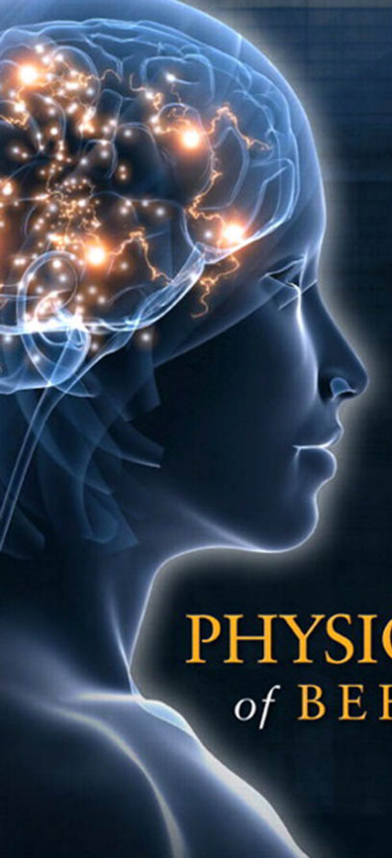

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PHYSIOLOGY *of* BEHAVIOR

Neil R. Carlson

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eleventh edition

Physiology of Behavior

NEIL R. CARLSON

University of Massachusetts, Amherst

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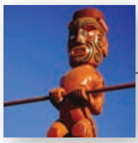

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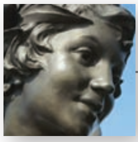

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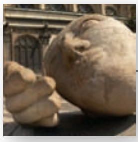

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Preface

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 eleventh 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.

The first part of the book is concerned with foundations: 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: 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 covers the neural and metabolic bases of drinking and eating.

The fourth part of the book deals with learning, including research on synaptic plasticity, the neural mechanisms that are responsible for perceptual learning and stimulus-response learning (including classical and instrumental conditioning), human amnesia, and the role of the hippocampal formation in relational learning. The final part of the book deals with verbal 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 the anxiety disorders, autism, attention deficit disorder, and stress disorders; and the third discusses drug abuse.

Each chapter begins with a *Case History,* which describes an episode involving a neurological disorder or an issue in neuroscience. Other case histories are included in the text of the chapters. *Section Summaries* with *Thought Questions* follow each major section of the book. They not only provide useful reviews, but also break each chapter into manageable chunks; the *Thought Questions* are designed to stimulate your own thinking about what you have just learned. *Review Questions* are provided at the end of each chapter to help you assess your understanding of the material. *Definitions of Key Terms* are printed in the margin near the places where the terms are first discussed. *Pronunciation Guides* for terms that might be difficult to pronounce are also found there.

New to This Edition

The research reported in this edition—approximately 400 new references—reflects the enormous advances made in research methods. Nowadays, 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. And more and more, researchers are combining techniques that converge upon the solution to a problem. In the past, individuals tended to apply their particular research method to a problem; now they are more likely to use many methods, often in collaboration with other laboratories.

The art in this book continues to evolve. With the collaboration of Jay Alexander of I-Hua Graphics, I have revised the existing art and prepared new art to illustrate research that is described for the first time in this edition. The result is a set of up-to-date, clear, consistent, and attractive illustrations.

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

Chapter 6

Animal research on gene therapy for color blindness
Congenital prosopagnosia
Williams syndrome and the fusiform face area
Enhanced connections between auditory cortex and visual cortex in blind people

Chapter 7

Reaction to dissonance in newborns
Kinesthesia from skin receptors
New research on placebo analgesia
New research on fat taste
New research on olfactory coding in the cortex

Chapter 8

Interhemispheric transfer of motor learning
Role of frontopolar cortex in decisions to move

The hyperdirect pathway of the cortico-basal ganglia circuitry

Chapter 9

Health effects of chronic sleep deprivation

Role of variants in the gene for adenosine deaminase in sleep need

New optogenetic studies on role of noradrenergic and orexigenergic neurons in sleep and waking

Chapter 10

Role of kisspeptin in stimulation of puberty and control of secretion of sex hormones

Stimulation of neurogenesis by odor of potential sex partners

New research on congenital adrenal hypertrophy

Research on the role of the uncinate nucleus on gender identity

Role of prolactin in parental behavior by human fathers

Chapter 11

New research on the role of the prefrontal cortex on courage

"Emotional contagion" in people with blindsight

The simulationist hypothesis of recognition of emotional expressions

Effects of Botox treatment of facial muscles on mood

Chapter 12

Role of the FTO gene in obesity

Chapter 13

Discovery of the role of PKM-zeta in longlasting long-term potentiation

Role of the basal ganglia in filtering irrelevant information out of short-term memory

New research on place cells, grid cells, head direction cells, and border cells

Role of sharp-wave-ripple complexes during slow-wave sleep in memory consolidation

New research on reconsolidation of memories

Chapter 14

Role of sensorimotor function and mirror-neuron circuits in speech perception

Role of subvocal articulation in word recognition in deaf people

New section on recognition of people's voices

Research on the relation between object recognition and reading

Chapter 15

Role of tumor initiating cells in malignant gliomas

New research on treatment for cerebral blood clots

New section on traumatic brain injury

Prion-like behavior of misfolded α-synuclein and Aβ proteins

Optogenetic methods in research on Parkinson's disease

Chapter 16

Research on the role of DISC1 in schizophrenia and other mental disorders

Role of maternal substance abuse in development of schizophrenia in offspring

Season of birth in development of depressive disorder

Deep brain stimulation as treatment for depression

New section on role of the frontal cortex in development of depression

Increased apoptosis and depressive behavior after prolonged exposure to darkness

Chapter 17

Role of variations in the gene for BDNF in anxiety disorders

Research on efficacy of a neurosteroid enhancer in treatment of anxiety disorders

Research on oxytocin treatment to improve social interactions in autism spectrum disorders

Role of prenatal androgens in development of autism spectrum disorders

Role of variations in the gene for COMT in development of PTSD

Transcranial magnetic stimulation of the dorsolateral PFC for treatment of PTSD

Chapter 18

Discovery of the role of orexin and MCH in addictions

Role of the medial habenula and the interpeduncular nucleus in nicotine addiction

Role of variations in the gene for α5 ACh receptors in nicotine addiction

Inhibitory role of cannabidiol on addictive potential of marijuana

Role of sirtuins in the addictive potential of cocaine

Deep brain stimulation and TMS as a treatment for drug addiction

Besides updating my discussion of research, I keep updating my writing. Writing is a difficult, time-consuming endeavor, and I find that I am still learning how to do it well. But I do think that with practice my writing is better organized, smoother, and more coherent.

Good writing means including all steps of a logical discourse. My teaching experience has taught me that an entire lecture can be wasted if the students do not understand all of the "obvious" conclusions of a particular experiment before the next one is described. Unfortunately, puzzled students sometimes write notes feverishly, in an attempt to get the facts down so they can study them—and understand them—later. A roomful of busy, attentive students tends to reinforce the lecturer's behavior. I am sure all my colleagues have been dismayed by a question from a student that reveals a lack of understanding of details long since passed, accompanied by quizzical looks from other students that confirm that they have the same question. Painful experiences such as these have taught me to examine the logical steps between the discussion of one experiment and the next and to make sure they are explicitly stated. A textbook writer must address the students who will read the book, not simply colleagues who are already acquainted with much of what he or she will say.

Because research on the physiology of behavior is an interdisciplinary effort, a textbook must provide the student with the background necessary for understanding a variety of approaches. I have been careful to provide enough biological background early in the book that students without a background in physiology can understand what is said later, while students with such a background can benefit from details that are familiar to them.

I designed this text for serious students who are willing to work. In return for their effort, I have endeavored to provide a solid foundation for further study. Those students who will not take subsequent courses in this or related fields should receive the satisfaction of a much better understanding of their own behavior. Also, they will have a greater appreciation for the forthcoming advances in medical practices related to disorders that affect a person's perception, mood, or behavior. I hope that students who read this book carefully will henceforth perceive human behavior in a new light.

MyPsychLab

The new MyPsychLab combines original online learning applications with powerful online assessments to engage students, assess their learning, and help them succeed. For each chapter of the text, MyPsychLab has a pre-test, post-test and chapter exam so both instructors and students can track progress and get immediate feedback. Each student receives a personalized study plan based on Bloom's Taxonomy, which arranges content requiring less complex thinking—such as remembering and understanding—to more complex critical thinking—such as applying and analyzing. This layered approach helps students succeed in the course and beyond. MyPsychLab also contains an eText so students can access their textbook anytime, anywhere, including listening online.

MyPsychLab for *Physiology of Behavior*, eleventh edition, contains simulations and animations of important figures and diagrams. The simulations and animations demonstrate some of the most important principles of neuroscience through movement and interaction, including modules on neurophysiology, neuroanatomy, psychopharmacology, audition, sleep, emotion, ingestive behavior, memory, and verbal communication. MyPsychLab also includes a 3D ***Virtual Brain*** application which allows students to take interactive tours through different sections of the brain while using real life scenarios to explain behavior. Also included are ***BioFlix*** animations, which are interactive tutoring on the toughest topics in biopsychology, such as how neurons and synapses work. References throughout the text direct students to content in MyPsychLab, and a new feature at the end of each chapter directs student to ***Virtual Brain*** modules.

Resources for Instructors

Several supplements are available for instructors who adopt *Physiology of Behavior,* eleventh edition.

Instructor's Manual (ISBN 020523951X): Written by Scott Wersinger, University of Buffalo, SUNY. Each chapter includes an Integrated Teaching Outline with teaching objectives, lecture material, demonstrations and activities, videos, suggested readings, web resources, and information about other supplements. An appendix contains a set of student handouts. Available online at www.pearsonhighered.com/irc.

Test Bank (ISBN 0205239501): Written by Paul Wellman, Texas A&M University. Includes over 2500 thoroughly reviewed multiple-choice, completion, short answer, and essay questions, each with answer skill justification, page references, difficulty rating, and skill type designation. The Test Bank is also available in Pearson *MyTest* (ISBN 0205239498), a powerful online assessment software program. Instructors can easily create and print quizzes and exams as well as author new questions online for maximum flexibility. Both the Test Bank and MyTest are available online at www.pearsonhighered.com/irc.

PowerPoint Slides (ISBN 0205239498): Written by Grant McLaren, Edinboro University of Pennsylvania. Provide a framework for lecture outlines with images from the text. For this edition, the slides have been enhanced with even more visual appeal to engage students. Available online at www.pearsonhighered.com/irc.

Acknowledgments

Although I must accept the blame for any shortcomings of the book, I want to thank the many colleagues who helped me by responding to my requests for reprints of their work, suggesting topics that I should cover, permitting me to reproduce their diagrams and photographs in this book, and pointing out deficiencies in the previous edition.

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Finally, I thank my wife Mary for her support. Writing is a lonely pursuit, because one must be alone with one's thoughts for many hours of the day. I thank her for giving me the time to read, reflect, and write without feeling that I was neglecting her too much.

I was delighted to hear from many students and colleagues who read previous editions of my book, and I hope that the dialogue will continue. Please write to me and tell me what you like and dislike about the book. My e-mail is nrc@psych.umass.edu. When I write, I like to imagine that I am talking with you, the reader. If you write to me, we can make the conversation a two-way exchange.

Introduction

Outline

Miss S. was a 60-year-old woman with a history of high blood pressure, which was not responding well to the medication she was taking. One evening she was sitting in her reclining chair reading the newspaper when the phone rang. She got out of her chair and walked to the phone. As she did, she began to feel giddy and stopped to hold onto the kitchen table. She has no memory of what happened after that.

The next morning, a neighbor, who usually stopped by to have coffee with Miss S., found her lying on the floor, mumbling incoherently. The neighbor called an ambulance, which took Miss S. to a hospital.

Two days after her admission, I visited her in her room, along with a group of neuropsychologists and neurological residents being led by the chief of neurology. We had already been told by the neurological resident in charge of her case that Miss S. had had a stroke in the back part of the right side of the brain. He had attached a CT scan to an illuminated viewer mounted on the wall and had showed us a white spot caused by the accumulation of blood in a particular region of her brain. (You can look at the scan yourself if you like; it is shown in Figure 5.19.)

About a dozen of us entered Miss S.'s room. She was awake but seemed a little confused. The resident greeted her and asked how she was feeling. "Fine, I guess," she said. "I still don't know why I'm here."

"Can you see the other people in the room?"

"Why, sure."

"How many are there?"

She turned her head to the right and began counting. She stopped when she had counted the people at the foot of her bed. "Seven," she reported. "What about us?" asked a voice from the left of her bed. "What?" she said, looking at the people she had already counted. "Here, to your left. No, toward your left!" the voice repeated. Slowly, rather reluctantly, she began turning her head to the left. The voice kept insisting, and finally she saw who was talking. "Oh," she said, "I guess there are more of you."

The resident approached the left side of her bed and touched her left arm. "What is this?" he asked. "Where?" she said. "Here," he answered, holding up her arm and moving it gently in front of her face.

"Oh, that's an arm."

"An arm? Whose arm?"

"I don't know…. I guess it must be yours."

"No, it's yours. Look, it's a part of you." He traced with his fingers from her arm to her shoulder.

"Well, if you say so," she said, still sounding unconvinced.

When we returned to the residents' lounge, the chief of neurology said that we had seen a classic example of unilateral neglect, caused by damage to a particular part of the right side of the brain. "I've seen many cases like this," he explained. "People can still perceive sensations from the left side of their body, but they just don't pay attention to them. A woman will put makeup on only the right side of her face, and a man will shave only half of his beard. When they put on a shirt or a coat, they will use their left hand to slip it over their right arm and shoulder, but then they'll just forget about their left arm and let the garment hang from one shoulder. They also don't look at things located toward the left or even the left halves of things. Once I visited a man in his hospital room who had just finished eating breakfast. He was sitting in his bed, with a tray in front of him. There was half of a pancake on his plate. 'Are you all done?' I asked. 'Sure,' he said. When he wasn't looking, I turned the plate around so that the uneaten part was on his right. He saw it, looked startled, and said, 'Where the hell did that come from?' "

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.

One of the most universal of all human characteristics is curiosity. We want to explain what makes things happen. In ancient times, people believed that natural phenomena were caused by animating spirits. All moving objects—animals, the wind and tides, the sun, moon, and stars—were assumed to have spirits that caused them to move. For example, stones fell when they were dropped because their animating spirits wanted to be reunited with Mother Earth. As our ancestors became more sophisticated and learned more about nature, they abandoned this approach (which we call *animism*) in favor of physical explanations for inanimate moving objects. But they still used spirits to explain human behavior.

From the earliest historical times, people have believed that they possess something intangible that animates them: a mind, or a soul, or a spirit. This belief stems from the fact that each of us is aware of his or her own existence. When we think or act, we feel as though something inside us is thinking or deciding to act. But what is the nature of the human mind? We each 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. 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 take an empirical, practical, and monistic approach to the study of human nature. Most of us believe that once we understand the workings of the human body—and, in particular, the workings of the nervous system—the mind–body problem will have been solved. We will be able to explain how we perceive, how we think, how we remember, and how we act. We will even be able to explain the nature of our own self-awareness. Of course, we are far from understanding the workings of the nervous system, so only time will tell whether this belief is justified. In any event there is no way to study nonphysical phenomena in the laboratory. All that we can detect with our sense organs and our laboratory instruments are manifestations of the physical world: matter and energy.

Understanding Human Consciousness: A Physiological Approach

As you will learn from subsequent chapters, scientists have discovered much about the physiology of behavior: of perception, motivation, emotion, memory, and control of specific movements. But before addressing these problems, I want to show you that a scientific approach to perhaps the most complex phenomenon of all—human consciousness—is at least possible.

The term *consciousness* can be used to refer to a variety of concepts, including simple wakefulness. Thus, a researcher may write about an experiment using "conscious rats," referring to the fact that the rats were awake and not anesthetized. However, in this context I am using the word *consciousness* to refer to the fact that we humans are aware of—and can tell others about—our thoughts, perceptions, memories, and feelings.

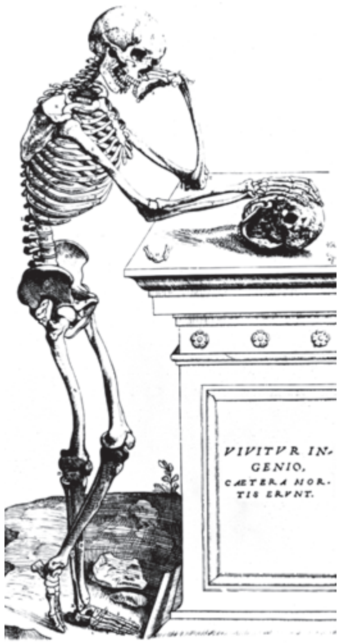

FIGURE 1.1 Studying the Brain
Will the human brain ever completely understand its own workings? A sixteenth-century woodcut from the first edition of *De humani corporis fabrica (On the Workings of the Human Body)* by Andreas Vesalius.
(Courtesy of National Library of Medicine.)

We know that consciousness can be altered by changes in the structure or chemistry of the brain; therefore, we may hypothesize that consciousness is a physiological function, just like behavior. We can even speculate about the origins of this self-awareness. Consciousness and the ability to communicate seem to go hand in hand. Our species, with its complex social structure and enormous capacity for learning, is well served by our ability to communicate: to express intentions to one another and to make requests of one another. Verbal communication makes cooperation possible and permits us to establish customs and laws of behavior. Perhaps the evolution of this ability is what has given rise to the phenomenon of consciousness. That is, our ability to send and receive messages with other people enables us to send and receive our own messages inside our own heads—in other words, to think and to be aware of our own existence. (See ***Figure 1.1.***)

▷ **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.

Blindsight

Several phenomena involving the human brain provide insights into the nature of consciousness. One of these phenomena, caused by damage to a particular part of the brain, is known as **blindsight** (Weiskrantz et al., 1974; Cowey, 2010). The symptoms of blindsight indicate that the common belief that perceptions must enter consciousness to affect our behavior is incorrect. Our behavior can be guided by sensory information of which we are completely unaware.

Natalie J. had brought her grandfather to see Dr. M., a neuropsychologist. Mr. J.'s stroke had left him almost completely blind; all he could see was a tiny spot in the middle of his visual field. Dr. M. had learned about Mr. J.'s condition from his neurologist and had asked Mr. J. to come to his laboratory so that he could do some tests for his research project.

Dr. M. helped Mr. J. find a chair and sit down. Mr. J., who walked with the aid of a cane, gave it to his granddaughter to hold for him. "May I borrow that?" asked Dr. M. Natalie nodded and handed the cane to Dr. M. "The phenomenon I'm studying is called blindsight," he said. "Let me see if I can show you what it is.

"Mr. J., please look straight ahead. Keep looking that way, and don't move your eyes or turn your head. I know that you can see a little bit straight ahead of you, and I don't want you to use that piece of vision for what I'm going to ask you to do. Fine. Now, I'd like you to reach out with your right hand and point to what I'm holding."

"But I don't see anything—I'm blind!" said Mr. J., obviously exasperated.

"I know, but please try, anyway."

Mr. J. shrugged his shoulders and pointed. He looked startled when his finger encountered the end of the cane, which Dr. M. was pointing toward him.

"Gramps, how did you do that?" asked Natalie, amazed. "I thought you were blind."

"I am!" he said, emphatically. "It was just luck."

"Let's try it just a couple more times, Mr. J.," said Dr. M. "Keep looking straight ahead. Fine." He reversed the cane, so that the handle was pointing toward Mr. J. "Now I'd like you to grab hold of the cane."

Mr. J. reached out with an open hand and grabbed hold of the cane.

"Good. Now put your hand down, please." He rotated the cane 90 degrees, so that the handle was oriented vertically. "Now reach for it again."

Mr. J. did so. As his arm came up, he turned his wrist so that his hand matched the orientation of the handle, which he grabbed hold of again.

"Good. Thank you, you can put your hand down." Dr. M. turned to Natalie. "I'd like to test your grandfather now, but I'll be glad to talk with you later."

As Dr. M. explained to Natalie afterward, the human brain contains not one but several mechanisms involved in vision. To simplify matters somewhat, let's consider two systems, which evolved at different times. The more primitive one, which resembles the visual system of animals such as fish and frogs, evolved first. The more complex one, which is possessed by mammals, evolved later. This second, "mammalian" system seems to be the one that is responsible for our ability to perceive the world around us. The first, "primitive," visual system is devoted mainly to controlling eye movements and bringing our attention to sudden movements that occur off to the side of our field of vision.

Mr. J.'s stroke had damaged the mammalian visual system: the visual cortex of the brain and some of the nerve fibers that bring information to it from the eyes. Cases like his show that after the mammalian visual system is damaged, people can use the primitive visual system of their brains to guide hand movements toward an object even though they cannot see what they are reaching for. In other words, visual information can control behavior without producing a conscious sensation. The phenomenon of blindsight suggests that *consciousness is not a general property of all parts of the brain;* some parts of the brain, but not others, play a special role in consciousness. Although we are not sure just where these parts are or exactly how they work, they seem to be related to our ability to communicate—with others and with ourselves. The primitive system, which evolved before the development of brain mechanisms that give rise to consciousness, does not have these connections, so we are not conscious of the visual information it detects. It *does* have connections with the parts of the brain responsible for controlling hand movements. Only the mammalian visual system in the human brain has direct connections with the parts of the brain responsible for consciousness. (See ***Figure 1.2.***)

Split Brains

Studies of humans who have undergone a particular surgical procedure demonstrate dramatically how disconnecting parts of the brain involved with perceptions from parts that are involved with verbal behavior also disconnects them from consciousness. These results suggest

▷ **blindsight** The ability of a person who cannot see objects in his or her blind field to accurately reach for them while remaining unconscious of perceiving them; caused by damage to the "mammalian" visual system of the brain.

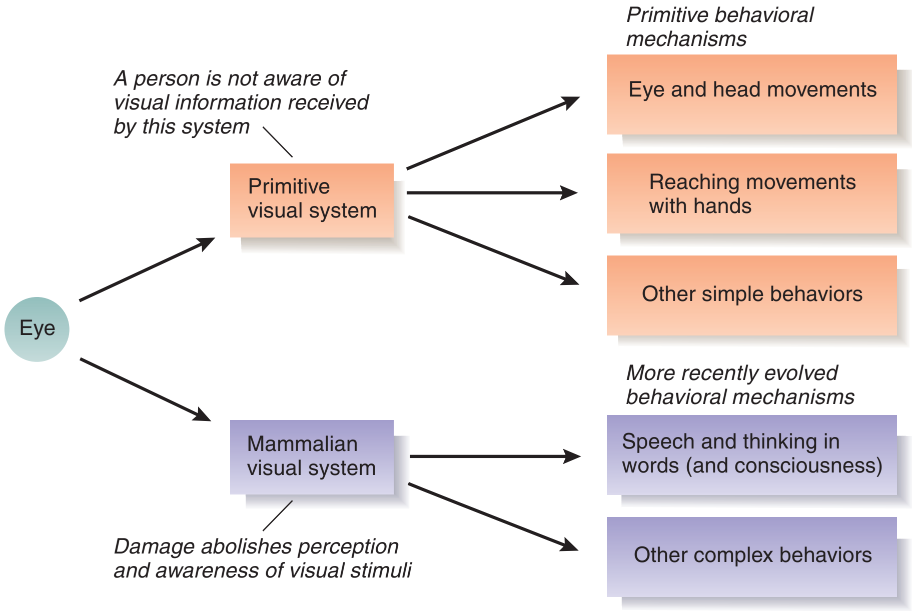

FIGURE 1.2 An Explanation of the Blindsight Phenomenon

that the parts of the brain involved in verbal behavior may be the ones responsible for consciousness.

The surgical procedure is one that has been used for people with very severe epilepsy that cannot be controlled by drugs. In these people, nerve cells in one side of the brain become uncontrollably overactive, and the overactivity is transmitted to the other side of the brain by the corpus callosum. The **corpus callosum** ("tough body") is a large bundle of nerve fibers that connect corresponding parts of one side of the brain with those of the other. Both sides of the brain then engage in wild activity and stimulate each other, causing a generalized epileptic seizure. These seizures can occur many times each day, preventing the patient from leading a normal life. Neurosurgeons discovered that cutting the corpus callosum (the **split-brain operation**) greatly reduced the frequency of the epileptic seizures.

Figure 1.3 shows a drawing of the split-brain operation. We see the brain being sliced down the middle, from front to back, dividing it into its two symmetrical halves. The artist has created a window in the left side of the brain so that we can see the corpus callosum being cut by the neurosurgeon's special knife. (See ***Figure 1.3***.)

Sperry (1966) and Gazzaniga and his associates (Gazzaniga and LeDoux, 1978; Gazzaniga, 2005) have studied these patients extensively. The largest part of the brain consists of two symmetrical parts, called the **cerebral hemispheres,** which receive sensory information from the opposite sides of the body. They also control movements of the opposite sides. The corpus callosum permits the two hemispheres to share information so that each side knows what the other side is perceiving

▷ **corpus callosum (*core* *pus ka* ***low*** *sum*)** The largest commissure of the brain, interconnecting the areas of neocortex on each side of the brain.

▷ **split-brain operation** Brain surgery that is occasionally performed to treat a form of epilepsy; the surgeon cuts the corpus callosum, which connects the two hemispheres of the brain.

▷ **cerebral hemispheres** The two symmetrical halves of the brain; constitute the major part of the brain.

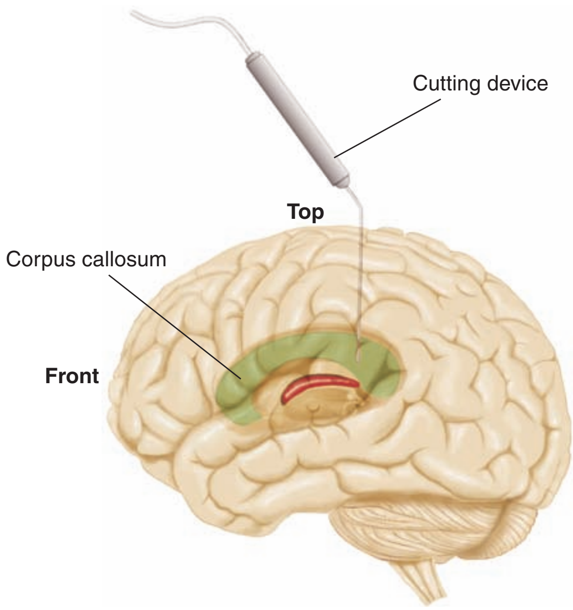

FIGURE 1.3 The Split-Brain Operation

A "window" has been opened in the side of the brain so that we can see the corpus callosum being cut at the midline of the brain.

and doing. After the split-brain operation is performed, the two hemispheres are disconnected and operate independently; their sensory mechanisms, memories, and motor systems can no longer exchange information. You might think that disconnecting the brain hemispheres would be devastating, but the effects of these disconnections are not obvious to the casual observer. The simple reason for this fact is that only one hemisphere—in most people, the left—controls speech. The right hemisphere of an epileptic person with a split brain appears able to understand instructions reasonably well, but it is totally incapable of producing speech.

Because only one side of the brain can talk about what it is experiencing, people speaking with a person who has a split brain are conversing with only one hemisphere: the left. The operations of the right hemisphere are more difficult to detect. Even the patient's left hemisphere has to learn about the independent existence of the right hemisphere. One of the first things that these patients say they notice after the operation is that their left hand seems to have a "mind of its own." For example, patients may find themselves putting down a book held in the left hand, even if they have been reading it with great interest. This conflict occurs because the right hemisphere, which controls the left hand, cannot read and therefore finds holding the book boring. At other times these patients surprise themselves by making obscene gestures (with the left hand) when they had not intended to. A psychologist once reported that a man with a split brain attempted to hit his wife with one hand and protect her with the other. Did he *really* want to hurt her? Yes and no, I guess.

The olfactory system is an exception to the general rule that of sensory information crosses from one side of the body to the opposite side of the brain. That is, when a person sniffs a flower through the left nostril, the *left* brain receives information about the odor. Thus, if the right nostril of a patient with a split brain is closed, leaving only the left nostril open, the patient will be able to tell us what the odors are because the information is received by the side of the brain that controls speech (Gordon and Sperry, 1969). However, if the odor enters only the right nostril, the patient will say that he or she smells nothing. But, in fact, the right brain *has* perceived the odor and *can* identify it. To show that this is so, we ask the patient to smell an odor with the right nostril and then reach for some objects that are hidden from view by a partition. If asked to use the left hand, which is controlled by the hemisphere that detected the smell, the patient will select the object that corresponds to the odor—a plastic flower for a floral odor, a toy fish for a fishy odor, a model tree for the odor of pine, and so forth. But if asked to use the right hand, the patient fails the test because the right hand is connected to the left hemisphere, which did not smell the odor presented to the right nostril. (See ***Figure 1.4.***)

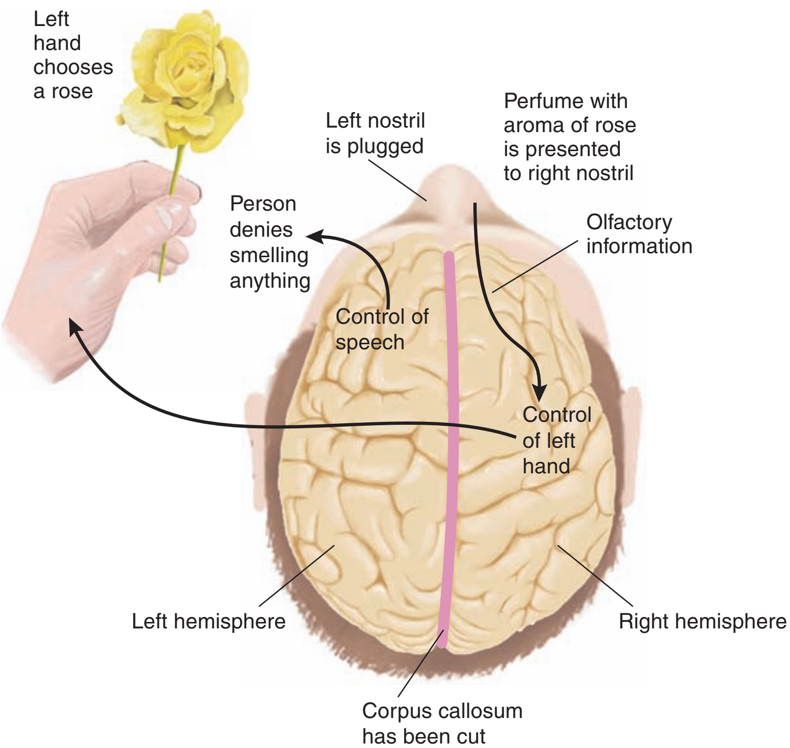

FIGURE **1.4** **Smelling with a Split Brain**
Identification of an object in response to an olfactory stimulus by a person with a split brain.

The effects of cutting the corpus callosum reinforce the conclusion that we become conscious of something only if information about it is able to reach the parts of the brain responsible for verbal communication, which are located in the left hemisphere. If the information does not reach these parts of the brain, then that information does not reach consciousness. We still know very little about the physiology of consciousness, but studies of people with brain damage are beginning to provide us with some useful insights. This issue is discussed in later chapters.

Unilateral Neglect

The phenomenon described in the case history at the beginning of this chapter—failure to notice things located to a person's left—is known as **unilateral neglect** (Adair and Barrett, 2008). Unilateral ("one-sided") neglect is produced by damage to a particular part of the right side of the brain: the cortex of the parietal lobe. (Chapter 3 describes the location of this region.) The parietal lobe receives information directly from the skin, the muscles, the joints, the internal organs, and the part of the inner ear that is concerned with balance. Thus, it is concerned with the body and its position. But that is not all; the parietal cortex also receives auditory and visual information. Its most important function seems to be to put together information about the movements and location of the parts of the body with the locations of objects in space around us. This information makes it possible for us to reach for and manipulate objects and to orient ourselves in space.

If unilateral neglect simply consisted of blindness in the left side of the visual field and anesthesia of the left side of the body, it would not be nearly as interesting. But individuals with unilateral neglect are neither half blind nor half numb. Under the proper circumstances, they *can* see things located to their left, and they *can* tell when someone touches the left side of their bodies. But normally they ignore such stimuli and act as if the left side of the world and the left side of their bodies do not exist. In other words, their inattention to things to the left means that they normally do not become conscious of them.

Volpe, LeDoux, and Gazzaniga (1979) presented pairs of visual stimuli to people with unilateral neglect—one stimulus in the left visual field and one stimulus in the right. Invariably, the people reported seeing only the right-hand stimulus. But when the investigators asked the people to say whether the two stimuli were identical, they answered correctly, *even though they said that they were unaware of the left-hand stimulus.*

If you think about the story that the chief of neurology told about the man who ate only the right half of a pancake, you will realize that people with unilateral neglect *must* be able to perceive more than the right visual field. Remember that people with unilateral neglect fail to notice not only things to their left but also the *left halves* of things. But to distinguish between the left and right halves of an object, you first have to perceive the entire object—otherwise, how would you know where the middle was?

FIGURE 1.5 Unilateral Neglect
When people with unilateral neglect attempt to draw simple objects, they demonstrate their unawareness of the left half of things by drawing only the features that appear on the right.

People with unilateral neglect also demonstrate their unawareness of the left half of things when they draw pictures. For example, when asked to draw a clock, they almost always successfully draw a circle; but then when they fill in the numbers, they scrunch them all in on the right side. Sometimes they simply stop after reaching 6 or 7, and sometimes they write the rest of the numbers underneath the circle. When asked to draw a daisy, they begin with a stem and a leaf or two and then draw all the petals to the right. (See ***Figure 1.5***.)

Bisiach and Luzzatti (1978) demonstrated a similar phenomenon, which suggests that unilateral neglect extends even to a person's own visual imagery. The investigators asked two patients with unilateral neglect to describe the Piazza del Duomo, a well-known landmark in Milan, the city in which they and the patients lived. They asked the patients to imagine that they were standing at the north end of the piazza and to describe what they saw. The patients duly named the buildings, but only those on the west, to their right. Then the investigators asked them to imagine themselves at the south end of the piazza. This time, they named the buildings on the east—again, to their right. Obviously, they knew about *all* of the buildings and their locations, but they visualized them only when the buildings were located in the right side of their (imaginary) visual field.

▷ **unilateral neglect** A syndrome in which people ignore objects located toward their left and the left sides of objects located anywhere; most often caused by damage to the right parietal lobe.

As you can see, there are two major symptoms of unilateral neglect: neglect of the left halves of things in the environment and neglect of the left half of one's own body. In fact, although most people with unilateral neglect show both types of symptoms, research indicates that they are produced by damage to slightly different regions of the brain (Hillis et al., 2005).

Perception of Self

Although neglect of the left side of one's own body can be studied only in people with brain abnormalities, an interesting phenomenon seen in people with undamaged brains confirms the importance of the parietal lobe (and another region of the brain) in feelings of body ownership. Ehrsson, Spence, and Passingham (2004) studied the *rubber hand illusion.* Normal subjects were positioned with their left hand hidden out of sight. They saw a lifelike rubber left hand in front of them. The experimenters stroked both the subject's hidden left hand and the visible rubber hand with a small paintbrush. If the two hands were stroked synchronously and in the same direction, the subjects began to experience the rubber hand as their own. In fact, if they were then asked to use their right hand to point to their left hand, they tended to point toward the rubber hand. However, if the real and artificial hands were stroked in different directions or at different times, the subjects did *not* experience the rubber hand as their own. (See ***Figure 1.6.***)

While the subjects were participating in the experiment, the experimenters recorded the activity of their brains with a functional MRI scanner. (Brain scanning is described in Chapter 5.) The scans showed increased activity in the parietal lobe and then, as the subjects began to experience the rubber hand as belonging to their body, in the *premotor cortex,* a region of the brain involved in planning movements. When the stroking of the real and artificial hands was uncoordinated and the subjects did not experience the rubber hand as their own, the premotor cortex did not become activated. The experimenters concluded that the parietal cortex analyzed the sight and the feeling of brush strokes. When the parietal cortex detected that they were congruent, this information was transmitted to the premotor cortex, which gave rise to the feeling of ownership of the rubber hand.

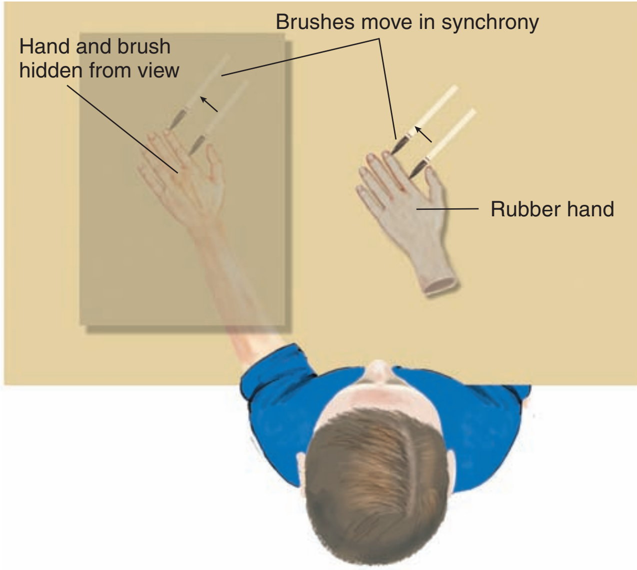

FIGURE 1.6 The Rubber Hand Illusion
If the subject's hidden left hand and the visible rubber hand are stroked synchronously in the same direction, the subject will come to experience the artificial hand as his or her own. If the hands are stroked asynchronously or in different directions, this illusion will not occur.
(Adapted from Botwinick, M. *Science*, 2004, *305*, 782–783.)

Another study from the same laboratory provided a particularly convincing demonstration that people experience a genuine feeling of ownership of the rubber hand (Ehrsson et al., 2007; Slater et al., 2009). The investigators used the procedure previously described to establish a feeling of ownership and then threatened the rubber hand by making a stabbing movement toward it with a needle. (They did not actually touch the hand with the needle.) Brain scans showed increased activity in a region of the brain (the anterior cingulate cortex) that is normally activated when a person anticipates pain and also in a region (the supplementary motor area) that is normally activated when a person feels the urge to move his or her arm (Fried et al., 1991; Peyron, Laurent, and Garcia-Larrea, 2000). So the impression that the rubber hand was about to receive a painful stab from a needle made people react as they would if their own hand were the target of the threat.

SECTION SUMMARY

Understanding Human Consciousness

The mind–body question has puzzled philosophers for many centuries. Modern science has adopted a monistic position—the belief that the world consists of matter and energy and that the human mind is a manifestation of the human brain. Studies of the functions of the human nervous system tend to support this position, as three specific examples show. These phenomena show that brain damage, by destroying conscious brain functions or disconnecting them from the speech mechanisms in the left hemisphere, can reveal the presence of perceptual mechanisms of which the person is *not* conscious and that a feeling of ownership of our own body is a function of the human brain.

Blindsight is a phenomenon that is seen after partial damage to the "mammalian" visual system on one side of the brain. Although the person is, in the normal meaning of the word, blind to anything presented to part of the visual field, the person can nevertheless reach out and point to objects whose presence he or she is not conscious of. Similarly, when sensory information about a particular object is presented to the right hemisphere of a person who has had a split-brain operation, the person is not aware of the object but can nevertheless indicate by movements of the left hand that the object has been perceived. Unilateral neglect—failure to become aware of the left half of one's body, the left half of objects, or items located to a person's left—reveals the existence of brain mechanisms that control our attention to things and hence our ability to become aware of them. These phenomena suggest that consciousness involves operations of the verbal mechanisms of the left hemisphere. Indeed, consciousness may be, in large part, a matter of our "talking to ourselves." Thus, once we understand the language functions of the brain, we may have gone a long way toward understanding how the brain can be conscious of its own existence. The rubber hand phenomenon suggests that a feeling of ownership of our own body is a result of brain mechanisms that can be studied with the methods of neuroscience.

■ THOUGHT QUESTIONS

1. Could a sufficiently large and complex computer ever be programmed to be aware of itself? Suppose that someone someday claims to have done just that. What kind of evidence would you need to prove or disprove this claim?
2. Is consciousness found in animals other than humans? Is the ability of some animals to communicate with each other and with humans evidence for at least some form of awareness of self and others?
3. Clearly, the left hemisphere of a person with a split brain is conscious of the information it receives and of its own thoughts. It is not conscious of the mental processes of the right hemisphere. But is it possible that the right hemisphere is conscious too but is just unable to talk to us? How could we possibly find out whether it is? Do you see some similarities between this issue and the one raised in the first question?

The Nature of Behavioral Neuroscience

Behavioral neuroscience was formerly known as *physiological psychology,* and it is still sometimes referred to by that name. Indeed, the first textbook of psychology, written by Wilhelm Wundt in the late nineteenth century, was titled *Principles of Physiological Psychology.* In recent years, with the explosion of information in experimental biology, scientists from other disciplines have become prominent contributors to the investigation of the physiology of behavior. The united effort of behavioral neuroscientists, physiologists, and other neuroscientists is due to the realization that the ultimate function of the nervous system is behavior.

When I ask my students what they think the ultimate function of the brain is, they often say "thinking," or "logical reasoning," or "perceiving," or "remembering things." Certainly, the nervous system performs these functions, but they support the primary one: control of movement. (Note that movement includes talking, an important form 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. Of course, once perceptual abilities have evolved, they can be used for purposes other than guiding behavior. For example, we can enjoy a beautiful sunset or a great work of art without the 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 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.

The modern history of investigating the physiology of behavior has been written 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. Thus, we