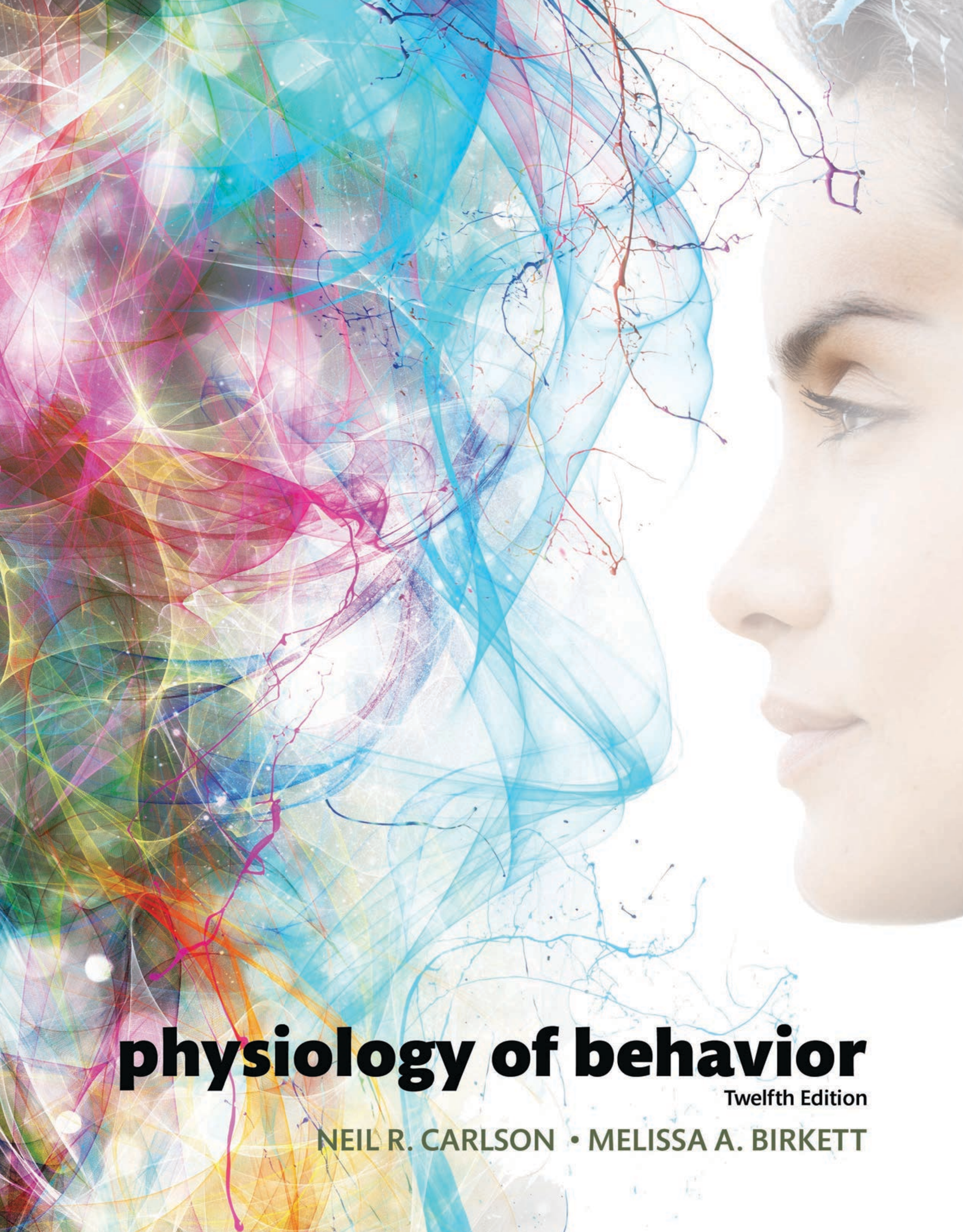

physiology of behavior

Twelfth Edition

NEIL R. CARLSON • MELISSA A. BIRKETT

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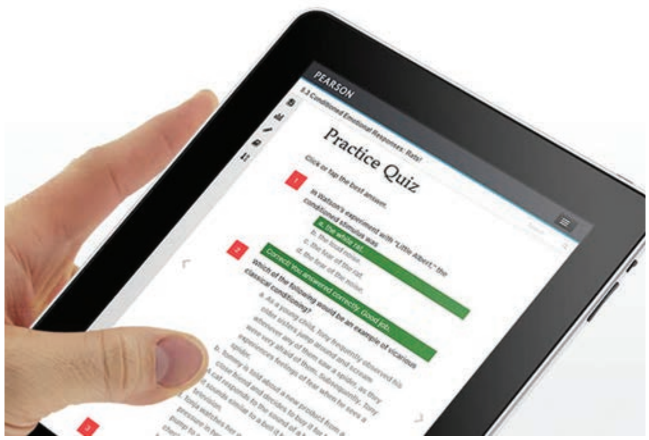

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Physiology of Behavior

twelfth edition

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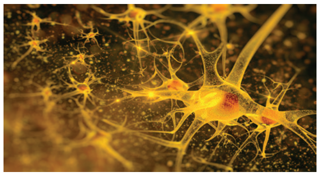

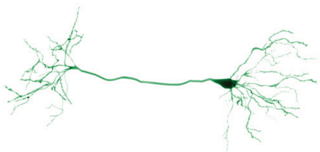

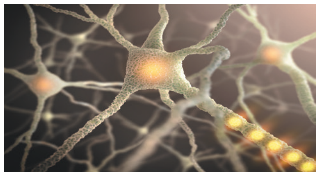

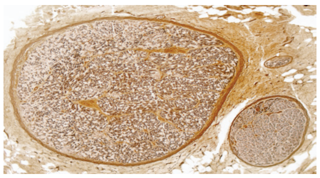

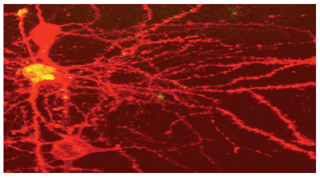

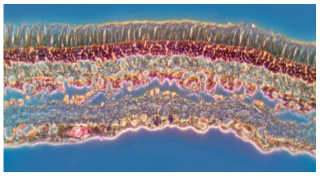

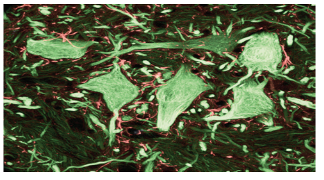

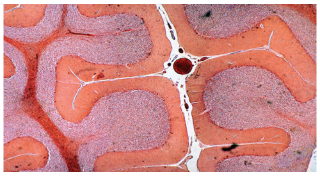

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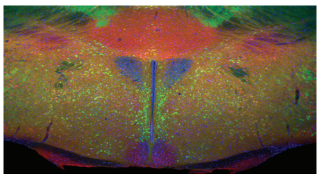

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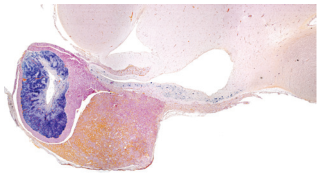

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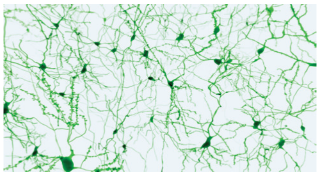

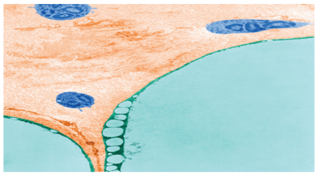

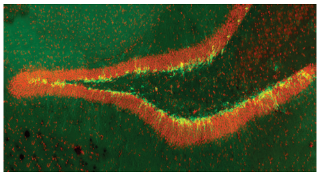

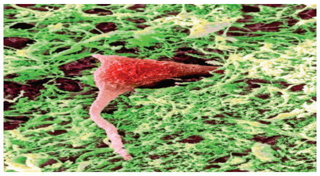

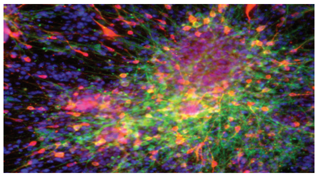

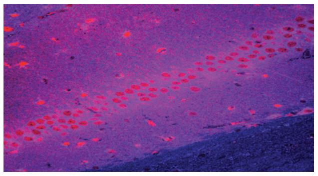

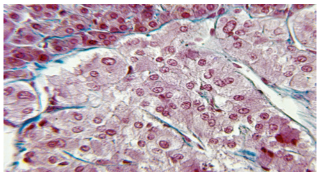

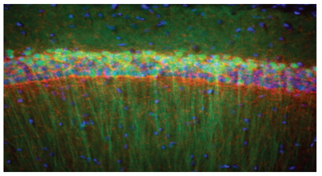

Preface

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.

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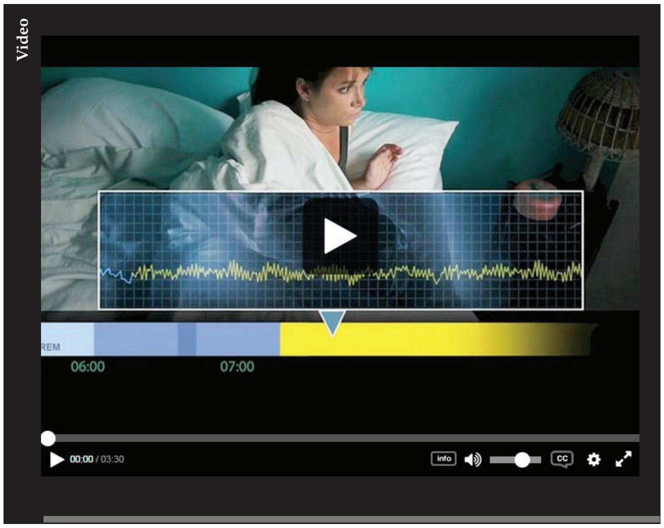

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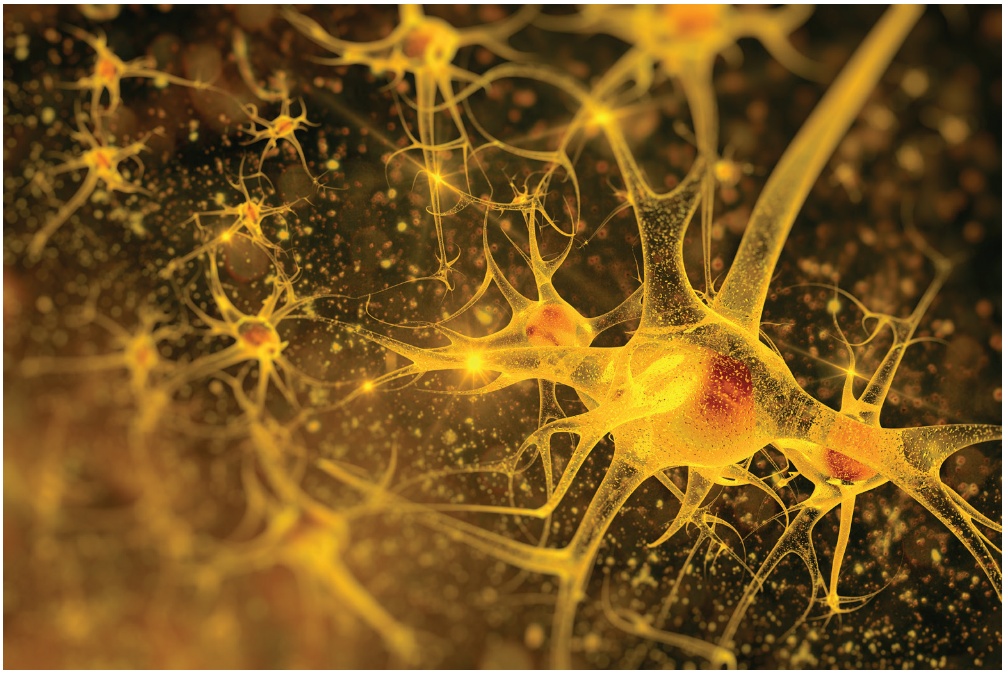
Please write to tell us what you like and dislike about the book at: nrc@psych.umass.edu.

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).

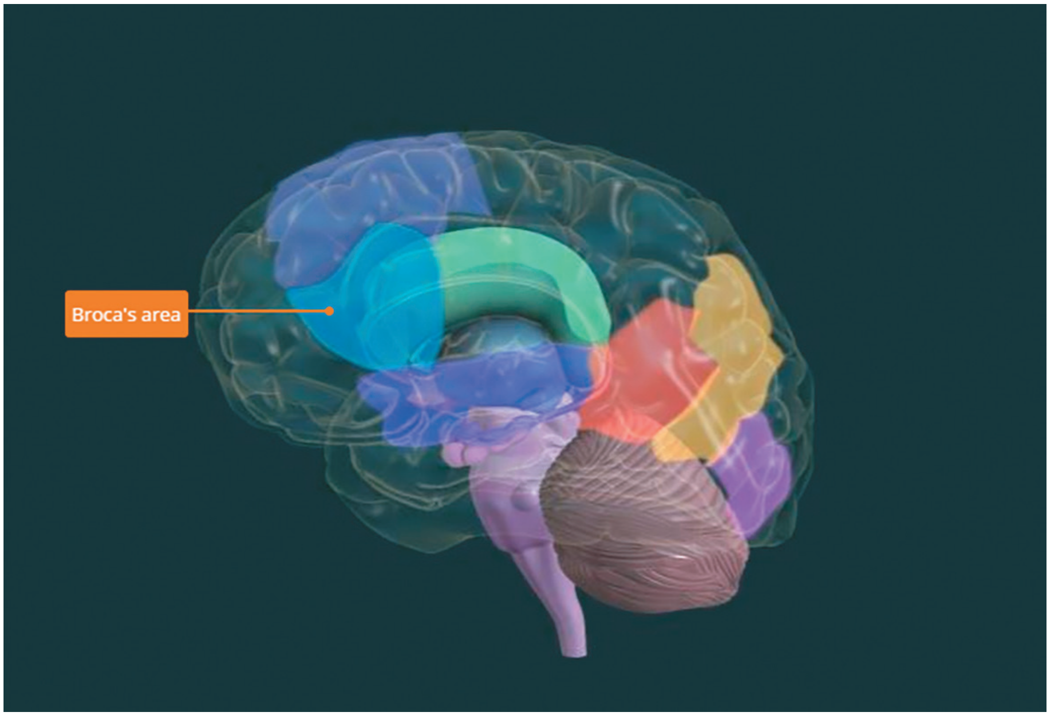
*****

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.

Watch A RESEARCHER SPEAKS ABOUT THE ROLE OF PSYCHOLOGY IN NEUROSCIENCE RESEARCH

Dr. Roberta Klatzky describes her research in neuroscience and psychology.

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

Watch WHAT ARE THE CHALLENGES IN BECOMING AN EXPERT IN THE STUDY OF BEHAVIOR AND PHYSIOLOGY?

John Cacioppo describes his work as an interdisciplinary neuroscientist, bringing together perspectives from biology and psychology.

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.)

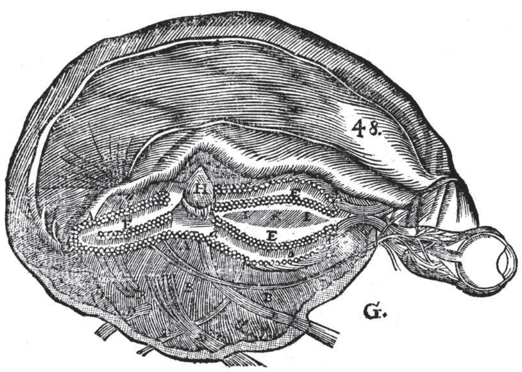
Descartes observed, some movements of the human body were automatic and involuntary. For example, if a person's finger touched a hot object, the arm would immediately withdraw from the source of stimulation. Reactions like this did not require participation of the mind; they occurred automatically. Descartes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

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.



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.

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.

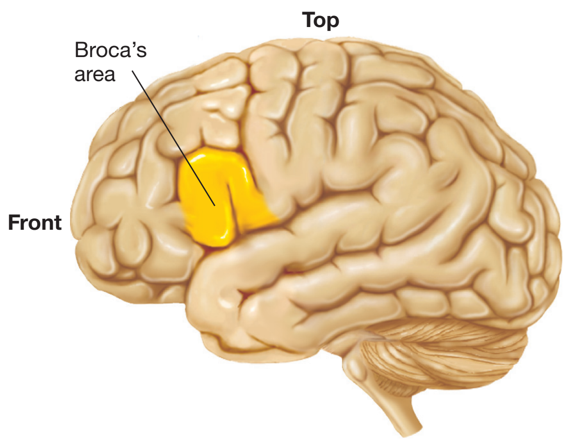
Müller's advocacy of experimentation and the logical deductions from his doctrine of specific nerve energies set the stage for performing experiments directly on the brain. Pierre Flourens, a nineteenth-century French physiologist, did just that. Flourens removed various parts of animals' brains and 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

Several new areas of research, such as the Brain Activity Map initiative and the Human Brain Project, are poised to shape the future of behavioral neuroscience. Write an e-mail message to a friend predicting future research in behavioral neuroscience and possible discoveries that may be made.

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.