10th EDITION

Foundations of Behavioral Neuroscience

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Melissa Birkett

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Tenth Edition

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Printer/Binder: *LSC Communications, Inc.*
Cover Printer: *LSC Communications, Inc.*

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Library of Congress Cataloging-in-Publication Data

Names: Carlson, Neil R., author.
Title: Foundations of behavioral neuroscience / by Neil R. Carlson.
Other titles: Physiology of behavior.
Description: 10e. | Upper Saddle River, NJ: Pearson, [2020] | Revision of: Physiology of behavior / Neil R. Carlson. c2004. 8th ed. | Includes bibliographical references and index.
Identifiers: LCCN 2018035111 | ISBN 9780134639796 (softcover)
Subjects: LCSH: Psychophysiology. | Neuropsychiatry.
Classification: LCC QP360 .C35 2020 | DDC 612.8—dc23
LC record available at https://lccn.loc.gov/2018035111

ScoutAutomatedPrintCode

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ISBN-10: 0-13-544912-X
ISBN-13: 978-0-13-544912-7

Revel Combo Card
ISBN-10: 0-13-519271-4
ISBN-13: 978-0-13-519271-9

Rental Edition
ISBN-10: 0-13-463979-0
ISBN-13: 978-0-13-463979-6

Loose-Leaf Edition
ISBN-10: 0-13-464142-6
ISBN-13: 978-0-13-464142-3

Instructor's Review Copy
ISBN-10: 0-13-464131-0
ISBN-13: 978-0-13-464131-7

Brief Contents

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Preface

The first edition of this text came at the request of fellow colleagues who teach the course and wanted a briefer version of *Physiology of Behavior* with more emphasis on research related to humans. The fascinating discoveries coming out of neuroscience labs provide us with something new to say with each edition. 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 revised learning objectives and thought questions. Her work on this text helped to focus the content around key 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.

The first part of this text is concerned with foundations: the history of the field, the structure and functions of neurons, neuroanatomy, psychopharmacology, and methods of research. The second part is concerned with inputs: the sensory systems. The third part deals with what might be called "motivated" behavior: movement, sleep, reproduction, emotion, and ingestion. The fourth part deals with learning and verbal communication. The final part deals with neurological and mental disorders.

New to This Edition

Of course, all chapters in this edition have been revised. Our colleagues keep us busy by providing us with interesting research results to describe in the text. The challenge is always to include the interesting new material without letting the length of the edition get out of hand.

Managing length became even more challenging this edition because we decided to add a new chapter on movement (chapter 8) based on reader feedback. Also in response to faculty feedback, we've integrated a completely new video program throughout the text that will help illustrate and explain the chapter concepts. Similarly, we've added a Key Concepts feature, which is an interactive feature that provides expanded coverage of particularly important, but also complex, concepts. Finally, we've also tried to provide more scaffolding in the chapters by way of chunking material into more manageable subheads and updated vignettes in many chapters.

The following list includes some of the information that is new to this edition:

- New areas of neuroscience and emphases in the field
- Additional ethical considerations
- Research on strategies for learning neuroscience
- Debate about adult neurogenesis in humans
- Estimates of cortical neurons
- Immunocytochemical methods
- Confocal microscopy methods
- CRISPR methods
- New discussion on itch sensation
- Treatments for phantom limb pain
- A new chapter on control of movement
- Research on mirror neurons
- Revised scoring for sleep stages
- Research on the function of sleep spindles and K complexes
- Eye movements and brain activity in REM sleep
- Research on sleep deprivation
- Sleep, neurotoxins, and the glymphatic system
- Sleep and physical exercise
- Allostatic factors
- Approaches to studying sexually dimorphic brain regions
- Discussion of sex, gender, and transgender
- Research on persistent Müllerian duct syndrome
- Female sexual behavior across the menstrual cycle
- Human pheromones
- Neural control of sexual behavior
- Effects of oxytocin administration
- Biological influences on sexual orientation
- Brain and gender identity
- Testosterone and aggression
- Expanded discussion of heredity and aggression
- Affective neuroscience
- Replications of facial feedback hypothesis research
- Research on obesity and eating disorders, including new treatments for anorexia nervosa
- Reorganization of Learning and Memory chapter
- Information about hippocampal structures and pathways
- Bilingualism in the brain
- Visual word form area and reading
- Brain regions involved in typing and texting
- Korsakoff's syndrome
- Stereotactic radiosurgery techniques
- Brain-computer interface for stroke rehabilitation
- Chronic traumatic encephalopathy

- Neuronal transplantation in Parkinson's disease
- Updated diagnostic criteria for disorders and mental illnesses
- Ketamine treatment for depression
- Reorganization of neurodevelopmental disorders section
- Autism and theory of mind research
- New treatment options for posttraumatic stress disorder

How Each Chapter Is Organized

- Each chapter begins with a **vignette** that profiles a person's real-life experience and a list of learning objectives for each module. The profiles 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 modules. A reader should be able to complete or address each of the learning objectives based on information presented in the section of the chapter.
- At the end of each module, you will find three different types of **review activities**: learning objective summaries, thought questions, and multiple-choice questions. The learning objective summaries will remind you of key points from the modules; 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; and the multiple-choice questions, which students will find in their Revel course, will help you assess how well you've learned many of the most important concepts in each chapter.
- At the end of each chapter in Revel, you will find key term **flashcards** to help you review. You will also find a **shared writing prompt**, which is meant to foster a dialogue among your classmates. Finally, there is a comprehensive multiple choice chapter test for self-assessment, a strategy to improve long-term retention of chapter information.

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Resources for Instructors

Several supplements are available for instructors who adopt this text.

- **Instructor's Manual** (ISBN 013466812X) Revised by Trisha K. Prunty, Professor of Psychology, Lindenwood University—Belleville, this manual provides a tool for classroom preparation and management. Each chapter includes a teaching outline with learning objectives, lecture material, demonstrations, activities and assignments, handouts, and lists of videos.
- **Test Bank** (ISBN 0134642953) Revised by Trisha K. Prunty, Professor of Psychology, Lindenwood University—Belleville, this resource contains questions that target key concepts. Each chapter has approximately 100 questions, including multiple choice, short answer, and essay. All questions are correlated to both chapter learning objectives and APA learning objectives. Instructors can easily create and print quizzes and exams as well as author new questions online for maximum flexibility. Each chapter of the Test Bank contains a Total Assessment Guide, an easy-to-reference grid that organizes all test items by learning objective and question type. The Test Bank is also available in Pearson MyTest (ISBN 0134678443), 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.
- **PowerPoint Slides** (ISBN 0134668103) These accessible PowerPoint slides facilitate the development of lectures and the encouragement of classroom discussions by pairing key points covered in the chapters with images from the text. In addition, the Video PowerPoint Slides (0134678419) are enhanced with selected videos, enabling instructors to show videos within the context of their lecture.

Acknowledgments

We wish to thank the following reviewers for their comments on this edition:

Todd Ahern, Quinnipiac University
Titus Asbury, Texas Woman's University
Holly Brothers, The Ohio State University
Tom Byrne, Massachusetts College of Liberal Arts
Kim Cronise, Middlebury College
Mark Krause, Southern Oregon University
Andrew Menatti, Ohio University—Athens
Brady Phelps, South Dakota State University
Juan Salinas, University of Texas—Austin
Glen Schafe, Hunter College
Joseph Stano, Springfield College
Sandra Trafalis, San Jose State University
Meg Waraczynski, University of Wisconsin—Whitewater
Wendy Yoder, University of Floriday

We also want to thank the people at Pearson: Kelli Strieby, portfolio manager; Chris Brown, marketing manager; Lisa Mafrici, content producer; Jennifer Gavigan, production project manager; and Lindsay Verge, digital producer. Finally, this text would not have been possible without Thomas Finn, freelance development editor, who made numerous invaluable contributions to preparing the content and format for this edition. Finally, Neil thanks his wife Mary for her support and Melissa thanks her family for their support.

To the Reader

We designed this text to be interesting and informative and endeavored to provide a solid foundation for further study. We hope that in reading and interacting with this material you will come not only to learn more about the brain but also to appreciate it for the marvelous organ it is. The brain is wonderfully complex, and perhaps the most remarkable thing is that we are able to use it in our attempt to understand it. Finally, we hope that this text provides you with a better understanding of your own behavior and a greater appreciation for the forthcoming advances in neuroscience.

About the Authors

Neil R. Carlson pursued his undergraduate studies at the University of Illinois. He had planned to study nuclear physics, but when he discovered in an introductory psychology course that psychology was really a science, he decided that was what he wanted to do. Before changing his major, Carlson talked with several professors and visited their laboratories, and when he saw what physiological psychologists do, he knew that he had found his niche. He stayed on at Illinois and received his Ph.D. Then, after a two-year postdoctoral fellowship at the University of Iowa, Carlson came to the University of Massachusetts, where he taught throughout his entire career. He retired from UMass in the fall of 2004 but continues to keep up with developments in the field of behavioral neuroscience and to revise his book.

As an undergraduate psychology major at Cornell University, Melissa A. Birkett discovered courses in biopsychology, behavior, endocrinology, and evolutionary psychology. There, she was introduced to interdisciplinary research incorporating multiple perspectives in the challenging task of understanding behavior. She became interested in learning about behavior and its underlying mechanisms. She worked as an undergraduate research assistant in several laboratories on projects ranging from insect behavior to sleep in undergraduates. Those formative experiences and interactions with several influential research mentors convinced her to pursue a career in research.

Melissa completed her Ph.D. in the Neuroscience and Behavior program at the University of Massachusetts Amherst (where Neil Carlson was a faculty member at the time). In 2007, she accepted a faculty position at Northern Arizona University in the Department of Psychological Sciences, and in the fall of 2018 became an Assistant Professor at Southern Oregon University. Melissa currently conducts research related to the stress response and teaches undergraduate courses in psychology, research methods, statistics, behavioral neuroscience, and psychopharmacology. Each semester, she supervises student researchers and seeks to provide them with the kinds of opportunities she found valuable as a student. Her work has been recognized with awards for both outstanding teaching and teaching innovation, and she has contributed to several publications on best practices in teaching neuroscience.

Chapter 1

Origins of Behavioral Neuroscience

Monty Rakusen/Getty Images

Learning Objectives

The Nature of Behavioral Neuroscience

LO 1.1 Compare the roles 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, and other disciplines.

Natural Selection and Evolution

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.

Ethical Issues in Research with Humans and Other Animals

LO 1.5 Outline reasons for the use of animals in behavioral neuroscience research and the regulations in place for oversight of this research.

LO 1.6 Discuss ethical considerations in research with human participants.

Careers in Behavioral Neuroscience and Strategies for Learning

LO 1.7 Identify careers in behavioral neuroscience.

LO 1.8 Identify effective learning strategies for studying behavioral neuroscience.

Seven-year-old Jeremiah had 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, or cerebrovascular accidents, in Chapter 14). After the stroke damaged the left side of his brain, Jeremiah lost all sensation on the right side of his body and had limited use of his right arm and leg. He received some rehabilitation immediately following the stroke and learned to walk with a cane. He learned to write with his left hand because the fine motor movements were too difficult with his right hand.

Even 40 years after the stroke, Jeremiah had not regained full movement of the right side of his body. Despite the progress he made, Jeremiah fell frequently, resulting in multiple injuries including bone fractures in his hand, foot, and hip. Jeremiah sought 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 focuses on strengthening the remaining neural pathways responsible for behaviors affected by the stroke. 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 or stacking blocks. 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 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 experienced as a child (Doidge, 2007).

At the end of the twentieth century, many researchers believed that the brain was not capable of change in adulthood. However, some neuroscientists suggested the cells and connections of the adult brain were flexible, or *plastic*, and attempted to change the view of the brain that had been held for more than a century. Eventually, as data accumulated, the scientific consensus became that the adult brain continues to experience neural changes. Regions of the adult brain in many species produce new cells called **neurons** throughout a lifetime. Researchers currently strive to better understand **neurogenesis**, the generation of new neurons.

However, understanding of this phenomenon (and others in the brain) remains incomplete. For example, new research reported little to no evidence of neurogenesis in the dentate gyrus of the hippocampus (an area of the brain typically associated with neurogenesis) of adult humans, and suggested that neurogenesis in this region declines throughout childhood in our species (Sorrells et al., 2018). In contrast, other researchers report evidence that generation of these cells continues throughout the human lifespan, into older adulthood (Boldrini et al., 2018). The neuroscience community is actively engaged in understanding these apparently conflicting results.

Behavioral neuroscience is a dynamic and ever-changing field. As you read this text, consider not only the facts, but also the research process used to obtain those facts, 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.

The Nature of Behavioral Neuroscience

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. 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. 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.

plasticity In the nervous system, this refers to change, flexibility, or adaptation, usually in response to an experience or learning.

neurons Nerve cell; the information-processing and information-transmitting cells of the nervous system.

neurogenesis Production of new neurons through the division of neural stem cells; occurs in the hippocampus and olfactory bulb and appears to play a role in learning.

The Goals of Research

LO 1.1 Compare the roles 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. A **generalization** is a broader explanation based on many different smaller observations of similar phenomena. For example, imagine if different researchers all find that a particular brain chemical seems to influence aggression in studies involving both nonhuman primates and humans. One possible generalization from such studies could be that this chemical is a key component of aggressive behavior in mammals. **Reduction** refers to the explanation of a broader complex phenomenon using a series of smaller ones. For example, consider the difficult task of trying to understand the motor behavior of people learning to walk. Some researchers choose to focus on understanding the functions of individual muscle cells, others focus on understanding the chemicals involved in communication between neurons and muscles, while still others focus on the motivation to walk. Each type of research contributes to an overall understanding of a complex behavior of walking.

The task of the behavioral neuroscientist is to explain behaviors by studying the smaller, microphysiological processes that control that behavior. But we 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 understand the overall function of a given behavior. In practice, the research efforts of behavioral neuroscientists involve both forms of explanation: generalization and reduction. Research is fueled both by psychological generalizations about behavior and the physiological mechanisms that underlie it. A behavioral neuroscientist must therefore be an expert in the study of behavior *and* the study of physiology.

Watch

ROLE OF PSYCHOLOGY IN NEUROSCIENCE RESEARCH

Watch

BRIDGING THE SOCIAL AND BIOLOGICAL SCIENCES

Biological Roots of Behavioral Neuroscience

LO 1.2 Summarize contributions to the modern field of behavioral neuroscience made by individuals involved in philosophy, physiology, and 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 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. People have generally 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.

Behavioral neuroscientists take an empirical, monistic approach to the study of human behavior. 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.

generalization A type of scientific explanation; a general conclusion based on many observations of similar phenomena.

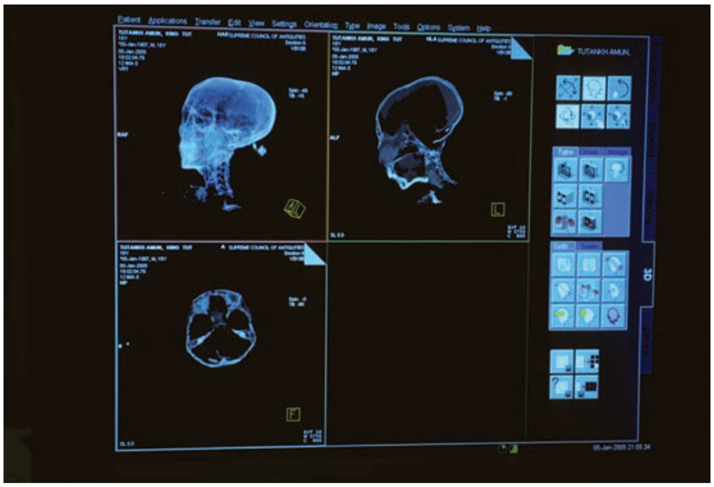
reduction A type of scientific explanation; a phenomenon is described in terms of the more elementary processes that underlie it.

dualism The belief that the body is physical but the mind (or soul) is not.

monism (*mahn ism*) The belief that the world consists only of matter and energy and that the mind is a phenomenon produced by the workings of the nervous system.

Figure 1.1 Imaging the Ancient World

Modern imaging techniques have been applied to learning more about the ancient world. This image reveals the internal structures of a mummified brain.



Kenneth Garrett/Danita Delimont/Alamy Stock Photo

ANCIENT WORLD Study of (or speculations about) the physiology of behavior has its roots in antiquity. 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. Galen (130–200 C.E.) dissected and studied brains of cattle, sheep, pigs, cats, dogs, weasels, monkeys, and apes (Finger, 1994). He found that all of the nerves were connected to the brain and concluded that Aristotle's theory about the brain's role was incorrect. (See Figure 1.1.)

Figure 1.2 Example of a Reflex

Descartes was among the first to describe reflexes as automatic and involuntary responses to stimuli, such as pulling your hand back after being burned.

PHOVOIR/Alamy Stock Photo

SEVENTEENTH CENTURY Philosophers and physiologists in the 1600s contributed greatly to the foundations of today's behavioral neuroscience. The French philosopher René Descartes's 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 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.) Though a dualist, Descartes 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.

Luigi Galvani, a seventeenth-century Italian physiologist, began exploring more precisely how the nervous system was connected to the body and behavior. He found that electrical stimulation of a frog's nerve caused a 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. 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 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 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. Müller suggested that some parts of the brain perform some functions, while other parts perform others.

reflex An automatic, stereotyped movement that is produced as the direct result of a stimulus.

doctrine of specific nerve energies Müller's conclusion that, because all nerve fibers carry the same type of message, sensory information must be specified by the particular nerve fibers that are active.

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*.

Soon after Flourens performed his experiments, Paul Broca, a French surgeon, applied the principle of experimental ablation to the human brain. He observed the behavior of people whose brains had been damaged by strokes, and 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. He concluded 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). Though this is not the sole neural component involved in speech, Broca's area is in fact integral to speech.

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 predominate 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. Figure 1.4 shows one of Cajal's drawings.

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.

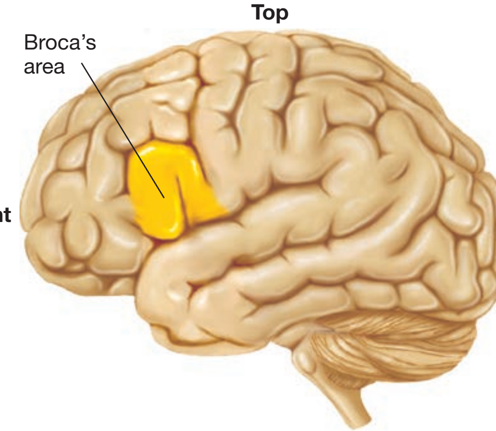
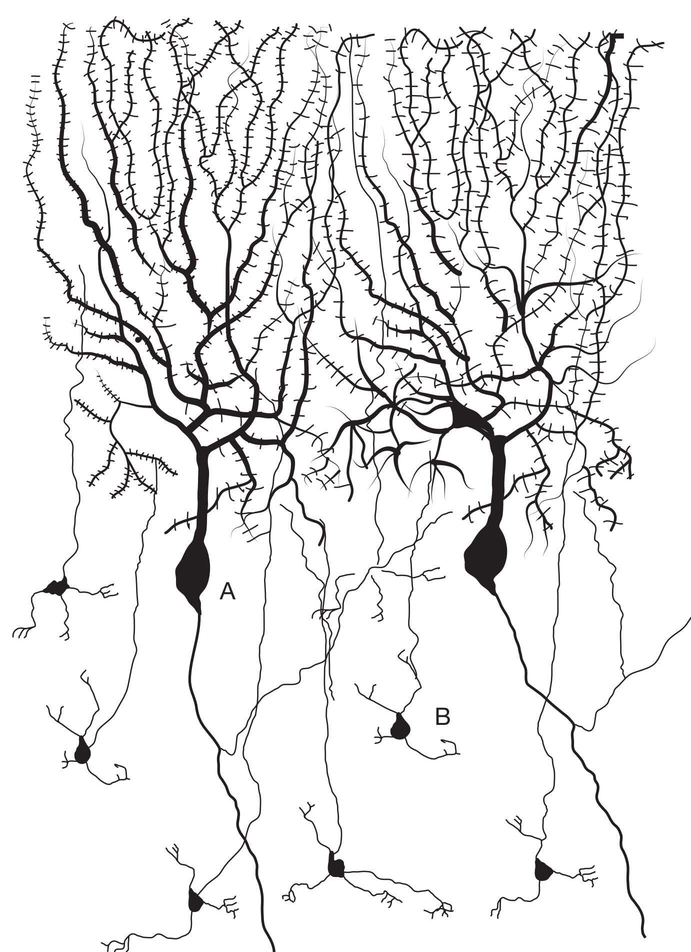


Figure 1.4 Golgi-Stained Neurons

Ramon Santiago y Cajal used Golgi staining to visualize neurons, revealing detailed structures of these cells for the first time. This shows a rendition of one of his drawings.

Santiago Ramón y Cajal, 1899; Instituto Cajal, Madrid, Spain.



CONTEMPORARY RESEARCH Twentieth-century developments in behavioral neuroscience 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.

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, ranging from the electrical and chemical messages used by neurons, to brain regions involved in a wide variety of behaviors, such as the mirror neuron system for coordinating social behavior (described in Chapter 11). 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 have enabled treatments for severe depression and Parkinson's disease using deep brain stimulation techniques (see Chapters 16 and 17).

New genetic techniques have spurred many exciting discoveries in neuroscience as well. The development of optogenetics provides researchers with the ability to selectively activate single neurons and observe changes in behavior—using light! (See Chapter 5.) The development of CRISPR-Cas9 techniques has enabled precise editing of genetic material (DNA). This technique uses an enzyme to cut out pieces of DNA (Cas9) paired with a set of replacement directions (guide RNA) to create modified genes. The impact of this technique on behavioral neuroscience is just beginning to be understood. The field of **epigenetics** focuses on the role of the environment in the expression of genes. Researchers continue to learn more about how environmental-dependent gene expression can have a profound impact on an individual's behavior.

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 37,000 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.

epigenetics Changes to gene expression induced by environmental factors.

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
2017	Jeffrey C. Hall (U.S.), Michael Rosbash (U.S.), Michael W. Young (U.S.)	Molecular mechanisms controlling circadian rhythms

Module Review

The Nature of Behavioral Neuroscience

LO 1.1 Compare the roles 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 smaller, discrete phenomena. Both are critical to understanding human behavior.

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

Ancient scholars disagreed on the importance of the brain in behavior. French philosopher Descartes was one of the first to speculate about the nature of reflexes and the interconnectedness between the mind, brain, and body. Galvani began exploring this relationship through a series of electrical stimulation experiments that showed how nerves and muscles functioned together. Müller proposed the doctrine of specific nerve energies while Flourens and Broca studied brain region functions using ablation. 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 email to a friend explaining the future research in behavioral neuroscience and predict possible discoveries that may be made.

Natural Selection and Evolution

During the nineteenth century, there were many biologists studying the world and making observations. One of the most important and influential of these scientists was Charles Darwin. Darwin formulated the principles of *natural selection* and the theory of *evolution*, which revolutionized biology at the time and continues to shape the field of behavioral neuroscience today. In science, a *theory* is an explanation that is supported by multiple lines of research with many converging results.

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, strong talons and sharp beaks help eagles 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.

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*—to help the organism survive. We can try to determine these mechanisms. 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 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-related 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).

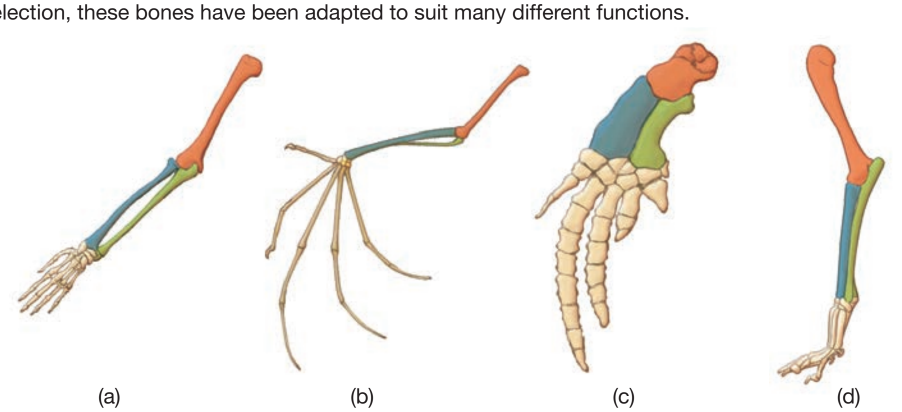
Darwin formulated his theory of evolution to explain the means by which species acquired their adaptive characteristics. The cornerstone of this theory is the principle of **natural selection**. Darwin noted that members of a species were not all identical and that some of the differences they exhibited 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.

functionalism The principle that the best way to understand a biological phenomenon (a behavior or a physiological structure) is to try to understand its useful functions for the organism.

natural selection The process by which inherited traits that confer a selective advantage (increase an animal's likelihood to live and reproduce) become more prevalent in a population.

Figure 1.5 Bones of 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.



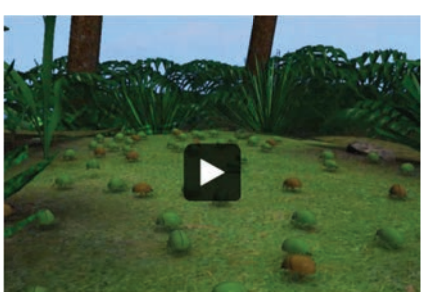
Over the course of time in the natural world, it was the environment, not the choices of the animal breeder, that shaped the process of evolution.

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 *genes,* the recipes for producing the proteins that cells need to grow and to perform their functions. Chromosomes contain pairs of genes called *alleles*. Each allele is a version of the gene inherited from one parent. 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 and 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 have a negative consequence; the offspring either fails to survive or survives with negative consequences of the mutation. However, a small percentage of mutations are beneficial and provide a **selective advantage** to the organism that possesses them. The animal is more likely than other members of its species to live long enough to reproduce and 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 capturing prey, and even a more attractive appearance to members of the other sex (after all, one must reproduce to pass on one's chromosomes).

Key Concepts

NATURAL SELECTION



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 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.

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.

mutation A change in the genetic information contained in the chromosomes of sperm or eggs, which can be passed on to an organism's offspring; provides genetic variability.

selective advantage A characteristic of an organism that permits it to produce more than the average number of offspring of its species.

evolution A gradual change in the structure and physiology of plant and animal species—generally producing more complex organisms—as a result of natural selection.

Evolution of the Human Brain

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 a 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.

Early human ancestors possessed several characteristics that enabled them to compete with other species to obtain resources. For example, agile hands enabled them to make and use tools; color vision helped them to spot ripe fruit, game animals, and dangerous predators. Their upright posture and bipedalism (ability to walk using two rear limbs) made it possible to walk long distances efficiently, with their eyes far enough from the ground to see long distances across the plains. 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 increased neural complexity and contributed to the development of a larger primate 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) require parental care for a period of time while the nervous system develops. Consequently, the evolutionary process did not have to result in a brain that consisted solely of specialized circuits of neurons that performed specialized tasks. Instead, it could simply result in 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. For the most part, 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 neither brain size nor proportion to overall body mass tells the whole story.

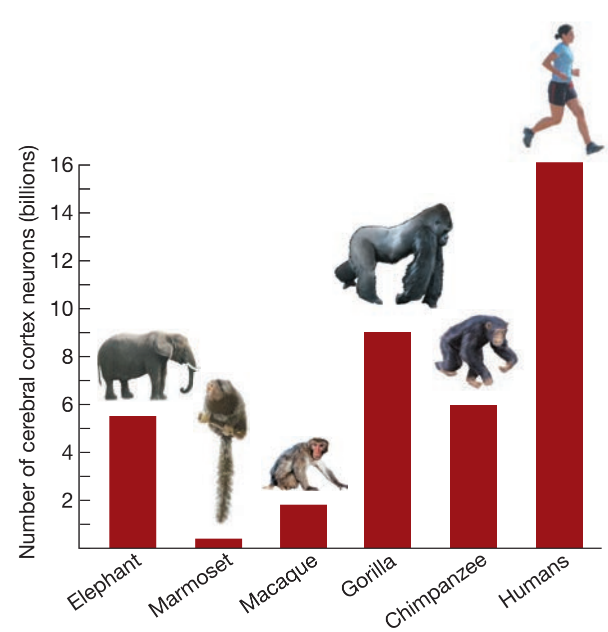
Ultimately, although bigger bodies require bigger brains, the size of the brain does not have to go up proportionally with that of the body. What counts, as far as intellectual ability goes, is having a brain with plenty of neurons that are available for behavior, learning, remembering, reasoning, and 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 brains of several species of rodents and primates and found that primate brains—especially large ones—contain many more neurons per gram than rodent brains do (see Figure 1.6). Among nonprimate mammals, this research group recently reported greater numbers of cerebral cortex neurons in dogs compared to cats. Of the eight species investigated, the group reported the greatest number of cerebral neurons in a golden retriever (627 million neurons) followed by a lion (545 million neurons) and a raccoon (512 million neurons). In comparison, the cerebral cortex of the cat contained 250 million neurons (Jardim-Messeder et al., 2017).

One key element to the evolution of a large human brain is a slowing of the process of brain development, allowing more time for growth. After birth, neurons grow and establish connections with each other, and other brain cells, which protect and support neurons, 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 1.6 **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.

Data from: Marino L. A Comparison of Encephalization between Odontocete Cetaceans and Anthropoid Primates. *Brain Behav Evol* 1998; 51: 230–238.



neoteny A slowing of the process of maturation, allowing more time for growth; an important factor in the development of large brains.

Module 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. Neoteny allows for the human brain to continue to develop after birth.

Thought Question

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

Figure 1.7 Research with Animals

Neuroscience research involving animals is reviewed for humane and ethical treatment of animals and strives to adhere to the the three Rs: Replacement (use non-animal models whenever possible), Reduction (use the smallest number of animals possible), and Refinement (minimize distress and improve welfare).

Fotografixx/Getty Images

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 the behavior of humans and animals. Neuroscience research involving humans and other animals is subject to important ethical considerations. This module addresses these issues in more detail.

Research with Animals

LO 1.5 Outline reasons for the use of animals in behavioral neuroscience research and the regulations in place for oversight of this research.

Throughout the history of our species, humans have and still do use animals for many purposes. People eat meat and eggs, and drink milk from various animals; turn animal hides into leather; extract insulin and other hormones from animal organs to treat people's diseases; train them to do useful work on farms; and provide companionship. We also use animals for scientific research to learn more about ourselves. Any time we use another species of animal for our own purposes, we should be sure that what we are doing is both humane and worthwhile. It is important that any use of animals for research in behavioral neuroscience qualifies on both counts, and we have oversight in place to ensure this is the case.

Most industrially developed societies have very strict regulations about the care of animals and require approval of the experimental procedures that are used. 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, and nonscientist members and community members not affiliated with the institution. This group reviews all proposals for research involving animals, with the 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. (See Figure 1.7.)

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. If they could not use animals in research, researchers could no longer develop or prepare many of the vaccines we now use to prevent disease.

Humans face medical, psychological, and behavioral challenges, many of which can be solved only through biological research. Let us consider some of the major neurological disorders. Strokes, such as Jeremiah's at the beginning of this chapter, are caused by bleeding or obstruction of a blood vessel within the brain, and may leave people partly paralyzed, unable to read, write, or communicate 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. 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, reducing the brain damage caused by strokes. We gain no such knowledge about strokes, nor possible ways to reduce or prevent the effects of strokes, without operating on a laboratory animal, to learn more about how to prevent or treat the effects of stroke.

As you will learn later in this book, research with laboratory animals has also 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.

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 that we already had all the answers. The only way to solve such human suffering is through conducting research on animals. In fact, animal research does not only help humans; it helps other animals. You may have a pet that receives vaccines for rabies or other diseases. All such medications for animals were originally developed for humans through research on animals.

Watch

HUMANE CARE AND HOUSING FOR ANIMALS INVOLVED IN RESEARCH

Research with Humans

LO 1.6 Discuss ethical considerations in research with human participants.

Not all neuroscience research is conducted with animals. 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) functions similarly to the IACUC to ensure ethical treatment of volunteers in research. (See Figure 1.8.)

Figure 1.8 Behavioral Neuroscience Research with Human Participants

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

Indiapicture/Alamy Stock Photo

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. For example, 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).

informed consent The process in which researchers must inform any potential participant about the nature of the research study, how any data will be collected and stored, and what the anticipated benefits and costs of participating will be.

neuroethics An interdisciplinary field devoted to understanding implications of and developing best practices in ethics for neuroscience research.

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 recent 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 hotly debated ethics of psychosurgery (Presidential Commission for the Study of Bioethical Issues, 2014). The panel generated a number of important recommendations, including integrating ethics and science through education at all levels. Today, an international professional organization (*International Neuroethics Society*) and research journals are dedicated to furthering dialogue about this important topic.

Module Review

Ethical Issues in Research with Humans and Other Animals

LO 1.5 Outline reasons for the use of animals in behavioral neuroscience research and the regulations in place for oversight of this 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 computer programs cannot adequately model the complexity of the nervous system. Regulation and oversight for animal research are important to ensure humane and ethical treatment of animals involved in research.

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 the 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 the creation of 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?