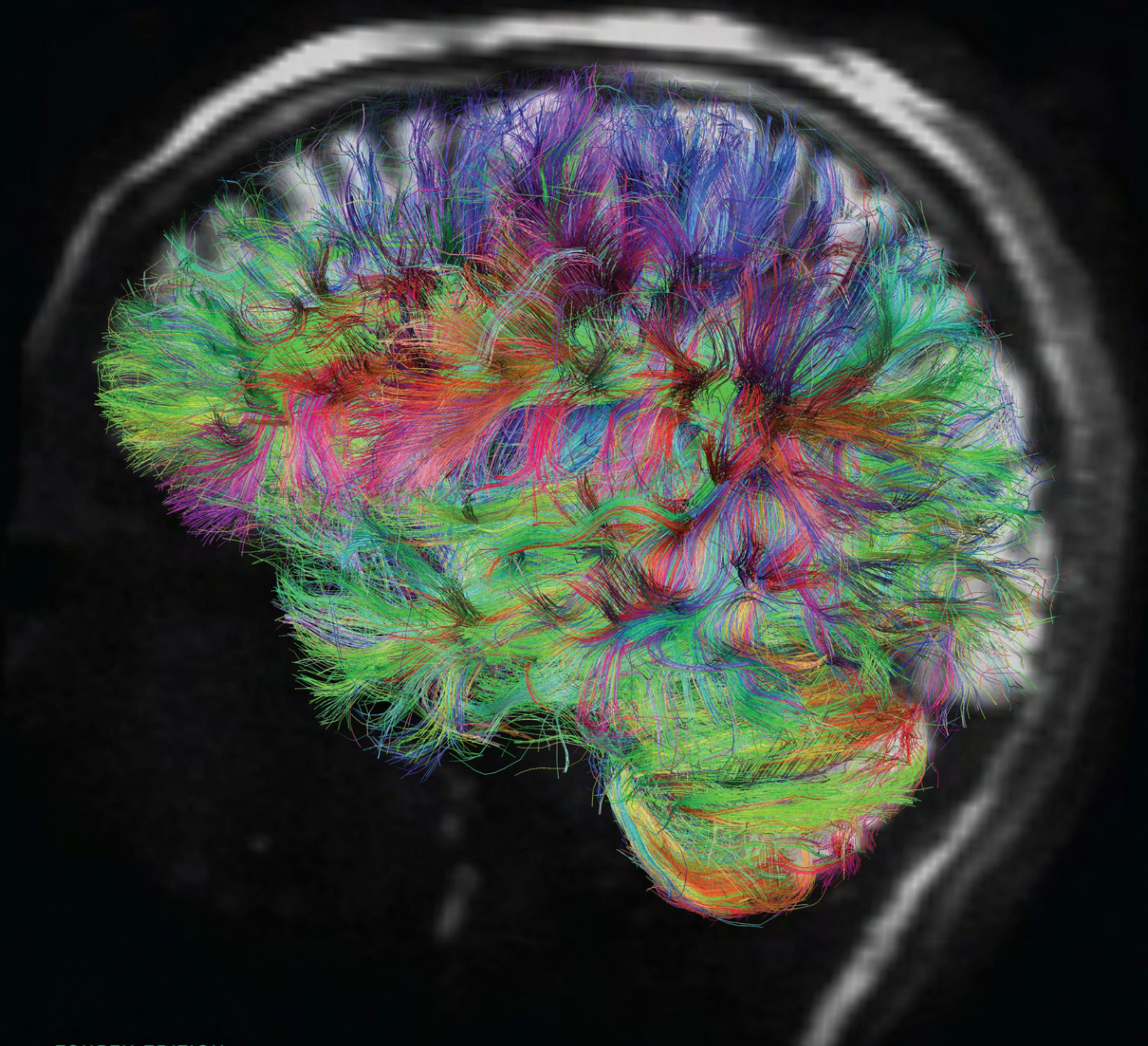
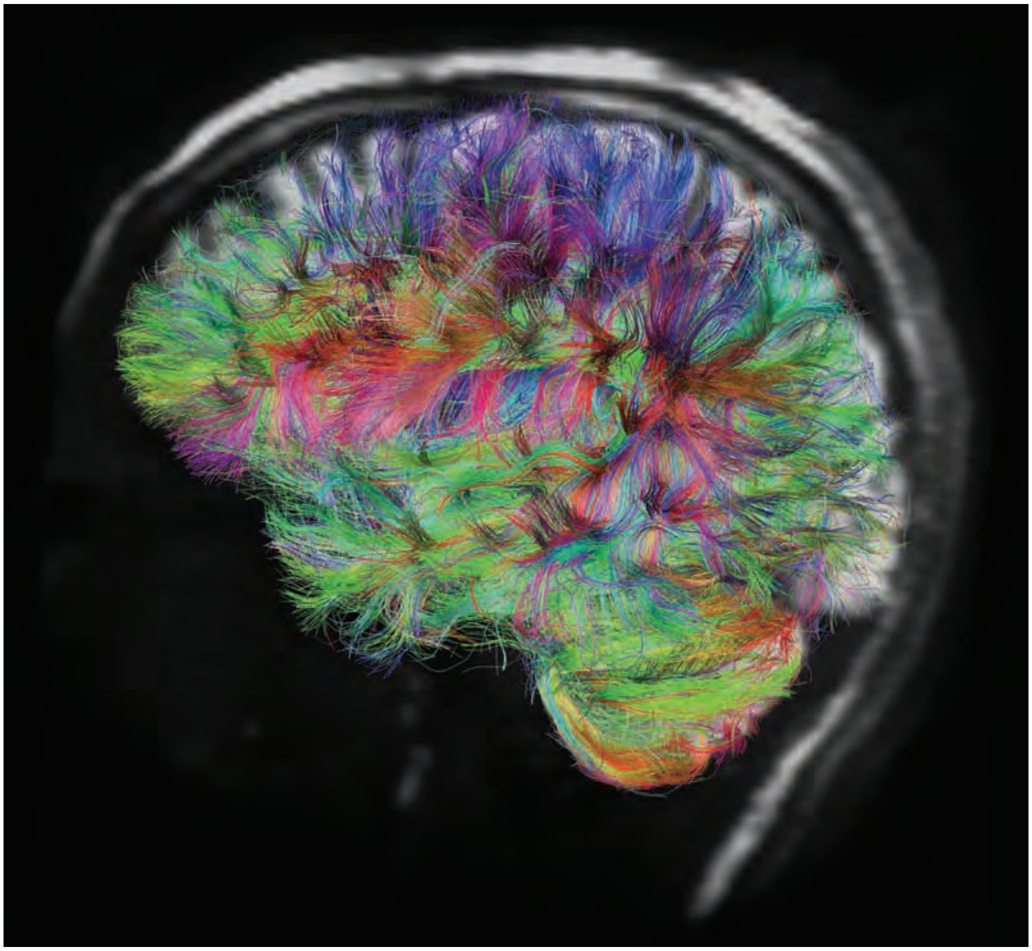
An Introduction to BRAIN AND BEHAVIOR



FOURTH EDITION

Bryan Kolb
Ian Q. Whishaw

An Introduction to
BRAIN AND BEHAVIOR



IMAGING THE BRAIN'S FIBER PATHWAYS

Commenting in *Nature* in 1993 on the "Backwardness of Human Neuroanatomy," Francis Crick and Edward Jones challenged the scientific community to map the human brain's connectivity. Rising to the challenge, scientists are exploiting MRI's sensitivity to motion to develop noninvasive methods for brain mapping in living humans, and the National Institutes of Health has launched the Human Connectome Project to catalyze new diagnostics based on connectivity (http://www.humanconnectomeproject.org/).

Diffusion MRI measures the microscopic, random movements of water molecules in living tissue. These movements act as a natural tracer of cellular architecture, including the orientations of axons, to create diffusion tractography: a virtual image representative of the brain's fiber pathways. The diffusion tractography shown on the cover was created under the aegis of NIH and employs the first in a new generation of MRI scanners designed and built to map human connectivity. The MGH/UCLA Siemens 3T Connectom affords gains in speed, sensitivity, and resolution up to tenfold over existing scanners.

On the cover, diffusion tractography images a typical human's left cerebral hemisphere, with the cerebellum at lower right and the nerve paths color-coded for clarity by their orientation in three-dimensional space. Each line represents hundreds of thousands of axons, primarily the short association pathways near the brain's surface. The image represents a milestone in answering the challenge of Crick and Jones and goes further—to the threshold of connectional imaging in mental health.

An Introduction to BRAIN AND BEHAVIOR

FOURTH EDITION

BRYAN KOLB
University of Lethbridge

IAN Q. WHISHAW
University of Lethbridge

WORTH PUBLISHERS

To the first neuron, our ancestors, our families, and students who read this book

Publisher: Kevin Feyen
Acquisitions Editor: Daniel DeBonis
Assistant Editor: Nadina Persaud
Marketing Manager: Jennifer Bilello
Developmental Editor: Barbara Brooks
Associate Media Editor: Betsy Block
Assistant Media Editor: Anthony Casciano
Supplements Project Editor: Edgar Bonilla
Senior Project Editor: Georgia Lee Hadler
Copy Editor: Penelope Hull
Production Manager: Sarah Segal
Art Director and Cover Design: Babs Reingold
Interior Design: Charles Yuen
Layout Designer and Chapter-Opening Photo Research: Lyndall Culbertson
Illustration Coordinator: Janice Donnola
Illustrations: Dragonfly Media Group and Northeastern Graphic, Inc.
Photo Editor: Cecilia Varas
Photo Researcher: Julie Tesser
Composition: Northeastern Graphic, Inc.
Printing and Binding: RR Donnelly

Library of Congress Control Number: 2012946361

ISBN-13: 9-781-4292-422-88
ISBN-10: 1-4292-4228-0

Printed in the United States of America
First printing
Worth Publishers
41 Madison Avenue
New York, NY 10010
www.worthpublishers.com

Credit is given to the following sources to use the chapter-opening images: Chapter 1: Jack Hollingsworth/Getty Images; Chapter 2: Dimitri Vervitsiotis/Getty Images; Chapter 3: (1) photosindia/Getty Images (2) Livet, Draft, Sanes, and Lichtman, Harvard University; Chapter 4: Take A Pix Media/Getty Images; Chapter 5: Diverse Images/Getty Images; Chapter 6: Image Source/Getty Images; Chapter 7: (1) Image Source/Getty Images (2) N. Kasthuri and J.W. Lichtman, Harvard University; Chapter 8: Priscilla Gragg/Getty Images; Chapter 9: (1) IMAGEMORE Co., Ltd./Getty Images (2) Novastock/StockConnection/PictureQuest; Chapter 10: Lane Oatey/Blue Jean/Getty Images; Chapter 11: Fotosearch/Getty Images; Chapter 12: Jupiterimages/Getty Images; Chapter 13: Brad Wilson/Getty Images; Chapter 14: Paula Hible/Getty Images; Chapter 15: (1) Nick Dolding/Getty Images (2) Image courtesy of Thomas Yeo and Fenna Krienen Yeo BTT, Krienen, F.M., Sepulcre, J., Sabuncu, M.R., Lashkari, L., Hollinshead, M., Roffman, J.L., Smoller, J.W., Zöllei, L., Polimeni, J.R., Fischl, B., Liu, H., Buckner, R.L.; Chapter 16: (1) Dimitri Vervitsiotis/Getty Images (2) Marcello Massimini/University of Wisconsin-Madison (3) Courtesy of Paul Thompson and Arthur W. Toga, University of California Laboratory of Neuro Imaging, Los Angeles, and Judith L. Rapoport, National Institute of Mental Health

Bryan Kolb received his Ph.D. from The Pennsylvania State University in 1973. He conducted postdoctoral work at the University of Western Ontario and the Montreal Neurological Institute. He moved to the University of Lethbridge in 1976, where he is currently Professor of Neuroscience and holds a Board of Governors Chair in Neuroscience. His current research examines how neurons of the cerebral cortex change in response to various factors, including hormones, experience, psychoactive drugs, neurotrophins, and injury, and how these changes are related to behavior in the normal and diseased brain. Kolb is a Fellow of the Royal Society of Canada, the Canadian Psychological Association (CPA), the American Psychological Association, and the Association of Psychological Science. He is a recipient of the Hebb Prize from CPA and from the Canadian Society for Brain, Behaviour, and Cognitive Science (CSBBCS) and has received honorary doctorates from the University of British Columbia and Thompson Rivers University. He is currently a member of the Experience-Based Brain and Behavioral Development program of the Canadian Institute for Advanced Research.

Ian Q. Whishaw received his Ph.D. from Western University and is a Professor of Neuroscience at the University of Lethbridge. He has held visiting appointments at the University of Texas, University of Michigan, Cambridge University, and the University of Strasbourg. He is a fellow of Clair Hall, Cambridge, the Canadian Psychological Association, the American Psychological Association, and the Royal Society of Canada. He is a recipient the Canadian Humane Society Bronze medal for bravery, the Ingrid Speaker Gold medal for research, and the distinguished teaching medal from the University of Lethbridge. He has received the Key to the City of Lethbridge and has honorary doctorates from Thompson Rivers University and the University of Lethbridge. His research addresses the neural basis of skilled movement and the neural basis of brain disease, and the Institute for Scientific Information includes him in its list of most cited neuroscientists. His hobby is training horses for western performance events.

this page left intentionally blank

CONTENTS IN BRIEF

this page left intentionally blank

CONTENTS

The Fourth Edition of *An Introduction to Brain and Behavior* continues to reflect the evolution of behavioral neuroscience. The major change in emphasis in this edition is the incorporation of epigenetics throughout. DNA, previously believed to be an unchanging template of heredity, is now known to respond to environmental events throughout life, leading to the concept of an *epigenome,* a record of the chemical changes to the DNA that regulate gene expression.

Epigenetics is especially important for understanding brain and behavior because environmentally induced modifications in gene expression alter the brain and ultimately behavioral development. Thus, experience—especially early experience—modifies how brain development unfolds. These modifications—of at least some behavioral traits—can be transferred across generations, as noted at the end of Section 3-3.

This edition fully addresses the advances in imaging technology, including the development and refinement of such MRI techniques as resting-state fMRI and diffusion tensor imaging, that are fueling the emerging field of *connectonomics.* As shown in the image on the book's cover, researchers are working to create a comprehensive map of neural connections—a "connectome" of the brain. These exciting advances are especially relevant in the second half of the book, where we review higher-level functions.

Imaging advances and epigenetics concepts and research are our prime focus in this revision but not our sole focus. The range of updates and new coverage in the Fourth Edition text and Focus features is listed, chapter-by-chapter, in the margins of these Preface pages. See for yourself the breadth and scope of the revision and then read on to learn more about the big-picture improvements in the Fourth Edition.

Our reviewers convinced us to move some material around. The chapter on Drugs and Hormones now follows Chapter 5, Neurotransmission. Long-term potentiation (LTP) has moved from Section 5-4 into an expanded discussion that begins Section 14-4 in the Learning and Memory chapter. And the Clinical Focus features on autism spectrum disorder and cerebral palsy have traded places: ASD now appears in Chapter 8, Development, and CP in Chapter 11, on Movement and Somatosensation.

In refining the book's learning apparatus, we have added sets of self-test questions at the end of the major sections in each chapter. These Section Reviews help students track their understanding as they progress. Answers appear at the back of the book.

We have expanded the popular margin notes, again thanks to feedback from readers, who confirm that the notes increase the reader's ease in finding information, especially when related concepts are introduced early in the text and then elaborated in later chapters. The addition of section numbers to each chapter's main headings makes it possible for readers to return quickly to an earlier discussion to refresh their knowledge or jump ahead to learn more. The margin notes also help instructors to move through the book to preview later discussions.

We have extended the appearance of illustrated Experiments that teach the scientific method visually from 8 to 13 chapters and the appearance of The Basics features that review scientific essentials from 4 to 6 chapters. The Experiments show readers how researchers design experiments—how they approach the study of brain–behavior relationships. The Basics let students brush up or get up to speed on their science foundation—knowledge that helps them comprehend behavioral neuroscience more fully.

We have made some big changes, yet much of the book remains familiar. Throughout, we continue to examine the nervous system with a focus on function, on how

FOURTH EDITION UPDATES CHAPTER-BY-CHAPTER

CHAPTER 1: ORIGINS

NEW Experiment 1-1 illustrates heritable factors and **genotype**.

UPDATED §1-2 defines **epigenetics**, adds case study on recovering consciousness post-TBI.

NEW The Basics: Classification of Life, in §1-3.

NEW Research Focus 1-3: climate change forced early hominids to develop more complex behaviors.

CHAPTER 2: NEUROANATOMY

NEW Figure 2-1 illustrates **phenotypic plasticity**.

NEW Experiment 2-1 demonstrates observational learning in the octopus.

NEW photo in §2-3: all sorts of activities can prove addictive.

CHAPTER 3: NEURONAL ANATOMY

NEW Research Focus 3-1: neuroscientists use genetics to investigate brain disorders.

NEW Experiment 3-1 tests how neural inhibition and excitation might produce behavior.

NEW Figure 3-6 contrasts early robots with contemporary social robots.

NEW coverage in §3-3: epigenetic mechanisms (Figure 3-25) and a case of "inheriting" experience.

CHAPTER 4: ELECTRICAL ACTIVITY IN THE NERVOUS SYSTEM

NEW Experiment 4-1 tests how motor neurons integrate information.

NEW Research Focus 4-3: the transgenic technique **optogenetics**.

FOURTH EDITION UPDATES CHAPTER-BY-CHAPTER

- **CHAPTER 5: NEUROTRANSMISSION**

  NEW Figure 5-3: **gap junction**; expanded coverage of electrical synapses in §5-1.

  UPDATED Research Focus 5-5: evidence that dendritic spines form the structural basis of behavior.

- **CHAPTER 6: DRUGS AND HORMONES**

  Chapter now follows Neurotransmission.

  NEW Clinical Focus 6-1: Cognitive Enhancement.

  NEW Table 6-1: streamlined grouping for psychoactive drugs in §6-2.

  UPDATED Clinical Focus 6-3: evidence for ketamine as an acute treatment for patients with major depression.

  UPDATED §6-4: coverage of drug abuse includes epigenetics-based explanations.

  UPDATED §6-5: epigenetic effects of long-term stress on susceptibility to PTSD.

- **CHAPTER 7: RESEARCH METHODS**

  NEW Research Focus 7-1: **optical tomography.**

  NEW Experiment 7-1 demonstrates how researchers tested the idea that hippocampal neurons contribute to memory formation.

  NEW coverage of state-of-the-art methods: **optogenetics** in §7-1, **electrocorticography** in §7-2, **resting-state fMRI** in §7-4, and "epigenetic drift" in §7-5.

  NEW Figure 7-16: a series of **diffusion tensor images** links tractography to research on the *brain connectome.*

  NEW §7-6 and Table 7-1 summarize neuroscience research methods.

our behavior and our brains interact, by asking key questions that students and neuroscientists ask:

- Why do we have a brain?
- How is the nervous system organized?
- How do drugs affect our behavior?
- How does the brain learn?
- How does the brain think?

As it was when we wrote the First Edition, our goal in this new edition is to bring coherence to a vast subject by helping students understand the big picture. Asking fundamental questions about the brain has another benefit: it piques students' interest and challenges them to join us on the journey of discovery that is brain science.

Scientific understanding of the human brain and human behavior continues to grow at an exponential pace. We want to communicate the excitement of recent breakthroughs in brain science and to relate some of our own experiences from 45 years of studying brain and behavior both to make the field's developing core concepts and latest revelations understandable and meaningful and to transport uninitiated students to the frontiers of physiological psychology.

Every chapter centers on the relation between the brain and behavior. When we first describe how neurons communicate in Section 5-4, for example, we also describe how synaptic plasticity serves as the basis of learning. Later, in Section 14-4, we expand on plasticity as we explore learning and memory.

Emphasis on Evolution, Genetics and Epigenetics, Plasticity, and Psychopharmacology

To convey the excitement of neuroscience as researchers currently understand it, we interweave evolution, genetics and epigenetics, neural plasticity, and psychopharmacology throughout the book.

We address nervous-system evolution in depth in Chapters 1 and 2 and return to this perspective—neuroscience in an evolutionary context—in almost every chapter. Examples range from the evolution of the synapse in Section 5-1 to the evolution of visual pathways in Section 9-2, from ideas about how natural selection might promote overeating in Section 12-5 to evolutionary theories of sleeping and dreaming in Section 13-3, and from the evolution of sex differences in spatial cognition and language in Section 15-5 to links between our evolved reactions to stress and the development of anxiety disorders in Section 16-4.

We introduce the foundations of genetic and epigenetic research in Sections 1-3 and 2-1 and begin to elaborate on them in Section 3-3. Chapter 5 includes discussions of metabotropic receptors and DNA and of learning and genes. The interplay of genes and drug action is integral to Chapter 6, as is the role of genes and gene methylation in development to Chapter 8. Section 9-4 explains the genetics of color vision, and the genetics of sleep disorders anchors Section 13-6. Section 14-4 now includes the role of epigenetics in memory. Section 16-1 considers the role of genetics in understanding the causes of behavioral disorders.

Chapter 6 investigates drugs and behavior, a topic we revisit often through the book. You will find coverage of drugs and information transfer in Section 4-3, drugs and cellular communication in Section 5-3, drugs and motivation in Section 12-6, drugs and sleep disorders in Section 13-6, neuronal changes with drug use in Section 14-4, and drugs as treatments for a range of disorders in Section 16-4.

Neural plasticity continues as a hallmark of the book. We introduce the concept in Section 1-5, define it in Section 2-1, develop it in Section 2-6, and expand on it throughout, elaborating on the Basic Principles of Brain Plasticity at the conclusion of Section 14-4.

Scientific Background Provided

We describe the journey of discovery that is neuroscience in a way that students just beginning to study the brain and behavior can understand. The illustrated Experiments help students visualize the scientific method and how scientists think. We developed The Basics features to address the fact that this course can sometimes be daunting, largely because understanding brain function requires information from all the basic sciences. These encounters with basic science can prove both a surprise and a shock to introductory students, who often come to the course without the necessary background.

Our approach provides all the background students require to understand an introduction to brain science. The Basics features in Chapters 1 and 2 address the relevant evolutionary and anatomical background. In Chapter 3, The Basics provides a short introduction to chemistry before describing the chemical activities of the brain and, in Chapter 4, to electricity before exploring the brain's electrical activity. Readers already comfortable with the material can easily skip it; less experienced readers can learn it.

Similarly, we review such basic psychological facts as stages of behavioral development in Chapter 8 and the forms of learning and memory in Chapter 14. With this background students can tackle brain science with greater confidence. Students in social science disciplines often remark on the amount of biology and chemistry in the book, whereas an equal number of students in biological sciences remark on the amount of psychology. More than half the students enrolled in our Bachelor of Science in Neuroscience program have switched from biochemistry or psychology majors after taking this course. We must be doing something right!

Finally, Chapter 7 showcases the range of methods behavioral neuroscientists use to study brain and behavior—traditional methods and such cutting-edge techniques as optical tomography and resting-state fMRI. Expanded discussions of techniques appear where appropriate, especially in Research Focus features. Examples include Research Focus 3-2, "Brainbow: Rainbow Neurons"; Research Focus 4-3, "Optogenetics and Light-Sensitive Channels"; and Research Focus 16-1, "Posttraumatic Stress Disorder," which includes treatments based on virtual-reality exposure therapies.

Clinical Focus Maintained

We repeatedly emphasize that neuroscience is a human science. Everything in this book is relevant to our lives, and everything in our lives is relevant to neuroscience. Understanding neuroscience helps us understand how we learn, how we develop, and how we can help people who suffer brain and behavioral disorders. Knowledge of how we learn, how we develop, and the symptoms that people suffering brain and behavioral disorders display provides insights into neuroscience.

Clinical material also helps to make neurobiology particularly relevant to students who are going on to careers in psychology, social work, or other professions related to mental health, as well as to students pursuing careers in the biological sciences. We integrate clinical information throughout the text and Clinical Focus features, and we expand on it in Chapter 16, the book's capstone, as well.

In all four editions of *An Introduction to Brain and Behavior,* the placement of some topics is novel relative to traditional treatments. We include brief descriptions of brain diseases close to discussions of basic associated processes, as exemplified in the

FOURTH EDITION UPDATES CHAPTER-BY-CHAPTER

CHAPTER 8: DEVELOPMENT

UPDATED §8-2: how **gene (DNA) methylation** alters gene expression during brain development.

NEW Clinical Focus 8-2: Autism Spectrum Disorder.

NEW Figure 8-18 maps frontal-lobe development in a new discussion that points up frontal sensitivity to epigenetic influences.

UPDATED §8-4: benefits to infants of tactile stimulation beyond bonding.

NEW Figure 8-31 charts onset of behavioral disorders during adolescence.

CHAPTER 9: SENSATION, PERCEPTION, AND VISION

NEW in The Basics: the worldwide increase in myopia.

NEW in §9-2: the **retinohypothalamic tract.**

NEW Figure 9-19: temporal- and parietal-lobe areas specialized.

UPDATED discussion in §9-4: Seeing Color.

CHAPTER 10: AUDITION

NEW Research Focus 10-2: Seeing with Sound.

NEW research in §10-3 on the ventral and dorsal auditory streams.

NEW coverage: music as therapy concludes §10-4.

CHAPTER 11: MOVEMENT AND SOMATOSENSATION

UPDATED Research Focus 11-1: the promise of **neuroprosthetics.**

NEW The Basics: Relating the Somatosensory and Motor Systems, in §11-1.

CONDENSED §11-2: coverage of motor system organization and skilled movement, including plasticity in the motor system.

FOURTH EDITION UPDATES CHAPTER-BY-CHAPTER

- **CHAPTER 12: EMOTION, MOTIVATION, CHEMICAL SENSES**

NEW §12-2 is devoted to taste and smell; §12-4: neuroanatomy of motivated and emotional behaviors integrated to streamline coverage.

UPDATED Clinical Focus 12-4: Weight-Loss Strategies charts foods most likely to lead to weight gain or loss over time.

UPDATED §12-5: epigenetic influences on brain organization.

NEW Figure 12-19: prefrontal subregions important in motivated and emotional behavior.

NEW Figure 12-27: bilateral activity in the male hypothalamus during sexual arousal.

NEW Figure 12-30: enhanced connectivity in addiction-related limbic and prefrontal networks imaged by resting-state fMRI.

- **CHAPTER 13: SLEEP**

NEW Clinical Focus 13-1: disrupting the biological clock contributes to **metabolic syndrome**.

NEW Figure 13-6: path of the **retinohypothalamic tract**.

NEW coverage in §13-2: genetic and epigenetic influences on **chronotype**, biorhythmic influences on cognitive and emotional behavior.

UPDATED Research Focus 13-3 diagrams the cellular clock that paces SCN function.

NEW coverage in §13-4: sleep's possible roles in memory.

- **CHAPTER 14: LEARNING AND MEMORY**

NEW research in §14-3: memory **consolidation** and **reconsolidation**.

UPDATED §14-4 includes **LTP** and **LTD**, epigenetics of memory, **metaplasticity**.

NEW Figure 14-20 images hippocampal neurogenesis among London taxi drivers.

integrated coverage of Parkinson's disease through Chapter 5, "How Do Neurons Communicate and Adapt?" This strategy helps first-time students repeatedly forge close links between what they are learning and real-life issues.

In this new edition, the range of disorders we cover has expanded to nearly 150, all cross-referenced in the Index of Disorders inside the book's front cover. Chapter 16 expands on the nature of neuroscience research and the multidisciplinary treatment methods for neurological and psychiatric disorders described in preceding chapters, and it includes a discussion of causes and classifications of abnormal behavior.

Another area of emphasis is questions that relate to the biological bases of behavior. For us, the excitement of neuroscience lies in understanding how the brain explains what we do, whether it is talking, sleeping, seeing, or learning. Readers will therefore find nearly as many illustrations about behavior as illustrations about the brain. This emphasis on explaining the biological foundation of behavior is another reason that we include both Clinical Focus and Research Focus features throughout the text.

Abundant Chapter Pedagogy

In addition to the innovative teaching devices described so far, numerous in-text pedagogical aids adorn every chapter, beginning with an outline and an opening Focus feature that draws students into the chapter's topic. Clinical, Research, and Comparative Focus features dot each chapter to connect brain and behavior to relevant clinical or research experience. Within the chapters, boldface key terms are defined in the margins to reinforce their importance, margin notes link topics together, and end-of-section Review self-tests help students check their grasp of major points.

Each chapter ends with a Summary—several include summary tables or illustrations to help students visualize or review concepts—and a list of Key Terms, each referenced to the page number on which the term is defined. As in the Third Edition, additional resources can be found on the Companion Web Site at www.worthpublishers.com/kolbintro4e. Other material on the Web site will broaden students' understanding of chapter topics.

Superb Visual Reinforcement

You can see our most important learning aid simply by paging through the book: an expansive and, we believe, exceptional set of illustrations that, hand in hand with our words, describe and illuminate the nervous system. On the advice of instructors and readers, important anatomical diagrams have been enlarged to ease perusal, and we have retained and added new "applications" photos that range from Tweeting in Section 2-3 to a dance class for Parkinson's patients in Section 5-3 to a seniors' bridge game in Section 16-3.

Illustrations are consistent from chapter to chapter and reinforce one another. We consistently color-code diagrams that illustrate each aspect of the neuron, depict each structural region in the brain, and demark the divisions of the nervous system. We include many varieties of micrographic images to show what a particular neural structure actually looks like. These illustrations and images are included on our PowerPoint presentations and integrated as labeling exercises in our Study Guide and Testing materials.

Teaching Through Metaphors, Examples, and Principles

If a textbook is not enjoyable, it has little chance of teaching well. We heighten students' interest through abundant use of metaphors and examples. Students read about patients whose brain injuries are sources of insight into brain function, and we examine car engines, robots, and prehistoric flutes for the same purpose. Frequent comparative biology examples, illustrated Experiments, and representative Comparative Focus features help students understand how much we humans have in common with creatures as far distant from us as sea slugs.

We also facilitate learning by reemphasizing main points and by distilling sets of principles about brain function that can serve as a framework to guide students' thinking. Thus, Section 2-6 introduces ten key principles that explain how the various parts of the nervous system work together. Section 14-4 summarizes seven guiding principles of neuroplasticity. These principles form the basis of many discussions throughout the book, and marginal notes remind readers when they encounter the principles again—as well as where to review them in depth.

Big-Picture Emphasis

One challenge in writing an introductory book on any topic is deciding what to include and what to exclude. We organize discussions to focus on the bigger picture—a focus exemplified by the ten principles of nervous-system function introduced in Section 2-6 and echoed throughout the book. Any set of principles may be a bit arbitrary; nevertheless, it gives students a useful framework for understanding the brain's activities.

In Chapters 8 through 16 we tackle behavioral topics in a more general way than most contemporary books do. In Chapter 12, for instance, we revisit experiments and ideas from the 1960s to understand why animals behave as they do then we consider emotional and motivated behaviors as diverse as eating and anxiety attacks in humans. In Chapter 14, the larger picture of learning and memory is presented alongside a discussion of recovery from traumatic brain injury.

This broad focus helps students grasp the big picture that behavioral neuroscience is all about. While broadening our focus requires us to leave out some details, our experience with students and teachers through the three earlier editions confirms that discussion of the larger problems and issues in brain and behavior is of greater interest to students, especially those who are new to this field, and is more often remembered than are myriad details without context.

As in preceding editions, we are selective in our citation of the truly massive literature on the brain and behavior because we believe that numerous citations can disrupt the text's flow and distract students from the task of mastering concepts. We provide citations to classic works by including the names of the researchers and by mentioning where the research was performed. In areas where controversy or new breakthroughs predominate, we also include detailed citations to papers (especially reviews) from the years 2010–2013 when possible. An end-of-book References section lists all the literature used in developing the book, reflecting the addition of more than 200 new citations in this new edition and elimination of other, now superseded, research.

Acknowledgments

As in past editions of this text and *Fundamentals of Human Neuropsychology,* we have a special debt to Barbara Brooks, our development editor. She has learned how to extract the best from each of us by providing a firm guiding hand to our thinking. While we don't always initially agree with her (or our wives), we have learned to listen carefully and discover that she is usually right (as they are). Also, because we have now worked together on multiple editions, each of us has learned something of how the others think. Barbara's sense of humor is infectious and her commitment to excellence has again left a strong imprint on the entire book. Once again thank you, Barbara. You make this whole experience fun—believe it or not!

FOURTH EDITION UPDATES CHAPTER-BY-CHAPTER

CHAPTER 15: COGNITION

NEW Research Focus 15-1: experiment conducted with split-brain patients.

NEW Figure 15-2: prefrontal subregions important in cognition.

UPDATED Research Focus 15-3: evidence on mirror-neuron dysfunction in autism.

NEW in §15-3: mapping the **brain connectome**, the emerging fields of **social neuroscience** and **neuroeconomics**.

NEW Figures 15-17 and 15-18: sex differences in brain architecture.

UPDATED §15-6: efficiency of cortical networks and epigenetic factors in individual differences in intelligence.

CHAPTER 16: DISORDERS AND DYSFUNCTION

UPDATES chapterwide on epigenetic factors and neuroplasticity.

UPDATED Research Focus 16-1: increasing effectiveness of **virtual-reality exposure therapies**.

NEW Figure 16-10: healthy adult brain and brain shriveled by Alzheimer's disease.

NEW Clinical Focus 16-3: Concussion images **chronic traumatic encephalopathy**.

UPDATED §16-5 concludes with some pros and cons of **cognitive enhancement**.

We must sincerely thank the many people who contributed to the development of this edition. The staff at Worth Publishers is remarkable and makes revisions a joy to do. We thank our sponsoring editor Daniel DeBonis, assistant editor Nadina Persaud, our long-time project editor Georgia Lee Hadler, and our production manager Sarah Segal. Our manuscript editor Penelope Hull ensured the clarity and consistency of the text. Kate Scully and her team at Northeastern Graphic ensured that the page proofs were set properly and included the necessary revisions. We thank art director Babs Reingold for a striking cover and Charles Yuen and Lyndall Culbertson for a fresh, inviting, accessible new interior design. Thanks also to Cecilia Varas for coordinating photo research and to Julie Tesser, who found photographs and other illustrative materials that we would not have found on our own. We remain indebted to the illustrators at Dragonfly Media for their excellent work in creating new illustrations.

Our colleagues, too, have helped in the development of every edition. For their contributions to the Fourth Edition, we are especially indebted to the reviewers who provided extensive comments on selected chapters and illustrations: Mark Basham, *Regis University*; Pam Costa, *Tacoma Community College*; Russ Costa, *Westminster College*; Renee Countryman, *Austin College*; Kristen D'Anci, *Salem State University*; Trevor James Hamilton, *Grant MacGewn University*; Christian Hart, *Texas Woman's University*; Matthew Holahan, *Carleton University*; Chris Jones, *College of the Desert*; Joy Kannarkat, *Norfolk State University*; Jennifer Koontz, *Orange Coast College*; Kate Makerec, *William Paterson University of New Jersey*; Daniel Montoya, *Fayatteville State University*; Barbara Oswald, *Miami University of Ohio*; Gabriel Radvansky, *University of Notre Dame*; Jackie Rose, *Western Washington University*; Steven Schandler, *Chapman University*; Maharaj Singh, *Marquette University*; Manda Williamson, *University of Nebraska—Lincoln.*

Likewise, we continue to be indebted to the colleagues who provided extensive comments on selected chapters and illustrations during the development of the Third Edition: Chana Akins, *University of Kentucky*; Michael Anch, *Saint Louis University*; Maura Mitrushina, *California State University, Northridge*; Paul Wellman, *Texas A&M University*; and Ilsun White, *Morehead State University.* The methods chapter was new to the Third Edition and posed the additional challenge of taking what easily could read like a seed catalogue and making it engaging to readers. We therefore are indebted to Margaret G. Ruddy, *The College of New Jersey,* and Ann Voorhies, *University of Washington,* for providing extensive advice on the initial version of Chapter 7.

We'd also like to thank the reviewers who contributed their thoughts to the Second Edition: Barry Anton, *University of Puget Sound*; R. Bruce Bolster, *University of Winnipeg*; James Canfield, *University of Washington*; Edward Castañeda, *University of New Mexico*; Darragh P. Devine, *University of Florida*; Kenneth Green, *California State University, Long Beach*; Eric Jackson, *University of New Mexico*; Michael Nelson, *University of Missouri, Rolla*; Joshua S. Rodefer, *University of Iowa*; Charlene Wages, *Francis Marion University*; Doug Wallace, *Northern Illinois University*; Patricia Wallace, *Northern Illinois University*; and Edie Woods, *Madonna University.* Sheri Mizumori, *University of Washington,* deserves special thanks for reading the entire manuscript for accuracy and providing fresh ideas that proved invaluable.

Finally, we must thank our tolerant wives for putting up with sudden changes in plans as chapters returned from Barbara or Penny with hopes for quick turnarounds. We also thank our colleague Robbin Gibb, who uses the book and has provided much feedback, in addition to our graduate students, technicians, and postdoctoral fellows who kept our research programs moving forward when were engaged in revising the book.

Bryan Kolb and Ian Q. Whishaw

An Introduction to Brain and Behavior, Fourth Edition, features a wide array of supplemental materials designed exclusively for students and teachers of the text. For more information about any of the items, please visit Worth Publishers' online catalog at www.worthpublishers.com.

For Students

NEW! ONLINE NEUROSCIENCE TOOL KIT **Available Spring 2013 at www.worthpublishers.com/ntk** The Neuroscience Tool Kit is a powerful Web-based tool for learning the core concepts of behavioral neuroscience—by witnessing them firsthand. These 30 interactive tutorials allow students to see the nervous system in action via dynamic illustrations, animations, and models that demystify the neural mechanisms behind behavior. Videos taken from actual laboratory research enhance student understanding of how we know what we know, and carefully crafted multiple-choice questions make it easy to assign and assess each activity. Based on Worth Publishers' groundbreaking *Foundations of Behavioral Neuroscience CD-ROM,* the Neuroscience Tool Kit is a valuable accompaniment to any biopsychology course.

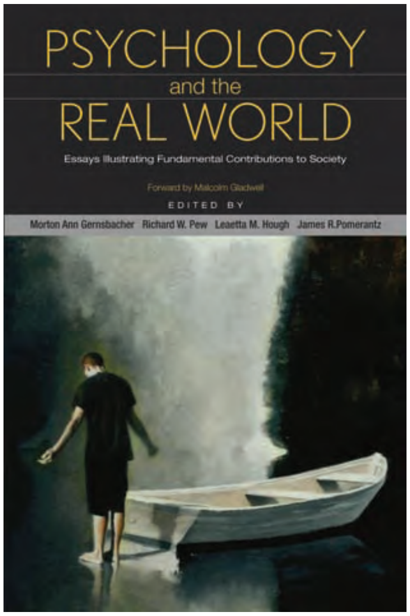
AN INTRODUCTION TO BRAIN AND BEHAVIOR, FOURTH EDITION, COMPANION WEB SITE www.worthpublishers.com/kolbintro4e Created by Joe Morrissey of Binghamton University, the companion Web site is an online educational setting for students that provides a virtual study guide, 24 hours a day, 7 days a week. Best of all, the resources are free and do not require any special access codes or passwords. Tools on the site include chapter outlines; learning objectives; interactive flashcards; research exercises; selections from PsychSim 5.0 by Thomas Ludwig, Hope College; and online quizzes with immediate feedback and instructor notification.

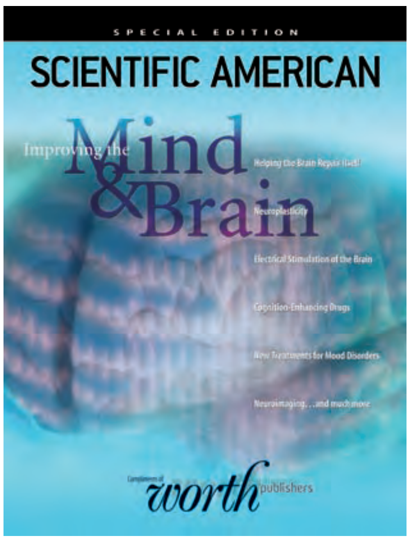
For the instructor, the site offers access to a quiz gradebook for viewing student results, a syllabus posting service, lecture slides, illustration slides, electronic versions of illustrations in the book, and links to additional tools including course cartridges for Blackboard, WebCT, Angel, Desire2Learn, and others.

REVISED! STUDY GUIDE FOR *AN INTRODUCTION TO BRAIN AND BEHAVIOR* Written by Terrence J. Bazzett of the State University of New York at Geneseo, the revised Study Guide is carefully crafted to help students master each chapter of *An Introduction to Brain and Behavior,* Fourth Edition. To aid learning and retention, the Study Guide includes a review of key concepts and terms, practice tests, short-answer questions, illustrations for identification and labeling, Internet activities, and crossword puzzles. In one of the most difficult courses in psychology, the Study Guide is a great help to students at all levels.

COURSESMART E-BOOK A complete electronic version of *An Introduction to Brain and Behavior,* Fourth Edition, can be previewed and purchased at www.coursesmart.com. Students can choose to view the CourseSmart e-Book online or download it to a personal computer or a portable media player such as a smart phone or iPad. This flexible, easy-to-use format makes the text more portable than ever before!

PSYCHOLOGY AND THE REAL WORLD: ESSAYS ILLUSTRATING FUNDAMENTAL CONTRIBUTIONS TO SOCIETY A superb collection of essays by major researchers describing their landmark studies. Published in association with the not-for-profit FABBS Foundation, this engaging reader includes Bruce McEwen's work on the neurobiology of stress





and adaptation, Elizabeth Loftus's own reflections on her study of false memories, and Daniel Wegner on his study of thought suppression. A portion of the proceeds is donated to FABBS to support societies of cognitive, psychological, behavioral, and brain sciences.

IMPROVING THE MIND AND BRAIN: A* SCIENTIFIC AMERICAN *SPECIAL ISSUE On request, this reader is free of charge when packaged with the textbook. This single-topic issue from *Scientific American* magazine features the latest findings from the most distinguished researchers in the field.

Worth Publishers is pleased to offer cost-saving packages of *An Introduction to Brain and Behavior,* Fourth Edition, with our most popular supplements. Below is a list of some of the most popular combinations available for order through your local bookstore.

Hardcover Text & Neuroscience Tool Kit Access Card
ISBN-10: 1464143676

Hardcover Text & Study Guide
ISBN-10: 1464143641

Hardcover Text & *Improving the Mind and Brain: A* Scientific American *Special Issue*
ISBN-10: 1464143668

Hardcover Text & *Psychology and the Real World*
ISBN-10: 1464145180

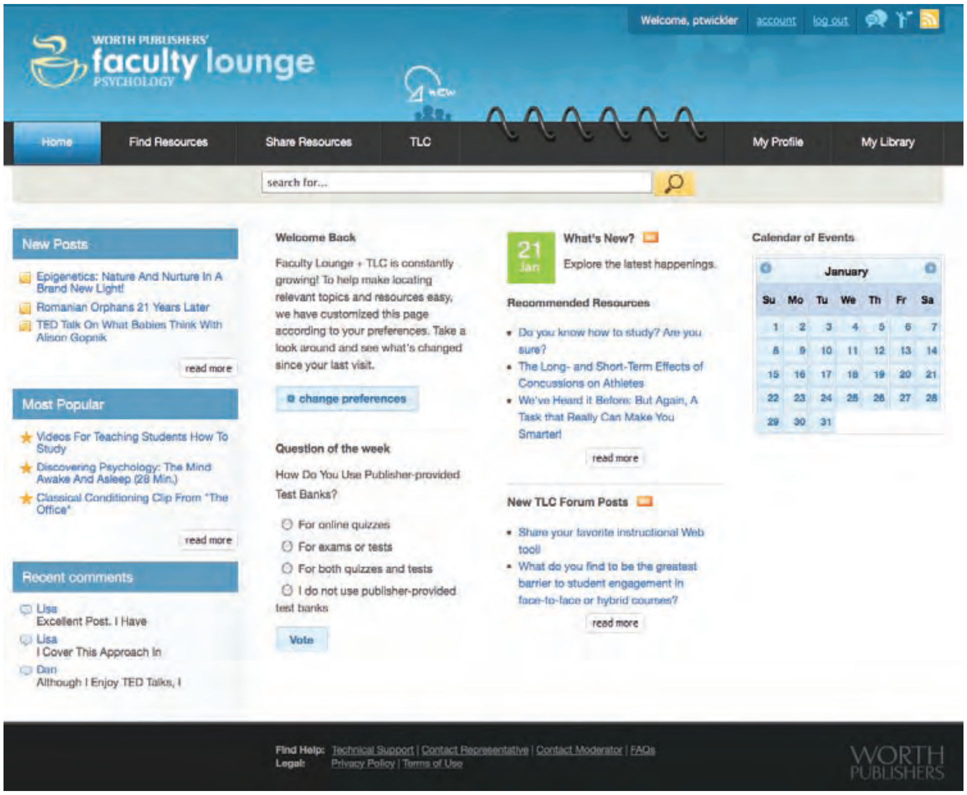
For Instructors

REVISED! INSTRUCTOR'S RESOURCES Revised by Manda Williamson, University of Nebraska—Lincoln, this invaluable tool for new and experienced instructors alike, the resources include chapter-by-chapter learning objectives and chapter overviews, detailed lecture outlines, thorough chapter summaries, chapter key terms, in-class demonstrations and activities, springboard topics for discussion and debate, ideas for research and term-paper projects, homework assignments and exercises, and suggested readings from journals and periodicals. Course-planning suggestions and a guide to videos and Internet resources also are included. The Instructor's Resources can be downloaded from the Companion Web Site at www.worthpublishers.com/kolbintro4e.

NEW! FACULTY LOUNGE Faculty Lounge is an online forum provided by Worth Publishers where instructors can find and share favorite teaching ideas and materials, including videos, animations, images, lecture slides, news stories, articles, Web links, and in-class activities. Sign up to browse the site or upload your favorite materials for teaching psychology at http://psych.facultylounge.worthpublishers.com.

Assessment Tools

DIPLOMA COMPUTERIZED TEST BANK Prepared by Christopher Striemer of Grant MacEwan University, the revised Test Bank includes a battery of more than 1300 multiple-choice and short-answer test questions as well as diagram exercises—500 of which are new. Each item is keyed to the page in the textbook on which the answer can be found. All the questions have been thoroughly reviewed and edited for accuracy and clarity. The Test Bank is available on a dual-platform CD-ROM. Instructors are guided step-by-step through the process of creating a test and can quickly add,



edit, scramble, or resequence items. The Test Bank will also allow you to export into a variety of formats that are compatible with many internet-based testing products. For more information on Diploma, please visit www.wimba.com/products/diploma.

ONLINE QUIZZES The Companion Web Site at www.worthpublishers.com/kolbintro4e features two multiple-choice quizzes to accompany each chapter of the text. Students can take each quiz multiple times and receive instant feedback. Instructors can then access student results in the online gradebook and view the results by quiz, student, or question, or they can obtain weekly results by email.

Presentation

ILLUSTRATION SLIDES AND LECTURE SLIDES Available at www.worthpublishers.com/kolbintro4e, these slides either can be used directly or customized to fit the needs of your course. There are two sets of slides for each chapter. One set features all the figures, photos, and tables, and the other features main points of the chapter with selected figures and illustrations.

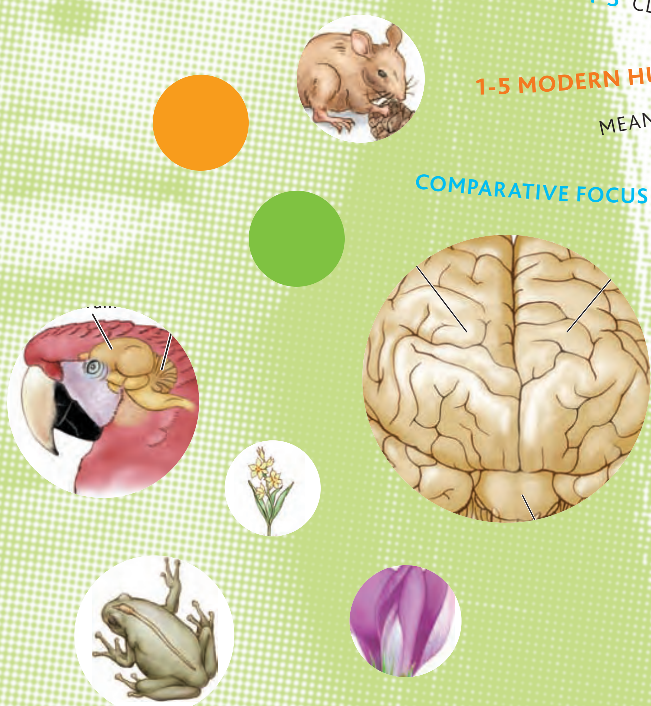
Video

WORTH PUBLISHERS' NEUROSCIENCE VIDEO COLLECTION Edited by Ronald J. Comer of Princeton University and available on DVD, this video collection consists of dozens of short video segments to enhance the biopsychology classroom and taken from clinical documentaries, television news reports, archival footage, and other sources. Each segment has been created to bring a lecture to life, engaging students and enabling them to apply neuroscience theory to the real world. This collection offers powerful and memorable demonstrations of the links between the brain and behavior, neuroanatomical animations, cutting-edge neuroscience research, brain assessment in action, important historical events, interviews, and a wide sampling of brain phenomena and brain dysfunction. A special cluster of segments reveals the range of research methods used to study the brain. The accompanying Faculty Guide (available at www.worthpublishers.com/kolbintro4e) offers a description of each segment so that instructors can make informed decisions about how to best use the videos.

COURSE MANAGEMENT The various resources for this textbook are available in the appropriate format for users of Blackboard, WebCT, Angel, Desire2Learn, and other systems. Course outlines, prebuilt quizzes, links, and activities are included, eliminating hours of work for instructors. For more information, please visit our Web site at www.macmillanhighered.com/lms.

CHAPTER 1

What Are the Origins of Brain and Behavior?



CLINICAL FOCUS 1-1

Living with Traumatic Brain Injury

Fred Linge, a clinical psychologist with a degree in brain research, wrote this description 12 years after his injury occurred:

> In the second it took for my car to crash head-on, my life was permanently changed, and I became another statistic in what has been called "the silent epidemic."
>
> During the next months, my family and I began to understand something of the reality of the experience of head injury. I had begun the painful task of recognizing and accepting my physical, mental, and emotional deficits. I couldn't taste or smell. I couldn't read even the simplest sentence without forgetting the beginning before I got to the end. I had a hair-trigger temper that could ignite instantly into rage over the most trivial incident. . . .

Two years after my injury, I wrote a short article: "What Does It Feel Like to Be Brain Damaged?" At that time, I was still intensely focusing on myself and my own struggle. (Every head-injured survivor I have met seems to go through this stage of narcissistic preoccupation, which creates a necessary shield to protect them from the painful realities of the situation until they have a chance to heal.) I had very little sense of anything beyond the material world and could only write about things that could be described in factual terms. I wrote, for example, about my various impairments and how I learned to compensate for them by a variety of methods.

At this point in my life, I began to involve myself with other brain-damaged people. This came about in part after the publication of my article. To my surprise, it was reprinted in many different publications, copied, and handed out to thousands of survivors and families. It brought me an enormous outpouring of letters, phone calls, and personal visits that continue to this day. Many were struggling as I had struggled, with no diagnosis, no planning, no rehabilitation, and most of all, no hope. . . . The catastrophic effect of my injury was such that I was shattered and then remolded by the experience, and I emerged from it a profoundly different person with a different set of convictions, values, and priorities. (Linge, 1990)

AP/Wide World Photos

AP/Wide World Photos

(*Left*) U.S. Representative Gabrielle Giffords (D-AZ) reenacts her swearing-in with House Speaker John Boehner in January 2011, days before a gunshot through the left side of her brain left her near death. (*Right*) One year later in Tucson, Rep. Giffords and her husband, former astronaut Mark Kelly, attend a candlelight vigil for all those who were shot, including the six who died. Giffords had regained limited speech, partly with the help of singing therapy, but mobility on her right side remained limited. Two weeks later she resigned her House seat to concentrate on recovering from the traumatic brain injury.

1-1 Neuroscience in the Twenty-First Century

In the years after his injury, Fred Linge made a journey. Before the car crash, he gave little thought to the relation between his brain and his behavior. After the crash, adapting to his injured brain and behavior dominated his life. On that journey he had to learn about his brain, he had to relearn many of his old skills, and he had learn to compensate for the impairments that his changed brain imposed on him.

The purpose of this book is to take *you* on a journey toward understanding the link between brain and behavior: how the brain is organized to create behavior. Evidence comes from studying three sources: (1) the evolution of brain and behavior in diverse animal species, (2) how the brain is related to behavior in normal people, and (3) how the brain changes in people who suffer brain damage or other brain abnormalities. The knowledge emerging from these lines of study is changing how we think about ourselves, how we structure education and our social interactions, and how we aid those with brain injury, disease, and disorder.

On our journey, we will learn about ourselves. We will learn how the brain stores and retrieves information, why we engage in the behaviors we engage in, and how we are able to read the lines on this page and generate ideas and thoughts. The coming decades will be exciting times for the study of brain and behavior. They will offer an opportunity for us to broaden our understanding of what makes us human.

We will marvel at the potential for future discoveries. We will begin to understand how genes control neural activity. The development of new imaging techniques will reveal how our own brains think. One day, we will be able to arrest the progress of brain disease. One day, we will be able to stimulate processes of repair in malfunctioning brains. One day, we will be able to make artificial brains that extend the functions of our own brains. One day, we will understand ourselves and other animals.

cerebrum (forebrain) Major structure of the forebrain that consists of two virtually identical hemispheres (left and right) and is responsible for most conscious behavior.

hemisphere Literally, half a sphere, referring to one side of the cerebrum.

Why Study Brain and Behavior?

The *brain* is a physical object, a living tissue, a body organ. *Behavior* is action, momentarily observable, but fleeting. Brain and behavior differ greatly but are linked. They have evolved together: one is responsible for the other, which is responsible for the other, which is responsible for the other, and so on and on. There are three reasons for linking the study of brain to the study of behavior:

1. *How the brain produces behavior is a major unanswered scientific question.* Scientists and students study the brain for the purpose of understanding humanity. Understanding brain function will allow improvements in many aspects of our world, including educational systems, economic systems, and social systems. Many chapters in this book touch on the relation between psychological questions related to brain and behavior and philosophical questions related to humanity. For example, in Chapters 14 and 15, we address questions related to how we become conscious, how we speak, and how we remember.
2. *The brain is the most complex living organ on Earth and is found in many different groups of animals.* Students of the brain want to understand its place in the biological order of our planet. Chapter 1 describes the basic structure and evolution of brains, especially the human brain, Chapter 2 surveys its structures and functions, and Chapters 3 through 5 describe the functioning of brain cells—the building blocks of the brains of all animals.
3. *A growing list of behavioral disorders can be explained and cured by understanding the brain.* Indeed, more than 2000 disorders may in some way be related to brain abnormalities. As indexed inside the front cover of this book, we detail relations between brain disorders and behavioral disorders in every chapter, especially in the "Focus" features.

None of us can predict the ways in which knowledge about the brain and behavior may prove useful. A former psychology major wrote to tell us that she took our course because she was unable to register in a preferred course. She felt that, although our course was interesting, it was "biology, not psychology." After graduating and getting a job in a social service agency, she has found to her delight that an understanding of the links between brain and behavior is a source of insight into the disorders of many of her clients and the treatment options for them.

A series of illustrated Experiments appears through the book to reveal how neuroscientists conduct research. Section 7-7 frames the debates on the benefits and the ethics of conducting research using nonhuman animals.

What Is the Brain?

For his postgraduate research, our friend Harvey chose to study the electrical activity given off by the brain. He said that he wanted to live on as a brain in a bottle after his body died. He expected that his research would allow his bottled brain to communicate with others who could "read" his brain's electrical signals. Harvey mastered the techniques of brain electrical activity but failed in his objective, not only because the goal was technically impossible but also because he lacked a full understanding of what "brain" means.

Brain is the Anglo-Saxon word for the tissue found within the skull, and it is this tissue that Harvey wanted to put into a bottle. As shown in **Figure 1-1,** the human brain comprises two major sets of structures, the cerebrum and the cerebellum. The **cerebrum** (*forebrain*), shown in Figure 1-1A, has two nearly symmetrical halves, called **hemispheres,**

Chapter 2 presents the brain's anatomical structures and functions in detail.

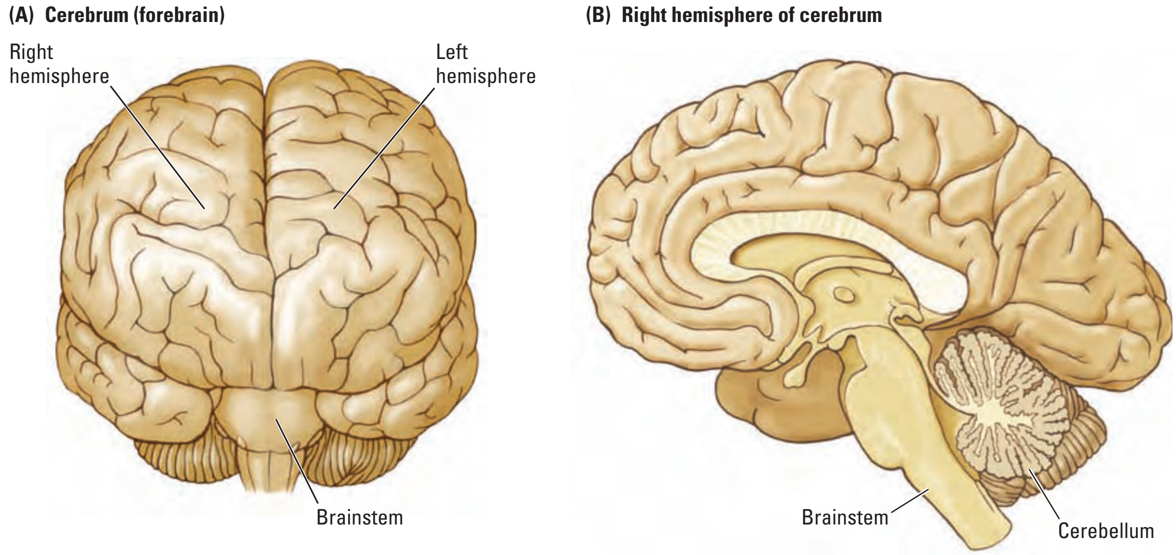
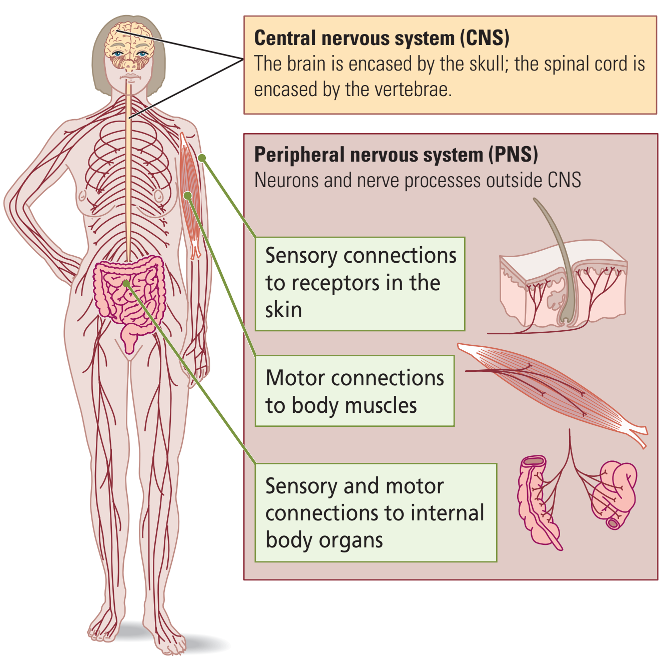


FIGURE 1-1 The Human Brain **(A)** Oriented within the human skull, the nearly symmetrical left and right hemispheres of the cerebrum shown head-on. **(B)** A cut through the middle of the brain from back to front reveals the right hemispheres of the cerebrum and cerebellum and the brainstem. The spinal cord emerges from the base of the brainstem.

one on the left and one on the right. The cerebrum is responsible for most of our conscious behaviors. It enfolds the **brainstem** (Figure 1-1B), which is responsible for most of our unconscious behaviors. The second major brainstem structure, the **cerebellum,** is specialized for learning and coordinating skilled movements.

Harvey clearly wanted to preserve not just his brain but his *self*—his consciousness, his language, and his memory. This meaning of the term *brain* refers to something other than the organ found inside the skull. It refers to the brain as that which exerts control over behavior. It is what we intend when we talk of someone smart being "a brain" or speak of the computer that guides a spacecraft as being the vessel's "brain." The term *brain,* then, signifies both the organ itself and the fact that this organ produces behavior. Why could Harvey not manage to preserve his control-exerting self inside a bottle? Read on to learn one answer to this question.

FIGURE 1-2 Major Divisions of the Human Nervous System The brain and spinal cord together make up the central nervous system. All the nerve processes radiating out beyond the brain and spinal cord and all the neurons outside the CNS connect to sensory receptors, muscles, and internal body organs to form the peripheral nervous system.



Gross Anatomy of the Nervous System

The major divisions of the human nervous system, illustrated in **Figure 1.2,** are composed of cells, as is the rest of the body, and these nerve cells, or **neurons,** most directly control behavior. Neurons in the brain communicate with one another, with sensory receptors in the skin, with muscles, and with internal body organs. Most of the connections between the brain and the rest of the body are made through the **spinal cord,** which descends from the brainstem through a canal in the backbone.

Together, the brain and spinal cord make up the **central nervous system** (CNS). The CNS is encased in bone, the brain by the skull and the spinal cord by the vertebrae. The CNS is "central" both because it is physically located to be the core of the nervous system and because it is the core structure mediating behavior. All the processes radiating out beyond the brain and spinal cord as well as all the neurons outside the brain and spinal cord constitute the **peripheral nervous system** (PNS).

To return to Harvey's brain-in-a-bottle experiment, the effect of placing the brain or even the entire CNS in a bottle would be to separate it from the PNS and thus to separate it from the sensations and movements mediated by the PNS. Could the brain function without sensory information and without the ability to produce movement?

In the 1920s, Edmond Jacobson wondered what would happen if our muscles completely stopped moving, a question relevant to Harvey's experiment. Jacobson believed that, even when we think we are entirely motionless, we still make subliminal movements related to our thoughts. The muscles of the larynx subliminally move when we "think in words," for instance, and we make subliminal movements of our eyes when we imagine or visualize a scene. So, in Jacobson's experiment, people practiced "total" relaxation and were later asked what the experience was like. They reported a condition of "mental emptiness," as if the brain had gone blank (Jacobson, 1932).

In 1957, Woodburn Heron investigated another question related to Harvey's experiment. How would the brain cope without sensory input? He examined the effects of sensory deprivation, including feedback from movement, by having each subject lie on a bed in a bare, soundproof room and remain completely still. Padded tubes covered the subjects' arms so that they had no sense of touch, and translucent goggles cut off their vision. The subjects reported that the experience was extremely unpleasant, not just because of the social isolation but also because they lost their normal focus in this situation. Some subjects even hallucinated, as if their brains were somehow trying to create the sensory experiences that they suddenly lacked. Most asked to be released from the study before it ended.

One line of research and philosophical argument, called **embodied language,** proposes that the movements we make and the movements we perceive in others are central to communication with others (Prinz, 2008). That is, we understand one another not only by listening to words but also by observing gestures and other body language, and we think not only with silent language but also with overt gestures and body language.

Findings from these lines of research suggest that (1) the CNS needs ongoing sensory stimulation from the world and from its own body's movement and (2) the brain communicates by producing movement and observing the movements of others. Thus, when we use the term *brain* to mean an intelligent, functioning organ, we should refer to an active brain that is connected to the rest of the nervous system and engaged in doing its job of producing behavior. Unfortunately for Harvey, the normal functioning of a brain in a bottle, disconnected from the PNS, seems unlikely.

What Is Behavior?

Irenäus Eibl-Eibesfeldt began his textbook *Ethology: The Biology of Behavior,* published in 1970, with the following definition: "Behavior consists of patterns in time." These patterns can be made up of movements, vocalizations, or changes in appearance, such as the facial movements associated with smiling. The expression "patterns in time" includes thinking. Although we cannot directly observe someone's thoughts, techniques exist for monitoring changes in the brain's electrical and biochemical activity that may be associated with thought. So thinking, too, is a behavior that forms patterns in time.

The behavioral patterns of animals vary enormously. Animals produce behaviors that are inherited ways of responding, and they also produce behaviors that are learned. Most behaviors probably consist of a mix of inherited and learned actions. An example of the difference between a mainly inherited behavior and a mainly learned behavior is

brainstem Central structure of the brain responsible for most unconscious behavior.

cerebellum Major structure of the brainstem specialized for coordinating and learning skilled movements. In large-brained animals, the cerebellum may also have a role in coordinating other mental processes.

neuron Specialized nerve cell engaged in information processing.

spinal cord Part of the central nervous system encased within the vertebrae (spinal column) that provides most of the connections between the brain and the rest of the body.

central nervous system (CNS) The brain and spinal cord that together mediate behavior.

peripheral nervous system (PNS) All the neurons in the body located outside the brain and spinal cord; provides sensory and motor connections to and from the central nervous system.

embodied language Hypothesis that the movements we make and the movements we perceive in others are central to communication with others.

Specialized "mirror" neurons, described in Sections 11-1 and 15-2, facilitate this nonverbal communication.

Find out more about sensory deprivation in Section 12-1, where Figure 12-1 illustrates Heron's setting for the experiments.

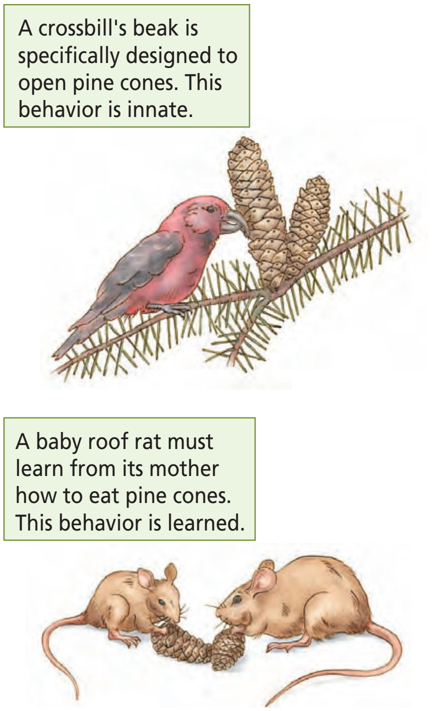


FIGURE 1-3 Innate and Learned Behaviors Some animal behaviors are largely innate and fixed (*top*), whereas others are largely learned (*bottom*). This learning is a form of cultural transmission. (*Top*) Adapted from *The Beak of the Finch* (p. 183), by J. Weiner, 1995, New York: Vintage. (*Bottom*) Adapted from "Cultural Transmission in the Black Rat: Pinecone Feeding," by J. Terkel, 1995, *Advances in the Study of Behavior, 24*, p. 122.

the contrast in the eating behavior of two different animal species—crossbills and roof rats—illustrated in **Figure 1-3.**

A crossbill is a bird with a beak that seems to be awkwardly crossed at the tips; yet this beak is exquisitely evolved to eat pinecones. If the shape of a crossbill's beak is changed even slightly, the bird is unable to eat preferred pinecones until its beak grows back. Thus, eating, for crossbills, is a fixed behavioral pattern that is inherited and does not require much modification through learning. Roof rats, in contrast, are rodents with sharp incisor teeth that appear to have evolved to cut into anything. But roof rats can eat pinecones efficiently only if they are taught to do so by an experienced mother.

The mixture of inherited and learned behaviors varies considerably in different species. Generally, animals with smaller, simpler nervous systems have a narrow range of behaviors that depend on *heredity.* Animals with complex nervous systems have more behavioral options that depend on *learning.* We humans believe that we are the animal species with the most complex nervous system and the greatest capacity for learning new responses.

But even most human behaviors involve some mixture of inheritance and learning because we humans have not thrown away our simpler nervous systems. For this reason, although human behavior depends mostly on learning, we, like other species, still possess many inherited ways of responding. The sucking response of a newborn infant is an inherited eating pattern in humans, for example.

REVIEW 1-1

Neuroscience in the Twenty-First Century

Before you continue, check your understanding.

1. One major set of brain structures, the ____________, or ____________, whose nearly symmetrical left and right ____________ enfold the ____________, connects to the spinal cord.
2. The brain and spinal cord together make up the ____________. All the nerve fibers radiating out beyond the brain and spinal cord as well as all the neurons outside the brain and spinal cord form the ____________.
3. A simple definition of behavior is any kind of movement in a living organism. All behaviors have both a cause and a function, but they vary in complexity and in the degree to which they are ____________, or automatic, and the degree to which they depend on ____________.
4. Explain the concept of *embodied language* in a statement or brief paragraph.

Answers appear at the back of the book.

1-2 Perspectives on Brain and Behavior

Returning to the central topic in the study of brain and behavior—how the two are related—we now survey three classic theories about the cause of behavior: mentalism, dualism, and materialism. Then we explain why contemporary brain investigators subscribe to the materialist view. In reviewing these theories, you will recognize that some familiar "commonsense" ideas you might have about behavior are derived from one or another of these long-standing perspectives.

Aristotle and Mentalism

The hypothesis that the mind (or soul or psyche) is responsible for behavior can be traced back more than 2000 years to ancient Greece. In classical mythology, Psyche was a mortal who became the wife of the young god Cupid. Venus, Cupid's mother, opposed his marriage to a mortal, so she harassed Psyche with almost impossible tasks.

E. Lessing/Art Resource, New York

François Gerard, *Psyche and Cupid* (1798)

Psyche performed the tasks with such dedication, intelligence, and compassion that she was made immortal, thus removing Venus's objection to her. The ancient Greek philosopher Aristotle was alluding to this story when he suggested that all human intellectual functions are produced by a person's **psyche.** The psyche, Aristotle argued, is responsible for life, and its departure from the body results in death.

Aristotle's account of behavior had no role for the brain, which Aristotle thought existed to cool the blood. To him, the nonmaterial psyche was responsible for human consciousness, perceptions, and emotions and for such processes as imagination, opinion, desire, pleasure, pain, memory, and reason. The psyche was an entity independent of the body. Aristotle's view that a nonmaterial psyche governs our behavior was adopted by Christianity in its concept of the soul and has been widely disseminated throughout the world.

Mind is an Anglo-Saxon word for "memory," and when "psyche" was translated into English, it became "mind." The philosophical position that a person's mind (psyche) is responsible for behavior is called **mentalism.** Mentalism has influenced modern behavioral science because many terms—*consciousness, sensation, perception, attention, imagination, emotion, motivation, memory,* and *volition* among them—remain in use for patterns of behavior today. Indeed, these terms are frequently used as chapter titles in contemporary psychology and neuroscience textbooks.

psyche Synonym for *mind,* an entity once proposed to be the source of human behavior.

mind Proposed nonmaterial entity responsible for intelligence, attention, awareness, and consciousness.

mentalism Explanation of behavior as a function of the nonmaterial mind.

dualism Philosophical position that holds that both a nonmaterial mind and a material body contribute to behavior.

Descartes and Dualism

In the first book on brain and behavior, René Descartes (1596–1650), a French philosopher, proposed a new explanation of behavior in which the brain played an important role. Descartes placed the seat of the mind in the brain and linked the mind to the body. In the first sentence of *Treatise on Man* (1664), he stated that mind and body "must be joined and united to constitute people."

To Descartes, most of the activities of the body and brain, such as motion, digestion, and breathing, could be explained by mechanical and physical principles. The nonmaterial mind, on the other hand, is responsible for rational behavior. Descartes's proposal that an entity called the mind directs a machine called the body was the first serious attempt to explain the role of the brain in controlling behavior.

The idea that behavior is controlled by two entities, a mind and a body, is called **dualism** (from Latin, meaning "two"). To Descartes, the mind receives information from the body through the brain. The mind also directs the body through the brain. The rational mind, then, depends on the brain both for information and to control behavior.

Descartes was also aware of the many new machines being built, including gears, clocks, and waterwheels. He saw mechanical gadgets on public display in parks. In the water gardens in Paris, one device caused a hidden statue to approach and spray water when an unsuspecting stroller walked past it. The statue's actions were triggered when the person stepped on a pedal hidden in the sidewalk. Influenced by these mechanical devices, Descartes developed mechanical principles to explain the functions of the body.

Descartes also developed a mechanical explanation of how the mind produces movement. He suggested that the mind works through a small structure in the center of the brain, the pineal body (now called the *pineal gland*), which is located beside fluid-filled cavities called *ventricles* (**Figure 1-4**). According to Descartes, the mind instructs the pineal body to direct fluid from the ventricles through nerves and into muscles. When the fluid expands the muscles, the body moves.

Descartes's dualistic theory faces many problems. It quickly became apparent to scientists that people who have damaged pineal bodies or even no pineal body at all still display normal intelligent behavior. Today, we understand that the pineal gland plays a role in behavior related to biological rhythms, but it does not govern human behavior. We now know that fluid is not pumped from the brain into muscles when they contract.

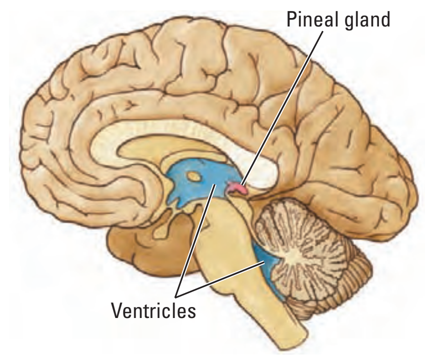


FIGURE 1-4 Dualist Hypothesis To explain how the mind controls the body, Descartes suggested that the mind resides in the pineal gland, where it directs the flow of fluid through the ventricles and into the body to investigate objects and to become informed about their properties.

Section 13-2 describes the pineal gland's function: it influences daily and seasonal biorhythms.

Placing an arm in a bucket of water and contracting the arm's muscles does not cause the water level in the bucket to rise, as it should if the volume of the muscle increased because fluid had been pumped into it. We now also know that there is no obvious way that a nonmaterial entity can influence the body, because doing so requires the spontaneous creation of energy, which violates the physical law of conservation of matter and energy.

The difficulty in Decartes's theory—how a nonmaterial mind and a physical brain might interact—has come to be called the **mind–body problem.** Nevertheless, Descartes proposed that his theory could be tested. To determine whether an organism possesses a mind, Descartes proposed the language test and the action test. To pass the language test, an organism must use language to describe and reason about things that are not physically present. The action test requires the organism to display behavior that is based on reasoning and is not just an automatic response to a particular situation. Descartes proposed that nonhuman animals and machines would be unable to pass the tests because they lack minds.

Descartes's theory of mind led to a number of unfortunate results. On the basis of it, some people argued that young children and the insane must lack minds, because they often fail to reason appropriately. We still use the expression "he's lost his mind" to describe someone who is "mentally ill." Some proponents of this view also reasoned that, if someone lacked a mind, that person was simply a machine not due normal respect or kindness. Cruel treatment of animals, children, and the mentally ill has been justified by Descartes's theory for centuries. It is unlikely that Descartes himself intended these interpretations. He was reportedly very kind to his own dog, Monsieur Grat.

Experimental research is also casting doubt on Descartes's view that only humans can pass the language and action tests. For example, studies of language in apes and other animals are partly intended to find out whether animals can describe and reason about things that are not present. Comparative Focus 1-2, "The Speaking Brain," summarizes a contemporary approach to studying language in animals. Computer specialists are also making progress on constructing robots with artificial intelligence—robots that think and remember.

Darwin and Materialism

By the mid-nineteenth century, another theory of brain and behavior emerged. This theory was **materialism**—the idea that rational behavior can be fully explained by the workings of the brain and the rest of the nervous system, without any need to refer to an immaterial mind. This perspective became prominent when supported by the evolutionary theory of Alfred Russel Wallace and Charles Darwin.

Evolution by Natural Selection

Wallace and Darwin independently arrived at the same conclusion—the idea that all living things are related. Both outlined this view in papers presented at the Linnaean Society of London in July 1858. Darwin further elaborated on the topic in his book *On the Origin of Species by Means of Natural Selection,* published in 1859. This book presented a wealth of supporting detail, which is why Darwin is regarded as the founder of modern evolutionary theory.

Both Darwin and Wallace had looked carefully at the structure of animals and at animal behavior. Despite the diversity of living animals, both men were struck by the myriad characteristics common to so many species. For example, the skeleton, muscles, and body parts of humans, monkeys, and other mammals are remarkably similar.

Such observations led first to the idea that living organisms must be related, an idea widely held even before Wallace and Darwin. But more important, these same observations led to Darwin's explanation of how the great diversity in the biological world

mind–body problem Quandary of explaining how a nonmaterial mind and a material body interact.

materialism Philosophical position that holds that behavior can be explained as a function of the brain and the rest of the nervous system without explanatory recourse to the mind.

natural selection Darwin's theory for explaining how new species evolve and how existing species change over time. Differential success in the reproduction of different characteristics (phenotypes) results from the interaction of organisms with their environment.

species Group of organisms that can interbreed.

phenotype Individual characteristics that can be seen or measured.

COMPARATIVE FOCUS 1-2

The Speaking Brain

Language is such a striking characteristic of our species that it was once thought to be a trait unique to humans. Nevertheless, evolutionary theory predicts that language is unlikely to have appeared full-blown in modern humans. Language does have antecedents in other species. Many species lacking a cerebral cortex, including fish and frogs, are capable of elaborate vocalizations, and vocalization is still more elaborate in species having a cerebral cortex, such as birds, whales, and primates. But can nonhuman animals speak?

In 1969, Beatrice and Alan Gardner taught a version of American Sign Language to a chimpanzee named Washoe, showing that nonverbal forms of language might have preceded verbal language. Sue Savage-Rumbaugh and her coworkers (1999) then taught a pygmy chimpanzee named Malatta a symbolic language called Yerkish. (The pygmy chimpanzee, or *bonobo,* is a species thought to be an even closer relative of humans than the common chimp.)

Malatta and her son Kanzi were caught in the wild, and Kanzi accompanied his mother to class. It turned out that, even though he was not specifically trained, Kanzi learned more Yerkish than his mother did. Remarkably, Kanzi also displayed clear evidence of understanding complex human speech.

While recording vocalizations made by Kanzi interacting with people and eating food, Jared Taglialatela and coworkers found that Kanzi made many sounds associated with their meanings, or semantic context. For example, various peeps were associated with specific foods. The research group also found that chimps use a "raspberry" or "extended grunt" sound in a specific context to attract the attention of others, including people.

Imaging of blood flow in the brain associated with the use of "chimpanzeeish" indicates that the same brain regions that are activated when humans speak are also activated when chimpanzees speak (Taglialatela, 2011). These findings strongly support the idea that human language has antecedents in the vocalizations and gestures of nonhuman animals.


AP Images/Great Ape Trust/dapd

Kanzi

could have evolved from common ancestry. Darwin proposed that animals have traits in common because these traits are passed from parents to their offspring.

Natural selection is Darwin's theory for explaining how new species evolve and how existing species change over time. A **species** is a group of organisms that can breed among themselves but not with members of other species. Individual organisms within any species vary extensively in their **phenotype,** the characteristics we can see or measure. No two members of the species are exactly alike. Some are big, some are small, some are fat, some are fast, some are light-colored, and some have large teeth.

Individual organisms whose characteristics best help them to survive in their environment are likely to leave more offspring than are less fit members. This unequal ability of individual members to survive and reproduce leads to a gradual change in a species' population over time, with characteristics favorable for survival in a particular habitat becoming more prevalent in succeeding generations. Natural selection is nature's equivalent of the artificial selection practiced by plant and animal breeders to produce organisms with desirable traits.

Natural Selection and Heritable Factors

Neither Darwin nor Wallace understood the basis of the great variation in plant and animal species they observed. Another scientist, the monk Gregor Mendel, discovered one principle underlying phenotypic variation and how traits are passed from parents