isolate synapses, limiting the dispersion of neurotransmitters that are released by the terminal buttons.

When cells in the central nervous system die, certain kinds of astrocytes take up the task of cleaning away the debris. These cells are able to travel around the CNS; they extend and retract their processes (*pseudopodia*, or "false feet") and glide about the way amoebas do. When these astrocytes contact a piece of debris from a dead neuron, they push themselves against it, finally engulfing and digesting it. We call this process **phagocytosis.** If there is a considerable amount of injured tissue to be cleaned up, astrocytes will divide and produce enough new cells to do the task. Once the dead tissue has been broken down, a framework of astrocytes will be left to fill in the vacant area, and a specialized kind of astrocyte will form scar tissue, walling off the area.

Oligodendrocytes The principal function of **oligodendrocytes** is to provide support to axons and to produce the

Figure 2.8 Structure and Location of Astrocytes

The processes of astrocytes surround capillaries and neurons of the central nervous system.

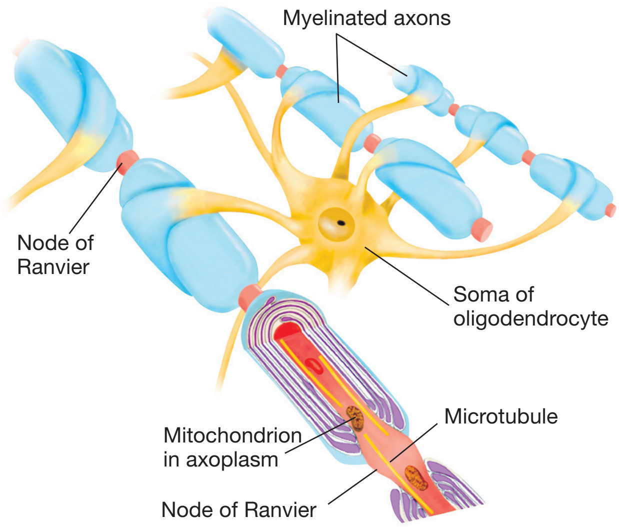


myelin sheath, which insulates most axons from one another. (Very small axons are not myelinated and lack this sheath.) Myelin, 80 percent lipid and 20 percent protein, is produced by the oligodendrocytes in the form of a tube surrounding the axon. This tube does not form a continuous sheath; rather, it consists of a series of segments, each approximately 1 mm long, with a small (1–2 µm) portion of uncoated axon between the segments. (A *micrometer,* abbreviated µm, is one-millionth of a meter, or one-thousandth of a millimeter.) The bare portion of axon is called a **node of Ranvier,** after the person who discovered it. The myelinated axon, then, resembles a string of elongated beads. (Actually, the beads are *very much* elongated—their length is approximately 80 times their width.)

A given oligodendrocyte produces up to 50 segments of myelin. During the development of the CNS, oligodendrocytes form processes shaped something like canoe paddles. Each of these paddle-shaped processes then wraps itself many times around a segment of an axon and, while doing so, produces layers of myelin. Each paddle thus becomes a segment of an axon's myelin sheath. (See Figure 2.9.)

Figure 2.9 Oligodendrocyte

An oligodendrocyte forms the myelin that surrounds many axons in the central nervous system. Each cell forms segments of myelin for several adjacent axons.



Microglia As their name indicates, **microglia** are the smallest of the glial cells. Like some types of astrocytes, they act as phagocytes, engulfing and breaking down dead and dying neurons. But, in addition, they serve as one of the representatives of the immune system in the brain, protecting the brain from invading microorganisms. They are primarily responsible for the inflammatory reaction in response to brain damage.

SUPPORTING CELLS OF THE PERIPHERAL NERVOUS SYSTEM In the central nervous system the oligodendrocytes support axons and produce myelin. In the peripheral nervous system the **Schwann cells** perform the same functions. Most axons in the PNS are myelinated. The myelin sheath occurs in segments, as it does in the CNS; each segment consists of a single Schwann cell wrapped many times around the axon. In the CNS the oligodendrocytes grow a