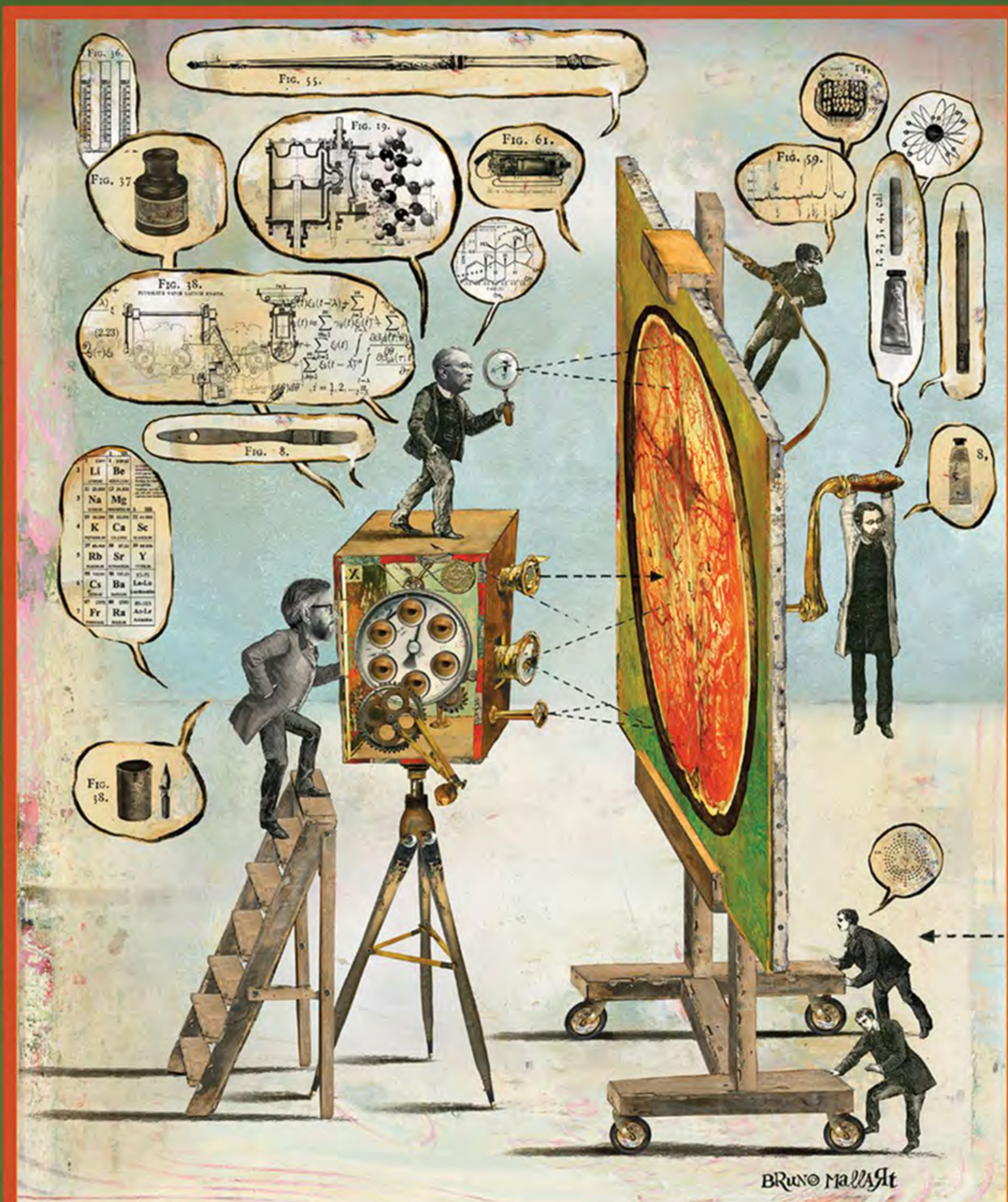
The Mind's Machine

Foundations of Brain and Behavior

FOURTH EDITION



Neil V. Watson • S. Marc Breedlove

The Mind's Machine

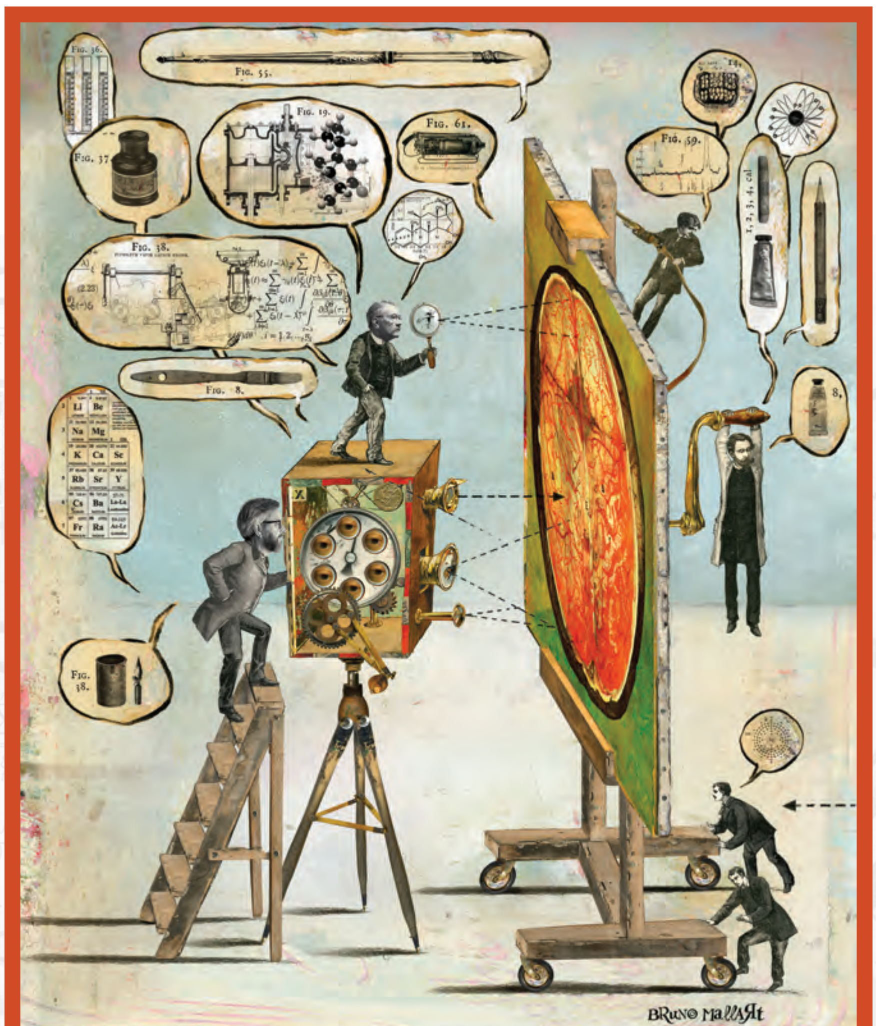
Foundations of Brain and Behavior

FOURTH EDITION

The Mind's Machine

Foundations of Brain and Behavior

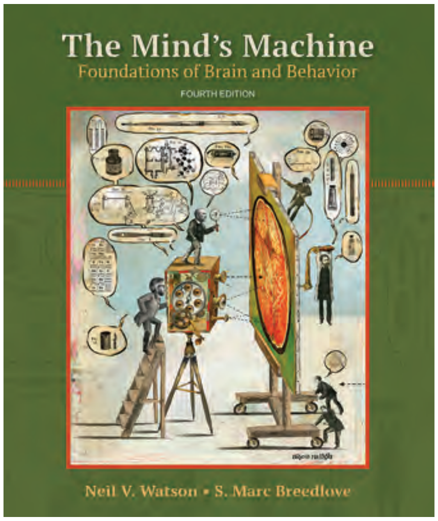
FOURTH EDITION



Neil V. Watson • **S. Marc Breedlove**
Simon Fraser University *Michigan State University*

SINAUER ASSOCIATES

NEW YORK OXFORD
OXFORD UNIVERSITY PRESS



About the Cover and Chapter Opener Images

Bruno Mallart is one of the most talented European artists, his work having appeared in some of the world's premier publications: The New York Times, The Wall Street Journal, and the New Scientist, to name a few. A freelance illustrator since 1986, Mallart first worked for several children's book publishers and advertising agencies, using a classical realistic watercolor and ink style. Some years later he began working in a more imaginative way, inventing a mix of drawing, painting, and collage. His work speaks of a surrealistic and absurd world and engages the viewer's imagination and sense of fun. Despite the recurring use of the brain in his art, Mallart's background is not scientific—though his parents were both neurobiologists. He uses the brain as a symbol for abstract concepts such as intelligence, thinking, feeling, ideas, and knowledge. Attracted to all that is mechanical, Mallart's art frequently includes machine parts such as gears and wheels that imply movement and rhythm. These features together, in their abstract representation, beautifully illustrate the topics discussed in *The Mind's Machine*, Fourth Edition, and even include a glimpse of Neil and Marc at work. To see more of Bruno Mallart's art, please go to his website: www.brunomallart.com.

Oxford University Press is a department of the University of Oxford. It furthers the University's objective of excellence in research, scholarship, and education by publishing worldwide. Oxford is a registered trade mark of Oxford University Press in the UK and certain other countries.

Published in the United States of America by Oxford University Press
198 Madison Avenue, New York, NY 10016, United States of America

Sinauer Associates is an imprint of Oxford University Press.

For titles covered by Section 112 of the US Higher Education Opportunity Act, please visit www.oup.com/us/he for the latest information about pricing and alternate formats.

Address editorial correspondence to:

Sinauer Associates
23 Plumtree Road
Sunderland, MA 01375 U.S.A.

Address orders, sales, license, permissions, and translation inquiries to:

Oxford University Press U.S.A.
2001 Evans Road
Cary, NC 27513 U.S.A.
Orders: 1-800-445-9714

ACCESSIBLE CONTENT Every opportunity has been taken to ensure that the content herein is fully accessible to those who have difficulty perceiving color. However, some of these Figures and activities will be less accessible to some readers due to the intrinsic nature of the colors and activities.

Library of Congress Cataloging-in-Publication Data

Names: Watson, Neil V. (Neil Verne), 1962- author. | Breedlove, S. Marc, author.

Title: The mind's machine : foundations of brain and behavior / Neil V. Watson, Simon Fraser University, S. Marc Breedlove, Michigan State University.

Description: Fourth edition. | New York, NY : Sinauer Associates/Oxford University Press, 2021. | Includes bibliographical references and index. | Summary: "The Mind's Machine, introduced in 2012, was written to present the interdisciplinary topics of introductory behavioral neuroscience to students from non-science majors, to psychology, life sciences, and neuroscience. This engaging and user-friendly text brings in relevance to students of all backgrounds through coverage of contemporary research, clinical cases and experimental studies, as well as through the use of clear learning objectives and concept checks, and Acrobatiq courseware for adaptive learning integrated with interactive learning tools"-- Provided by publisher.

Identifiers: LCCN 2020030747 (print) | LCCN 2020030748 (ebook) | ISBN 9781605359731 (paperback) | ISBN 9780197542248 (epub)

Subjects: LCSH: Brain--Textbooks. | Brain--Physiology--Textbooks. | Human behavior--Physiological aspects--Textbooks. | Psychobiology--Textbooks. | Neurophysiology--Textbooks. | Neuropsychology--Textbooks.

Classification: LCC QP376 .W26 2021 (print) | LCC QP376 (ebook) | DDC 612.8/2--dc23

LC record available at https://lccn.loc.gov/2020030747

LC ebook record available at https://lccn.loc.gov/2020030748

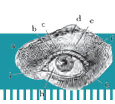
9 8 7 6 5 4 3 2 1
Printed in the United States of America

For Kathaleen Emerson and Sydney Carroll,
with affection and appreciation for their sharp eyes, calm nerves, and warm friendship.
Their fingerprints—and red pencil marks—are all over our books.

N.V.W. S. M. B.

Brief Contents

Table of Contents



6 Hearing, Balance, Taste, and Smell 176

7 Vision From Eye to Brain 210

9 Homeostasis Active Regulation of the Internal Environment 290

10 Biological Rhythms and Sleep 316

Preface

Who has not pondered their own consciousness, marveled at their many sensory experiences, or wondered how a small and lumpy organ can process so much information? Neuroscience boils down to the mind studying its own machine, an intrinsically fascinating topic that seems to fill every media channel nowadays. But another reason neuroscience is in the news so frequently is simply that it has become one of the most active branches of science. The pace of discoveries about brain and behavior has increased at an exponential rate over the last few decades, and continues to accelerate.

Every new edition of one of our books requires substantial updating because so much is happening all the time. (It's exciting, but wow, do we read a lot of reports and articles!) In fact, by far the hardest part of our job as authors lies in deciding which discoveries to include and which to (reluctantly) leave out: As the Red Queen remarked to Alice in Wonderland, "it takes all the running you can do, to keep in the same place." Our neuroscience news website (oup.com/he/watson-breedlove4e/news) boasts a collection of more than 25,000 news stories, drawn from the mainstream media, relating to the topics of this book. You can follow updates on the website, via email, or Facebook (www.facebook.com/BehavioralNeuroscience).

While we are sampling from this almost boundless scientific smorgasbord, we have to watch our weight. Our goal for *The Mind's Machine*, Fourth Edition is to introduce you to the basics of behavioral neuroscience in a way that focuses on the foundational topics in the field—with a generous sprinkling of the newest and most fascinating discoveries—and leaves you with an appetite for more. Whether you are beginning a program of study centered on the brain and behavior, or are just adding some breadth to your education, you will find that behavioral neuroscience now permeates all aspects of modern psychology, along with related life sciences like physiology, biology, and the health sciences. But that's not all. The tools and techniques of behavioral neuroscience also create new ways of looking at questions in many other areas, such as economics, the performing arts, anthropology, sociology, computer science, and engineering. Researchers are beginning to probe mental processes that seemed impenetrable only a decade or two ago: the neural bases of decision making, love and attachment, memory and learning, consciousness, and much of what we call the mind. Our aim in *The Mind's Machine*, Fourth Edition is to provide a foundation that places these and other important topics in a unified scientific context, delivered in clear, inclusive, and gender-neutral language.

We've found that students enrolled in our courses have diverse academic backgrounds and personal interests. In this book, we've tried to avoid making too many assumptions about our readers, and have focused on providing both behavioral and biological perspectives on major topics. If you've had some high-school level biology you should have no trouble with most of the material in the book.

For those readers who have more experience in science—or who want more detail—we have peppered the chapters with embedded links to more advanced material located in Oxford Learning Link. These links, called *A Step Further*, are just one of several novel features we have included to aid your learning. Throughout the book you will find web links that will connect you to animated versions of many figures, video clips, and more.

Each chapter also features at least one segment called *Researchers at Work*, which illustrates the nuts and bolts of experimentation through real-world examples, and a segment called *Signs & Symptoms* that relates a real-world clinical issue relevant to the chapter topic. To help you gauge your progress, each chapter is divided into several major topics bracketed by features called *The Road Ahead*, specifying your learning objectives for the material that follows, and *How's It Going?*, providing self-test conceptual questions. Every chapter also ends with a Visual Summary, an innovative combination of the main points and figures from the chapter, which you can also view in an interactive format in Oxford Learning Link. We encourage you to explore Oxford Learning Link (oup.com/he/watson-breedlove4e), which contains a comprehensive set of study questions. This tool is a powerful companion to the textbook that enhances the learning experience with a variety of multimedia resources.

The chapter lineup in this edition of *The Mind's Machine* encompasses several major themes. In the opening chapters, we trace the origins of behavioral neuroscience and introduce you to the structure of the brain, both as seen by the naked eye and as revealed through the microscope. We discuss how the cells of the brain use electrical signals to process information, and how they transmit that information to other cells within larger circuits. Along the way we'll look at the ways in which drugs affect nerve cells in order to change behavior, as well as some of the remarkable technology that lets us study the activity of the conscious brain as it perceives and thinks. New for this edition, Chapter 4 delves into developmental neuroscience: the continual remodeling of the nervous system and behavior as we grow up and grow old.

In the middle part of the book we look at the neural systems that underlie fundamental capabilities like feeling, moving, seeing, smelling, and hearing. We'll also consider biological and behavioral aspects of "mission-critical" functions such as feeding, sleeping, and sexual behavior. And we'll look at how the endocrine system acts as an interface between the brain and the rest of the body, as well as the reverse—ways in which the environment and behavior alter hormones and thus alter brain activity.

In the latter part of the book we turn to high-level emotional and cognitive processes that color our lives and define us as individuals. We'll survey the systems that allow us to learn and remember information and skills, and the brain systems dedicated to language and spatial cognition. Research on processes of attention has made great progress in recent years, and we'll also consider consciousness and decision-making from a neuroscientific perspective. Finally, we'll review some of the consequences of brain dysfunction, ranging from psychopathology to behavioral manifestations of brain damage, and some of the innovative strategies being developed to counter these problems.

As you make your way through the book, you'll learn that one of the outstanding features of the brain is its ability to remodel. Every new experience, every piece of information that you learn, every skill that you master, causes changes in the brain that can alter your future behavior. The changes may involve physical alterations in the connections between cells, or in the chemicals they use to communicate, or even the addition of whole new cells and circuits. It's a property that we neuroscientists refer to as "plasticity." And it's something that we aim to exploit—if we've done our job properly, *The Mind's Machine*, Fourth Edition should cause lots of changes in your brain. We hope you enjoy the process.

Neil V. Watson

S. Marc Breedlove

We welcome feedback
on any aspect of
The Mind's Machine, Fourth Edition.
Simply drop us a line at
themindsmachine@gmail.com.

Acknowledgments

This book bears the strong imprint of our late colleagues and coauthors Arnold L. Leiman (1932–2000) and Mark R. Rosenzweig (1922–2009). Arnie and Mark prepared the earliest editions of our more advanced text, *Behavioral Neuroscience*, and many illustrations and concepts in *this* book originated in their minds' machines.

In writing this book we benefited from the help of many highly skilled people. These include members of the staff of the Sinauer Associates branch of Oxford University Press: Jess Fiorillo, Editor; Alison Hornbeck and Kathaleen Emerson, Production Editors; Joan Gemme, Production Manager and Book Designer; Richard Neilsen and Meg Britton Clark, Production Specialists; Jason Dirks, Digital Resource Development Manager; and Peter Lacey, Digital Resource Development Editor. Copy Editor Lou Doucette skillfully edited the text, and Photo Researchers Mark Siddall and David McIntyre sourced many of the photographs. For over 25 years now we've been working with Mike Demaray, Craig Durant, and colleagues at Dragonfly Media Group, who so skillfully transform our rough sketches and wish lists into the handsome and dynamic art program you'll enjoy throughout the book.

Our greatest source of inspiration (and critical feedback) has undoubtedly been the thousands of students to whom we have had the privilege of introducing the mysteries and delights of behavioral neuroscience, over the past decade (or two or three or <ahem> four). We have benefited from wisdom generously contributed by a legion of academic colleagues, whose advice and critical reviews have enormously improved our books. In particular we are grateful to: Brian Adams, John Agnew, Duane Albrecht, David L. Allen, Dionisio A. Amodeo, A. Michael Anch, Anne E. Powell Anderson, Michael Antle, Benoit Bacon, Francis R. Bambico, Scott Baron, Alo C. Basu, Jeffrey S. Bedwell, Mark S. Blumberg, William Boggan, Beth Bowin, Sunny K. Boyd, Eliot A. Brenowitz, Chris Brill, Susanne Brummelte, Peter C. Brunjes, Rebecca D. Burwell, Aryn Bush, Joshua M. Carlson, Vanessa Cerda, Evangelia Chrysikou, Suzanne Clerkin, Kenneth J. Colodner, Catherine P. Cramer, Jennifer A. Cummings, Gregory L. Dam, Derek Daniels, Katherine M. Daniels, Heidi Day, Betty Deckard, Brian Derrick, Karen De Valois, Russell De Valois, Rachel A. Diana, Tiffany Donaldson, Gary L. Dunbar, Rena Durr, Steven I. Dworkin, Lena Ficco, Thomas Fischer, Julia Fisher, Loretta M. Flanagan-Cato, Francis W. Flynn, Lauren A. Fowler, Michael Foy, Joyce A. Furfaro, Philip A. Gable, Kara Gabriel, John D. E. Gabrieli, Jack Gallant, Eric W. Gobel, Kimberley P. Good, Christopher Goode, Diane C. Gooding, Janet M. Gray, Gary Greenberg, James Gross, Ervin Hafter, Ian A. Harrington, Mary E. Harrington, Ron Harris, Laura M. Harrison, Christian Hart, Chris Hayashi, Steven J. Hayduk, Wendy Heller, Brian J. Hock, Mark Hollins, Dave Holtzman, Rick Howe, Karin Hu, Richard Ivry, Lucia Jacobs, Karen Jennings, Tephillah Jeyaraj-Powell, Janice Juraska, Jessica M. Karanian, Erin Keen-Rhinehart, Dacher Keltner, Raymond E. Kesner, Mike Kisley, Keith R. Kluender, Leah A.

Krubitzer, Joseph E. LeDoux, Diane Lee, Robert Lennartz, Michael A. Leon, Simon LeVay, Jeannie Loeb, Stephen G. Lomber, Jeffrey Love, Christopher M. Lowry, Donna Maney, Stephen A. Maren, Joe L. Martinez, Jr., Melissa Masicampo, John J. McDonald, Robert J. McDonald, James L. McGaugh, Robert L. Meisel, Paul Merritt, Julia E. Meyers-Manor, Ralph E. Mistlberger, Jeffrey S. Mogil, Daniel Montoya, Randy J. Nelson, Chris Newland, Miguel Nicolelis, Michelle Niculescu, Antonio A. Nunez, Lee Osterhout, Kathleen Page, John Pellitteri, Linda Perrotti, James Pfaus, John D. Pierce, Jr., Eleni Pinnow, Helene S. Porte, Joseph Porter, George V. Rebec, Thomas Ritz, Scott R. Robinson, David A. Rosenbaum, Jennifer K. Roth, Lawrence Ryan, Stephen Sammut, Martin F. Sarter, Jeffrey D. Schall, Stan Schein, Frederick Seil, Andrea J. Sell, Dale R. Sengelaub, Victor Shamas, Matthew Shapiro, Arthur Shimamura, Kezia C. Shirkey, Rachel Shoup, Rae Silver, Cheryl L. Sisk, Laura Smale, Ken Sobel, D. J. Spear, Robert L. Spencer, Scott F. Stoltenberg, Jeffrey Stowell, Steve St. John, Patrick Steffen, Steven K. Sutton, Bruce Svare, Harald K. Taukulis, Earl Thomas, Jessica Thompson, Jennifer L. Thomson, Oscar V. Torres, Sandra Trafalis, Brian Trainor, Lucy J. Troup, Meg Upchurch, Franco J. Vaccarino, David R. Vago, Thomas E. Van Cantfort, Cyma Van Petten, Charles J. Vierck, Beth Wee, Carmen Westerberg, Robert Wickesberg, Christoph Wiedenmayer, Eric P. Wiertelak, Walter Wilczynski, Christina L. Williams, S. Mark Williams, Adrienne Williamson, Guangying Wu, Richard D. Wright, Melana Yanos, Heather J. Yu, Mark C. Zrull, and Irving Zucker.

The following external reviewers read and critiqued chapters of the Third Edition of *The Mind's Machine*; their contributions and corrections really helped us to hone this, the Fourth Edition. Any errors that remain are thus entirely our fault.

Katelyn Black, *Tulane University*
Renee A. Countryman, *Austin College*
Sarah E. Holstein, *Lycoming College*
Paul Meyer, *University of Buffalo*
Daniel Montoya, *Fayetteville State University*
John Moore, *Olivet College*
Mark Schmidt, *Columbus State University*
Rachel J. Smith, *Texas A&M University*
Steven St. John, *Rollins University*
Alicia A. Walf, *Rensselaer Polytechnic Institute*
Eric P. Wiertelak, *Macalester College*

Finally, we would like to thank all our colleagues whose ideas and discoveries make behavioral neuroscience so much fun.

Digital Resources

to accompany **The Mind's Machine:**
Foundations of Brain and Behavior, Fourth Edition

Oxford Learning Link
(oup.com/he/watson-breedlove4e)

For the Student

The Mind's Machine, Fourth Edition Oxford Learning Link contains a wide range of study and review resources to help students master the material presented in the text and to help engage them in the subject with fascinating examples. Tightly integrated with the text, these online resources greatly enhance the learning experience. Oxford Learning Link includes:

- *The Mind's Machine*, Fourth Edition e-book, with all the print book's contents in a digital format.
- *Animations* and *Videos* that illustrate dynamic processes and show examples of interesting phenomena.
- *Activities* that help the student learn and understand complex concepts and anatomical (and other) terms.
- *"A Step Further"* readings that offer additional coverage of selected topics.
- Online, interactive versions of the *Visual Summaries*, with links to key chapter figures, animations and videos, and activities.
- *Flashcards*, to help the student master the hundreds of new terms introduced in the textbook.
- *Biological Psychology NewsLink* (www.biopsychology.com/news), an invaluable online resource, has thousands of news stories updated 3-4 times a week to help students make connections between the science of biological psychology and their daily lives.

Optimize Student Learning with Oxford Insight

The Mind's Machine, Fourth Edition is available powered by Oxford Insight. Oxford Insight delivers the trusted and student-focused content of *The Mind's Machine* within powerful, data-driven courseware designed to optimize student success. Developed with a foundation in learning science, Insight enables instructors to deliver a personalized and engaging learning experience that empowers students by actively engaging them with assigned reading. This adaptivity, paired with real-time actionable data about student performance, helps instructors ensure that each student is best supported along their unique learning path.

For more information on how *The Mind's Machine*, Fourth Edition powered by Oxford Insight can enrich the teaching and learning experience in your course, please visit **oxfordinsight.oup.com** or contact your Oxford University Press representative.

For the Instructor

Oxford Learning Link provides instructors using *The Mind's Machine*, Fourth Edition with a wealth of resources for use in course planning, lecture development, and assessment. Content includes:

- *Textbook Figures and Tables*: All the figures and tables from the textbook are provided in a PowerPoint presentation.
- *PowerPoint Lecture presentations* that include text covering the entire chapter, with selected figures.
- *Videos* that illustrate interesting concepts and phenomena.
- *Instructor's Manual* that provides instructors with a variety of resources to aid in planning their course and developing their lectures. For each chapter, the manual includes:
    - Chapter overview
    - Chapter outline
    - Detailed key concepts
    - References for lecture development, including books, journal articles, and online resources
    - Detailed media references for animations and videos
    - Key terms
- *Test Bank*: The Test Bank consists of a broad range of questions covering all the key facts and concepts in each chapter. Each chapter includes multiple choice, short answer, and essay questions.
- *Computerized Test Bank*: The entire test bank is provided in TestGen software. This software makes it easy to assemble quizzes and exams from any combination of publisher-provided questions and instructor-created questions.
- *Test Bank Only cartridge*: The entire test bank is offered in an interoperable cartridge that is compatible with all major learning management systems.

Value Options

eBook

(ISBN 978-0-19754-224-8)
The Mind's Machine is available as an eBook, in several different formats, including RedShelf, VitalSource, and Chegg. All major mobile devices are supported.

The Mind's Machine, Fourth Edition
Oxford Learning Link animations, videos, and activities:

Animations & Videos

1.1	Inside the Brain
1.2	Brain Explorer
1.3	Brain Development
1.4	Visualizing the Living Human Brain
2.1	Electrical Stimulation of the Brain
2.2	Brain Explorer
2.3	The Resting Membrane Potential
2.4	The Action Potential
2.5	Action Potential Propagation
2.6	Spatial Summation
2.7	Synaptic Transmission
3.1	Synaptic Transmission
3.2	Brain Explorer
3.3	Neurotransmitter Pathways
3.4	Agonists and Antagonists
4.1	Blindness and the Brain
4.2	Brain Explorer
4.3	Stages of Neuronal Development
4.4	Migration of a Neuron along a Radial Glial Cell
5.1	Sensory Systems
5.2	Brain Explorer
5.3	Somatosensory Receptive Fields
5.4	The Stretch Reflex Circuit
6.1	Inside the Ear
6.2	Brain Explorer
6.3	Sound Transduction
6.4	Mapping Auditory Frequencies
6.5	The Vestibular System
6.6	The Human Olfactory System
7.1	Object Recognition
7.2	Brain Explorer
7.3	Visual Pathways in the Human Brain
7.4	Receptive Fields in the Retina
7.5	Spatial Frequencies
8.1	Gender
8.2	Brain Explorer
8.3	Chemical Communication Systems
8.4	Mechanisms of Hormone Action
8.5	The Hypothalamus and Endocrine Function
8.6	Organizational Effects of Testosterone
9.1	Regaining the Weight
9.2	Brain Explorer
9.3	Negative Feedback
9.4	Thermoregulation in Humans
9.5	Anorexia
10.1	Narcolepsy
10.2	Brain Explorer
10.3	Biological Rhythms
10.4	A Molecular Clock
10.5	Animal Sleep Activity
10.6	Narcoleptic Dogs
10.7	REM Behavior Disorder
11.1	The Case of S.M.
11.2	Brain Explorer
11.3	Stress
12.1	Lobotomy
12.2	Brain Explorer
12.3	Tardive Dyskinesia
13.1	Memory
13.2	Brain Explorer
13.3	AMPA and NMDA Receptors
13.4	Morris Water Maze
14.1	Attention and Perception
14.2	Brain Explorer
14.3	Inattentional Blindness
14.4	From Input to Output
14.5	Reconstructing Brain Activity
15.1	Global Aphasia
15.2	Brain Explorer
15.3	Split-Brain Research
15.4	Face Blindness
A.1	Gel Electrophoresis

Activities

The Mind's Machine

Foundations of Brain and Behavior

FOURTH EDITION

Introduction: Building the Mind's Machine

We humans have a long history of using contemporary technology as a metaphor for the mysterious workings of the brain, so today it is commonplace to see the brain described as a computer, complete with "hardware" and "software." Perhaps tomorrow's neuroscientists will describe the brain in terms of quantum devices, wormholes, or a technology that has yet to be imagined. But while modern research aims to describe the complicated machine within each of our heads, we also want to know how the operation of the brain produces the *mind*—the perceptions, emotions, thoughts, self-awareness, and other cognitive processes that inform our behavior.

During the twentieth century, a lot of ink was spilled over the "nature–nurture" controversy, with scholars arguing passionately about the extent to which mental characteristics and abilities are the result of learning experiences versus "innate, hardwired" genetic programs. The two perspectives have often been presented as mutually incompatible alternatives, but thanks to more-powerful techniques, we have come to realize that there is nothing controversial about nature versus nurture: they are two sides of the same coin. Consider the case of rat pups who have inattentive mothers. As adults, the formerly neglected pups show elevated stress hormone responses to stressors that have little effect on rats that were not neglected as pups (O'Donnell and Meaney, 2020). How does this lasting reactivity develop—through experience or as a result of inborn biological factors? Both, it turns out. As we'll see later in this Introduction, and throughout the book, the mind and its machine are shaped by a precise combination of genes and experience, inextricably tied together.

There are now nearly 8 billion of us, and while we can debate whether to fear or celebrate that number, there is no doubt that each of those billions of human brains will at times contemplate its own existence and meaning. How does the operation of a three-pound organ generate our sense of self, express our unique personalities, record information, and guide our actions? Evolution has shaped our bodies and brains so that we closely resemble one another, yet our brains remain malleable throughout life, continually remolded by our environments, experiences, and interactions with other people. So, through a remarkable intersection of genetic heritage and environmental influences, billions of unique individuals have been formed, and we literally change each other's minds on a daily basis.

See Video Intro.1: Nature and Nurture

What is this?

In each chapter of the book, you will find several of these small features, entitled **THE ROAD AHEAD.** They are intended to provide you with a road map for the reading you are about to do, giving you a sense of where the following section is going and what we hope you will get from it (i.e., your learning objectives).

Intro.1 Behavioral Neuroscience Spans Past, Present, and Future

THE ROAD AHEAD

We open the book by situating behavioral neuroscience in its historical context, considering its relationship to different branches of brain science, and reviewing some of the important developments that will propel brain research into the future. Reading this section should prepare you to:

Intro.1.1 Define *behavioral neuroscience*, identify its synonyms, describe the scope of the field, and situate it relative to other branches of brain science.

Intro.1.2 Trace the history of our understanding of the role of the brain, as articulated by scholars across the millennia.

Intro.1.3 Name and briefly describe some of the most influential concepts, emerging topics, and future goals for brain research.

The general field of **neuroscience**—the scientific study of the nervous system—is divided into many subdisciplines because the topic is so vast. The first scholars to study the relationships between brain and behavior called themselves philosophers, because it was philosophy that established the *scientific method* as our best tool for finding new knowledge. Philosophers had long been concerned with the sources of human behavior, so **behavioral neuroscience**, the field that relates behavior to bodily processes, naturally evolved from those beginnings. The names *biological psychology*, *brain and behavior*, and *physiological psychology* are all synonyms for *behavioral neuroscience*, but whichever name is used, the main goal of this field is to understand the brain structures and functions that respond to experiences and generate behavior.

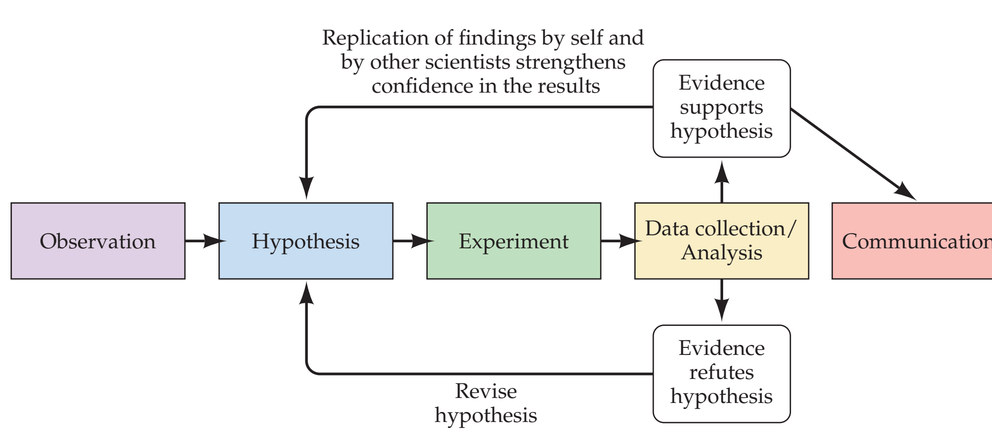
Researchers with dramatically varied backgrounds—psychologists, biologists, physiologists, engineers, neurologists, psychiatrists, and many others—together make up the field of behavioral neuroscience. It is a field that spans both academia and industry, with focus that ranges from pure research on basic processes to entirely applied work directly translating findings into goods and services (Hitt, 2007). The diverse branches of science that overlap with behavioral neuroscience are mapped in **FIGURE Intro.1**.

An early textbook famously opened with the observation that, as a science, "psychology has a long past but only a short history" (Ebbinghaus, 1908). That's certainly an apt description of behavioral neuroscience. The modern era of behavioral neuroscience—characterized by objective experimentation and use of the scientific method to test hypotheses—has a formal history of only 100 years or so. But curiosity about the genesis of behavior reaches much further into the past, shaped by religious ideas, folk knowledge, and ancient observations about the biology of humans and nonhuman animals.

View Animation Intro.2: Brain Explorer

neuroscience The scientific study of the nervous system.

behavioral neuroscience Also called *biological psychology*, *brain and behavior*, and *physiological psychology*. The study of the biological bases of psychological processes and behavior.

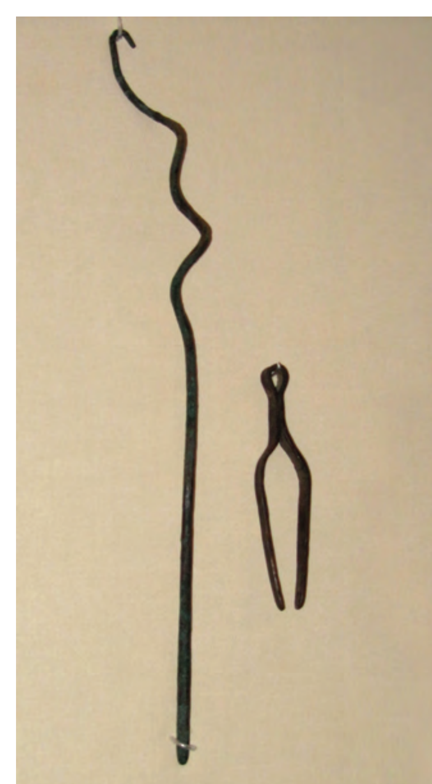


The Scientific Method Scientists use a formal system of hypothesis testing and refinement to gradually develop understanding of neural processes.

FIGURE Intro.1 How Behavioral Neuroscience Relates to Other Fields

An understanding of the brain's role in behavior has developed over centuries

The elaborate preparation of tombs and careful mummification of important people in ancient Egypt (especially about 1500–1000 BCE) reflected the belief that the dead would enter an afterlife that entailed both struggle and—for the adequately equipped individual—great reward. So, in addition to embalming the body with special salts and oils, the usual practice was to preserve four important organs in alabaster jars in the tomb: liver, lungs, stomach, and intestines. The heart, being especially esteemed, was preserved in its place within the body. The brain, however, was picked out though the nostrils and thrown away; apparently, it was considered to be of little value in the afterlife.



Photograph by Neil Watson

Brain Extraction Kit It seems the ancient Egyptians had little regard for the brain. During the mummification process, embalmers used specialized tools, like these examples in the British Museum, to first break up the small bones behind the nose and then extract the brain through the opening. Unlike other major organs, the brain was discarded, and the cranium was stuffed with linen or straw.

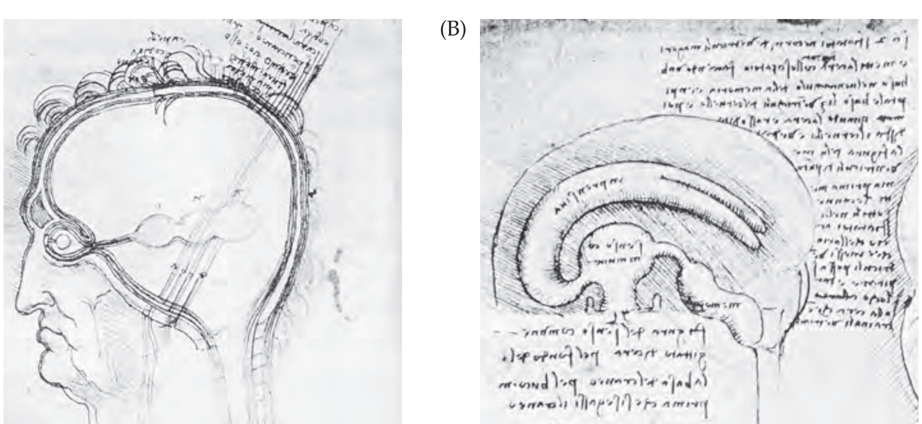
A Brain on the Ceiling of the Sistine Chapel? Between 1508 and 1512, Michelangelo painted the Sistine Chapel in the Vatican. In one panel of Michelangelo's masterpiece, God is depicted reaching out to bestow the gift of life upon humanity, through Adam. But neuroscientists have noted that the oddly shaped drapery behind God, and the arrangement of his attendants, closely resembles the human brain (Meshberger, 1990); compare it with the midsagittal view in Figure 1.16A. A keen student of anatomy, Michelangelo probably knew perfectly well what a dissected human brain looks like. So, was Michelangelo having some fun, making a subtle commentary about the origins of human behavior? We probably will never know, but modern research tools are helping us to understand how our distinctive human qualities—language, reason, emotion, and the rest—are products of the brain.

There is little or no mention of the brain in the Quran, and it is likewise never mentioned in either the Old Testament or New Testament of the Bible, but the heart is mentioned hundreds of times, along with several references each to the liver, the stomach, and the bowels as the seats of passion, courage, and pity, respectively. Aristotle (about 350 BCE), the most prominent scientist of ancient Greece, likewise considered mental capacities to be properties of the heart. When we call people kindhearted, openhearted, fainthearted, hardhearted, or heartless, and when we speak of learning by heart, we are using language echoing this ancient notion. Aristotle thought the brain was little more than a cooling system for hot blood from the heart. But Aristotle's near contemporary, the great Greek physician Hippocrates (about 400 BCE), already suspected that Aristotle's view was—ahem—wrongheaded, and he instead ascribed emotion, perception, and thought to the functioning of the brain.

By the second century CE, this brain-centered view of mental processes had become more accepted, appearing in the writings of the Greco-Roman physician Galen (the "Father of Medicine"). Galen's experiences in treating head injuries of gladiators led him to propose that behavior results from the movement of "animal spirits" from the brain through nerves to the body, but his understanding of the relevant anatomy was poor because the dissection of humans was outlawed in Rome at that time. Not until much later were techniques developed for making highly detailed anatomical studies of the fine structure of the brain.

Skillfully applying newly developed innovations in drawing technique, Renaissance painter and scientist Leonardo da Vinci (1452–1519) produced exquisite neuroanatomical illustrations of nerves and brain structures (**FIGURE Intro.2**). Religious dogma dominated Renaissance science—just ask Galileo—with the result that scientific writing from that era often presents the brain as a mysterious and intricate gift from God. But perhaps some thinkers of the day secretly held a more secular view of neuroscience; for example, it

(A) (B)



In an early sketch, Leonardo simply copied old drawings that bore little resemblance to the actual structure of the brain, showing the fluid-filled ventricles as a balloon connected to the eye.

Leonardo's later drawings, made from direct observations, were much more anatomically correct.

FIGURE Intro.2 Leonardo da Vinci's Changing View of the Brain has been observed that certain depictions of God on the ceiling of the Sistine Chapel, painted by Michelangelo (1475–1564), bear a striking resemblance to the human brain (Meshberger, 1990; Suk and Tamargo, 2010). It is believed that Michelangelo was conducting dissections of cadavers at about the time that the painting was created.

In any event, weighing religious notions of the soul against increasingly mechanistic views of the brain became a major preoccupation for later scholars. Among his many contributions to math and science, René Descartes (1596–1650) tried to explain how the control of behavior might resemble the workings of a machine, proposing the concept of spinal reflexes and a neural pathway for them (**FIGURE Intro.3**). But Descartes also argued (perhaps in order to deflect criticism) that free will and moral choice could not arise from a mere machine. So Descartes asserted that humans, at least, had a nonmaterial soul as well as a material body and that the soul governed behavior through a point of contact (possibly the pineal gland) in the brain. This notion of **dualism** spread widely and left other thinkers with the task of trying to explain *how* a nonmaterial soul could exert influence over a material body and brain. Today, almost all neuroscientists have discarded dualism in favor of the much simpler view that the workings of the mind can be understood as purely physical processes taking place in the material brain.

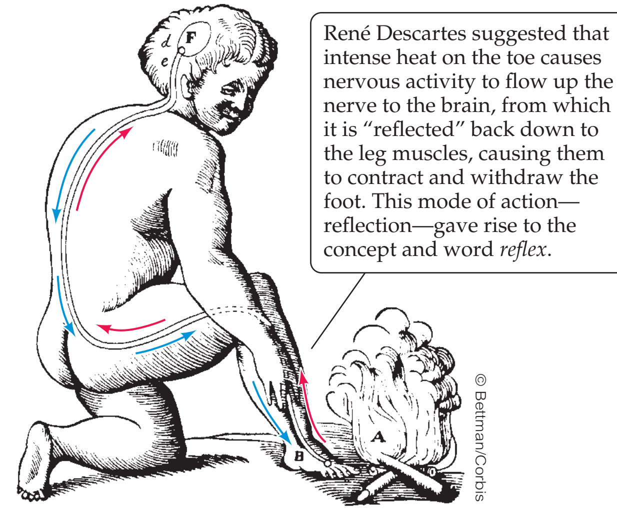


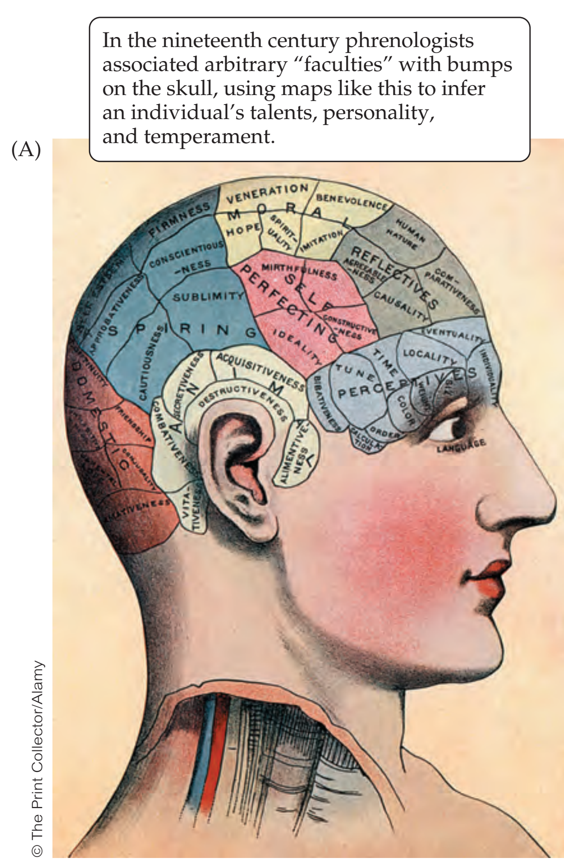
FIGURE Intro.3 An Early Account of Reflexes

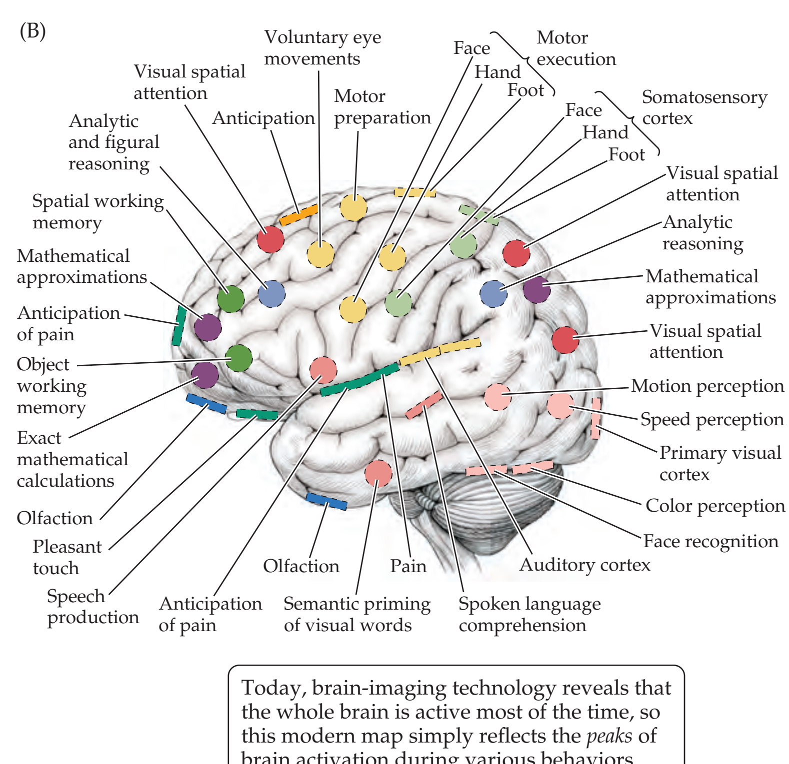
Thanks in large part to systematic studies of the relation between various disorders and damage to regions of the human brain that were conducted by the English physician Thomas Willis (1621–1675), the notion that the brain coordinates and controls behavior eventually became widely accepted (Zimmer, 2004). A pseudoscientific fad of the early 1800s called **phrenology** (**FIGURE Intro.4A**) capitalized on the emerging idea that specific behaviors, feelings, and personality traits were controlled by corresponding specific regions of the brain. Although phrenology was plainly wrong in several fundamental

dualism The notion, promoted by René Descartes, that the mind has an immaterial aspect that is distinct from the material body and brain.

phrenology The belief that bumps on the skull reflect enlargements of brain regions responsible for certain behavioral faculties.

FIGURE Intro.4 Mapping Behavior: Then and Now (B after M. J. Nichols and W. T. Newsome, 1999. *Nature* 402: C35.)





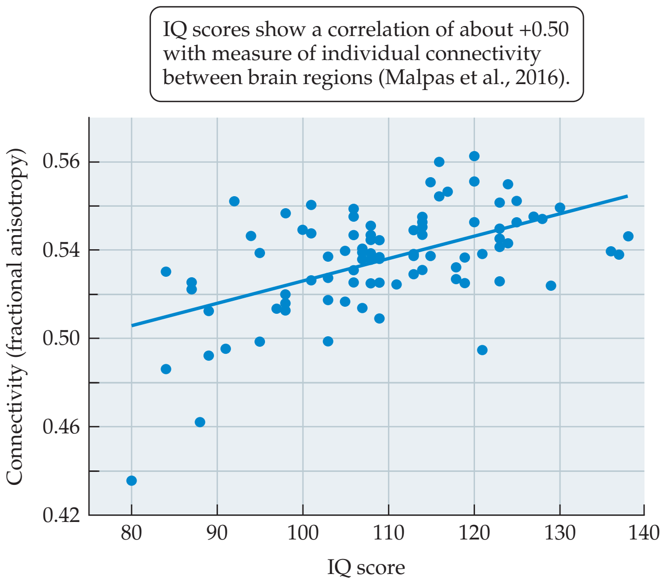


FIGURE Intro.5 Does Size Matter? (After C. B. Malpas et al. 2016. *J. Clin. Neurosci*. 24: 128.)

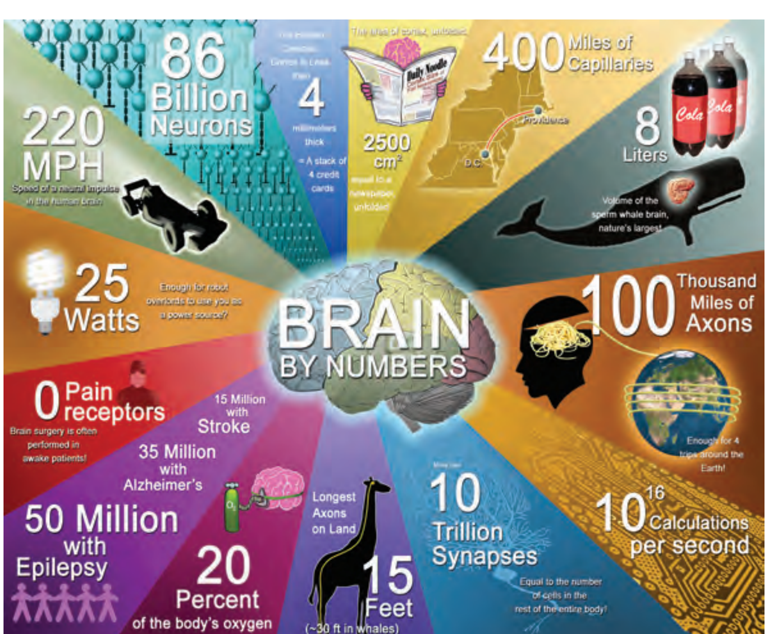
localization of function The concept that different brain regions specialize in specific behaviors.

ways—for example, phrenologists believed they could "read" a person's character by feeling the bumps on that person's head—the field helped establish the concept of **localization of function**, which asserts that different brain regions specialize in specific behaviors.

Later researchers found that damage to specific regions of the brain causes predictable impairments in people; for example, Paul Broca (1824–1880) noted that damage to a particular region of the left side of the brain reliably causes problems with speech production (see Chapter 15). Neuroscientists today accept that the localization of function within the brain is more or less true. Although the whole brain is active most of the time, when we are performing particular tasks, certain brain regions become even more activated, and different tasks activate different networks of brain regions. So modern functional maps of the human brain track the locations where these peaks of activation occur (**FIGURE Intro.4B**). A parallel concern that harks back to the phrenologists has been the importance of brain size to intellectual function. After a couple of centuries of study, the evidence indicates that while the overall size of your brain matters, it matters a lot less than you might expect. Initial evidence suggests that IQ measures may instead show a stronger relationship to individual differences in connectivity than to brain size (**FIGURE Intro.5**; Malpas et al., 2016).

In 1890, William James's book *Principles of Psychology* signaled the beginnings of a modern approach to behavioral neuroscience. In James's work, psychological ideas such as consciousness and other aspects of human experience came to be seen as properties of the nervous system. A true behavioral neuroscience began to emerge from this approach. By the beginning of the twentieth century, researchers were applying newly developed tools to study mental processes that had previously seemed unknowable. Rapid progress was made in developing techniques for measuring learning and memory in humans and animals, and Russian physiologist Ivan P. Pavlov (1849–1936) made his landmark discoveries of classical conditioning in animals—Nobel Prize–winning work that influences scientists to this day.

This rapid progress prompted a parallel interest in understanding the neural basis of learning, marked by one of the first true behavioral neuroscience research programs: the "search for the engram" by Karl Lashley (1890–1958). Although he would not accomplish his goal of linking a specific brain region to the formation of a specific long-term memory (an "engram"), Lashley gave us the idea (now well established) that memory is not localized to only one region of the brain. Behavioral neuroscience also bears the strong imprint of Canadian psychologist Donald O. Hebb (1904–1985), who showed that cognitive processing could be accomplished by networks of active neurons, molded by repeated activation patterns into functional circuits. His hypothesis about how neurons strengthen their connections as a consequence of experiences led to the idea of the *Hebbian synapse*, a type of plastic (changeable) connection between neurons that remains a hot topic in contemporary neuroscience research, as discussed in Chapter 13.



Your Brain, by the Numbers

Research objectives reflect specific theoretical orientations

In designing their research programs, present-day behavioral neuroscientists seek answers to well-defined, specific questions that build on the discoveries of scientists who have gone before. In developing the questions that they wish to study, researchers draw on multiple different research perspectives. Here are some of the major ones:

1. *Systematic description of behavior* Until we describe what we want to study, we cannot accomplish much. Depending on our goals, we may describe behavior in terms of detailed acts or processes, or in terms of results or functions. To be useful for scientific study, a description must be precise, using accurately defined terms and units.
2. *The evolution of brain and behavior* Charles Darwin's theory of evolution through natural selection is central to all modern biology and psychology. Behavioral neuroscientists employ evolutionary theory in two ways: by evaluating similarities among species that reflect shared ancestry, and by looking for species-specific differences in behavior and biology that have evolved as adaptations to different environments. We will discuss many examples of both perspectives in this book.
3. *Life span development of the brain and behavior* **Ontogeny** is the process by which an individual changes in the course of its lifetime—that is, grows up and grows old. Observing the way a particular behavior changes during ontogeny may give us clues to its functions and mechanisms. For example, we know that learning and memory abilities in monkeys increase over the first years of life. Therefore, we can speculate that prolonged maturation of brain circuits is required for complex learning tasks.
4. *The biological mechanisms of behavior* To understand the underlying mechanisms of behavior, we must regard the organism (with all due respect) as a "machine." Accordingly, behavior is the collaborative project of nerve cells, or **neurons**: about 86 billion of them in the case of the human brain (Herculano-Houzel, 2012). In a sense, the mechanistic questions are the "how" questions of behavioral neuroscience, in contrast to the "why" questions that derive from the evolutionary and developmental perspectives. So in the case of learning and memory, for example, we might try to understand how a sequence of electrical and biochemical processes allows us to store information in our brains, and how a different process retrieves it.
5. *Applications of behavioral neuroscience discoveries* The practical application of fundamental discoveries in behavioral neuroscience can improve our lives, and as in so many other branches of science, basic and applied research inform each other in a reciprocal manner. We'll see numerous examples of this reciprocity in the book, ranging from genome-based treatment of brain diseases to technological approaches for understanding brain mechanisms of learning, memory, and consciousness.

The future of behavioral neuroscience is in interdisciplinary discovery and knowledge translation

New discoveries from behavioral neuroscience labs are leading to greater understanding of brain disorders and, with time, will result in the development of effective treatments. This is an urgent problem of much greater scale than many people realize: even excluding addiction and developmental disorders, one in five U.S. residents lived with a mental illness in 2016 (SAMHSA, 2017), and for many disorders the prevalence appears to be on the rise (Hidaka, 2012; Duffy et al., 2019). Neurological and psychiatric disorders vary tremendously both in their severity—from illnesses that can be managed with suitable treatments, to devastating conditions that completely disable—and

ontogeny The process by which an individual changes in the course of its lifetime.

neuron Also called *nerve cell*. The basic unit of the nervous system.