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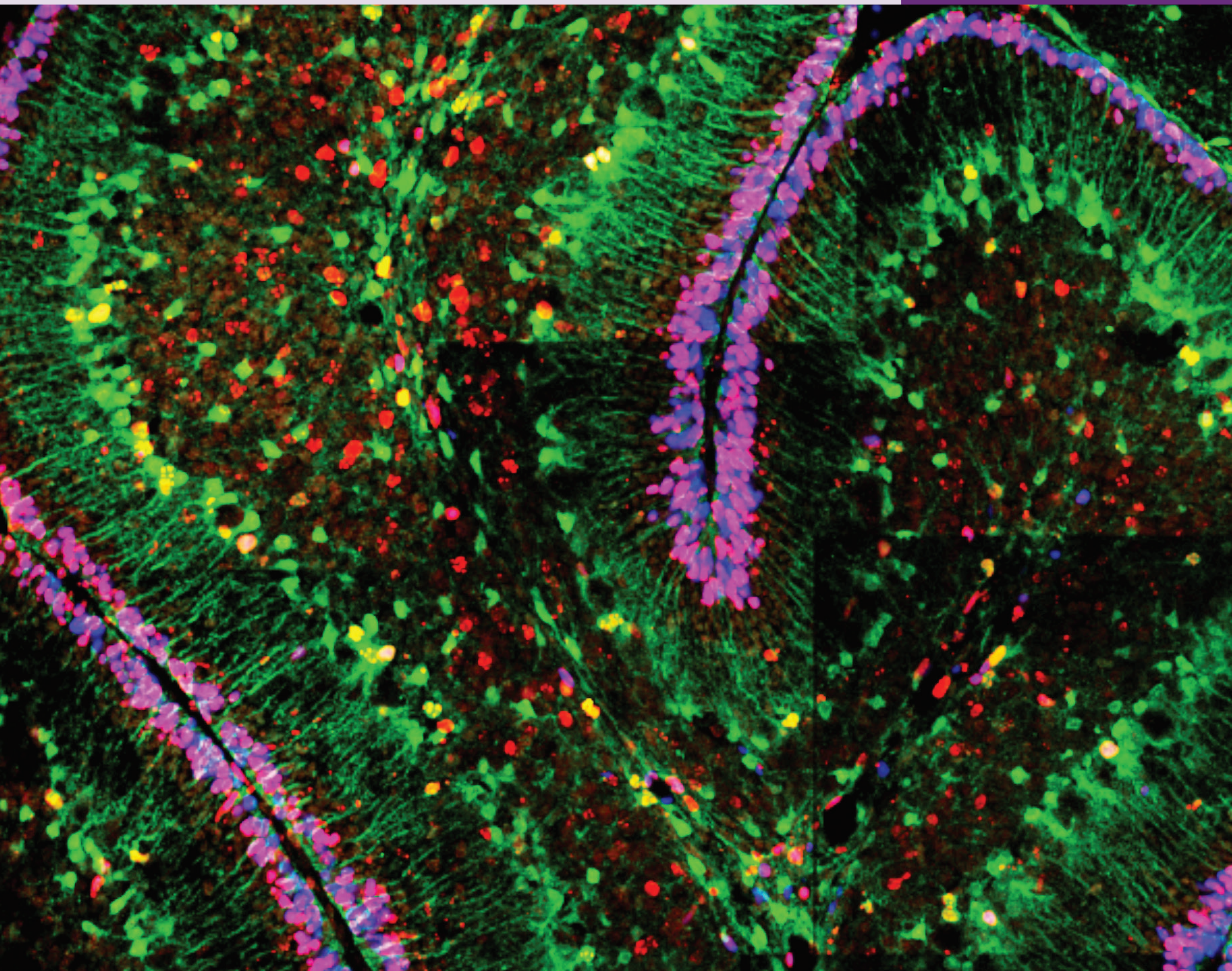
Laura A. Freberg

Discovering Behavioral Neuroscience

An Introduction to Biological Psychology

5th Edition



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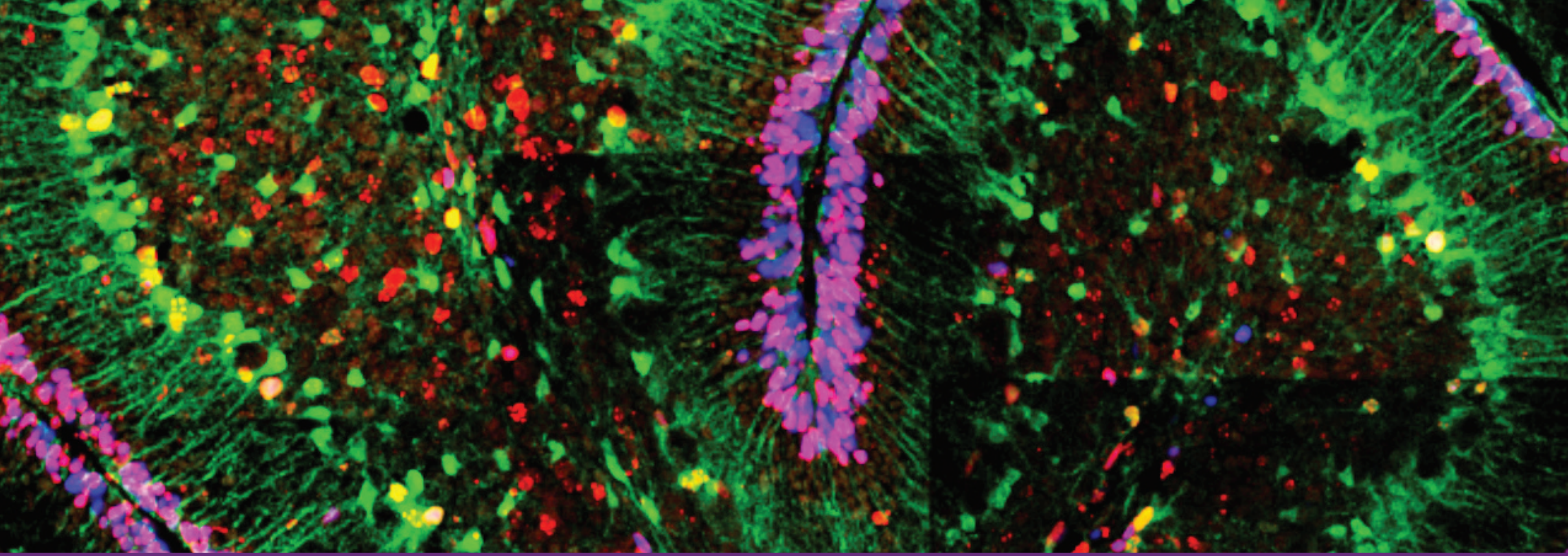

Fifth Edition

Discovering Behavioral Neuroscience

An Introduction to Biological Psychology

Laura A. Freberg

California Polytechnic State University,
San Luis Obispo

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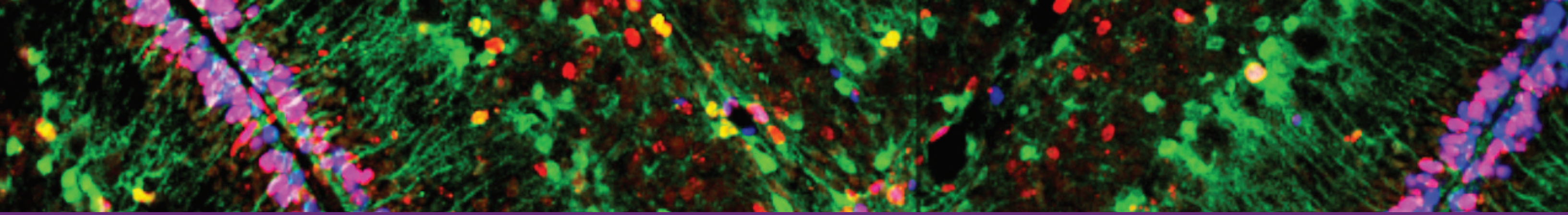
To My Family

Roger, Kristin and Scott, Karen, Karla, and Marcus



About the Author

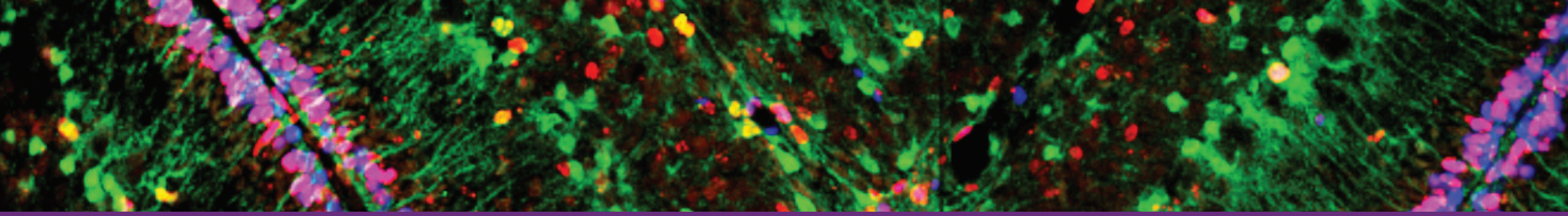
Courtesy of Laura A. Freberg

Laura A. Freberg is Professor of Psychology at California Polytechnic State University, San Luis Obispo, where she teaches courses in Introductory Psychology and Biological Psychology. With the late John Cacioppo and Steph Cacioppo of the University of Chicago, Laura is the co-author of four editions of *Discovering Psychology: The Science of Mind* for Cengage. She is author of *An Introduction to Applied Behavioral Neuroscience: Biological Psychology in Everyday Life* for Taylor & Francis. She is also lead author of *Research Methods in Psychological Science*.

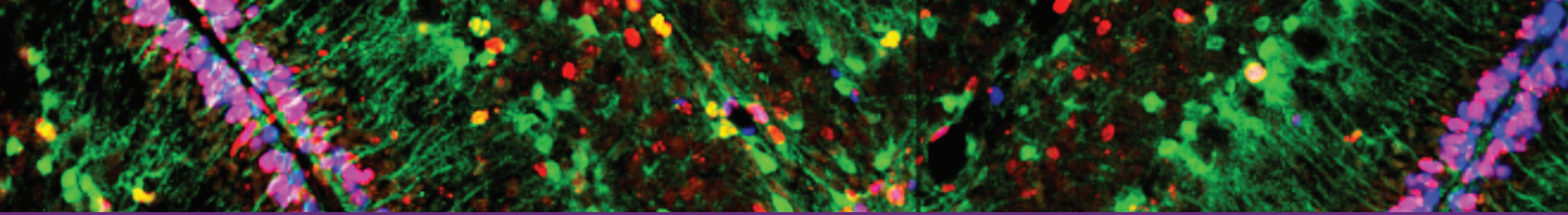
Laura completed her undergraduate and graduate studies at UCLA, where her thinking about psychology and neuroscience was shaped by Eric Holman, John Garcia, O. Ivar Lovaas, Larry Butcher, Jackson Beatty, John Libeskind, Donald Novin, Frank Krasne, and F. Nowell Jones. She was privileged to study neuroanatomy with Arnold Scheibel, and she investigated the effects of psychoactive drugs on learning and memory under the direction of Murray Jarvik and Ronald Siegel in the UCLA Neuropsychiatric Institute. As a capstone to her education, Laura completed her dissertation with Robert Rescorla, then at Yale University.

Laura's teaching career began when she taught her first college course at Pasadena City College at the age of 23 while still a graduate student at UCLA. Beginning in 2011, to better understand the needs of the online education community, she also began teaching for Argosy University Online, including courses in Social Psychology, Sensation/Perception, Cognitive Psychology, Statistics, Research Methods, and Writing in Psychology. She has also redesigned her Cal Poly introductory and biopsychology courses according to QOLT standards to be administered completely online. She has received Faculty Member of the Year recognition from the Cal Poly Disabilities Resource Center three times (1991, 1994, and 2009) for her work with students with disabilities. She enjoys experimenting with technology and social media in the classroom. Laura enjoys collaborating with daughters Kristin Saling (Systems Engineering—U.S. Military Academy at West Point) and Karen Freberg (Communications—University of Louisville) on a variety of research projects in crisis management and public relations as well as in psychology. She served as President of the Western Psychological Association (WPA) in 2018–2019.

In her spare time, Laura enjoys family time with her husband, Roger, their youngest daughter Karla, who has autism spectrum disorder, and an active menagerie including two Australian shepherds, two cats, a parakeet, who can usually be heard in her recordings for online courses, according to her students. She usually writes while consuming vast quantities of Gevalia coffee and listening to the Rolling Stones (which might be apparent in the book's writing style), and she has been known to enjoy college football, Harley Davidsons, episodes of House of the Dragon that do not feature weddings, and The Great British Baking Show. Her ringtone is from Nintendo's *Legend of Zelda*.



Brief Contents



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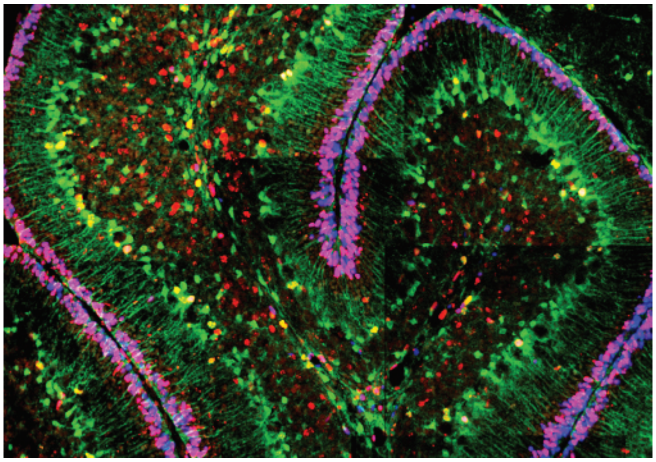
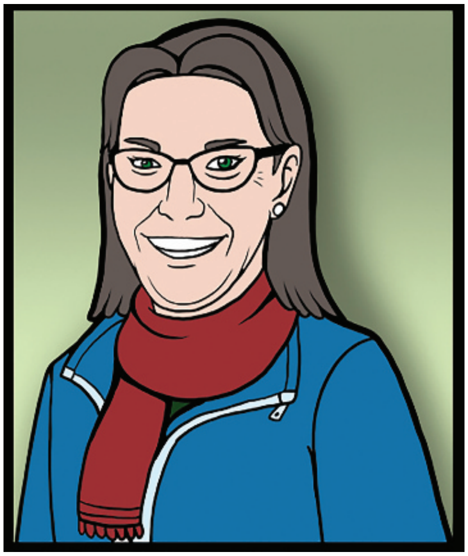
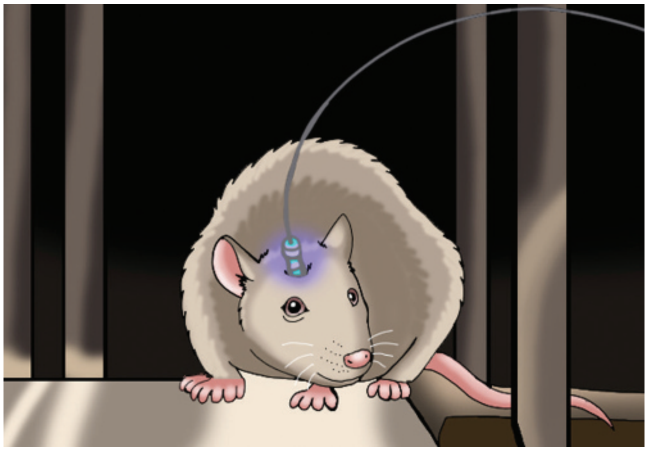
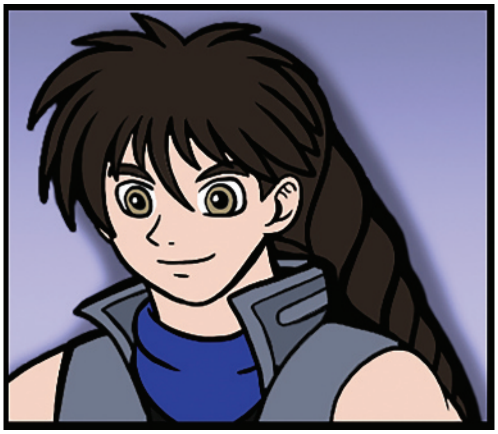


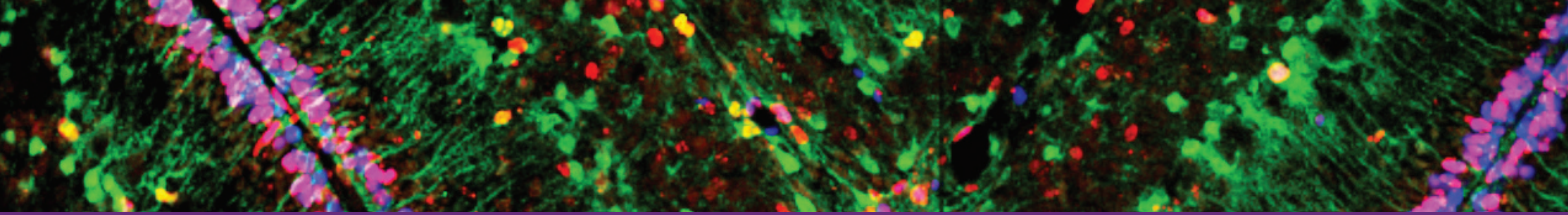
If you are familiar with the first four editions of this textbook, you know that we like to pick colorful visuals that portray the biology behind the behavior. For this fifth edition, we selected a confocal image of a sagittal section of a mouse cerebellum at postnatal day 7, by Valentina Cerrato. It is titled "Neuroscience is Heart." Immunofluorescence was used to label cerebellar astrocytes (green) and proliferating cells, which incorporated BrdU (red) and Edu (blue) at postnatal day 1 and 7, respectively. Distinct 20X images were collected and automatically realigned using Photoshop © software. More striking images may be found at NeuroArt.com



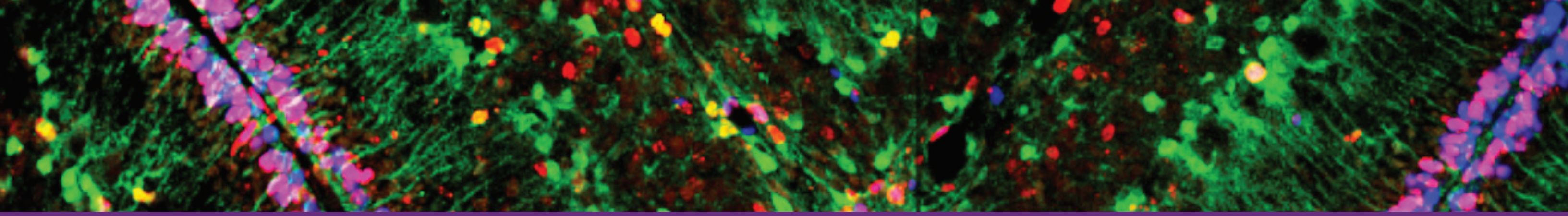
Many of the illustrations in this edition were the work of my daughter, Karla, who has autism spectrum disorder. Karla loves to draw and is very excited to see her work in print. She drew these portraits of herself and of me. You will see her version of a rat in an optogenetics experiment again in Chapter 1.







Contents



Preface

> "[I]n teaching, you must simply work your pupil into such a state of interest in what you are going to teach him that every other object of attention is banished from his mind; then reveal it to him so impressively that he will remember the occasion to his dying day; and finally fill him with devouring curiosity to know what the steps in connection with the subject are."
>
> —William James (1899, p. 10)

James' goals for the classroom instructor might seem lofty to some, but many of us who teach neuroscience have enjoyed the peak experience of seeing students "turn on" to the material in just the way James describes.

This is an exciting time to be a neuroscientist. Every day, science newsfeeds announce some new and dramatic breakthroughs in our knowledge about the nervous system and the human mind. Important questions raised in the past now have definitive answers. In 1890, James commented that "blood very likely may rush to each region of the cortex according as it is most active, but of this we know nothing" (vol. 1, p. 99). With today's technology, it is safe to say we now know much more than "nothing" about this phenomenon James described.

Much has changed in the field of neuroscience since our first edition of this textbook in 2006. I was unprepared, however, for the extent of the changes and updates that were needed in this 5th edition. The quantity of change far exceeded that made in any of the previous updates. The following trends shaped the changes that were made:

DSM-5-TR: All diagnostic criteria have been updated to reflect this latest edition of the DSM (2022).

Open Science methods: Issues of statistical power and researcher degrees of freedom have affected neuroscience as much as they have other facets of science. Students need to be aware of what constitutes good methodology before they can critically evaluate the research presented in the narrative.

ENIGMA, the UK Biobank, 23andMe and other large collaborations: One creative solution to the issues of expense and statistical power in neuroscience research is the formation of large collaborative working groups. Whenever available, these studies with many thousands of diverse participants were used as the basis for conclusions.

Meta-analyses, mega-analyses, and systemic reviews: Another solution to the expense of running studies with large numbers of participants is the "meta" approach. Granted, these analyses are only as good as the quality of the underlying studies, but they're a step in the right direction.

Social trends: Today's students expect to see themselves reflected in the material they're asked to study. While much of neuroscience qualifies as basic science, applications to everyday life are emphasized as frequently as space allows. This edition of the text has also been subject to an expert diversity, equity, and inclusion (DEI) review.

More than half of the four-year universities in the United States now offer bachelor's degrees in neuroscience, and most offer at least a minor in the discipline. Neuroscience reflects a general academic trend of the twenty-first century, in which the walls separating specializations are giving way to new, transdisciplinary research teams, courses, and educational programs. In recognition of these changes, we modified the title of the third edition of this textbook from *Discovering Biological Psychology* to *Discovering Behavioral Neuroscience: An Introduction to Biological Psychology.* This change was welcomed by our faculty and student audiences. A greater emphasis on the neurosciences in general is also achieved by renaming some chapter titles. Psychology still provides a foundation for the study of behavioral neuroscience, as without the ability to ask the right questions about behavior and mental processes, all of the technology on the planet wouldn't do us much good. Our current behavioral neuroscience students, however, are just as likely to be preparing for careers in the health professions, biomedical engineering, or even scientific journalism as they are in psychology.

A major reflection of the transdisciplinary approach exemplified by the neurosciences is the inclusion of psychology and behavioral neuroscience content in the revised edition of the Medical College Admission Test (MCAT), beginning in 2015. One hundred years ago, the leading killers of humans were infectious diseases. Today's top killers—heart disease, diabetes, and cancer—have far stronger relationships with behavior, not only in their causes but also in their treatments. A simple five-minute conversation with a health professional about the need to quit smoking is sufficient to lead to abstention for one year by 2 percent of patients (Law & Tang, 1995). This might not sound like much, but given the 13 percent or so of American adults who smoke and the billions of dollars their health care and lost productivity represent, the stakes are high. Imagine what could be accomplished by health care providers who have a deep understanding of learning, motivation, and social influences on behavior. In response to these and similar trends, the current edition of the textbook explores relevant applications to students pursuing fields of study other than psychology whenever these are relevant.

This fifth edition continues and expands on the goals of the previous four:

- To provide challenging, current content in a student-friendly, accessible form.
- To stimulate critical thinking about neuroscience by presenting controversial and cutting-edge material.
- To promote active student engagement and excitement about the neurosciences.
- To integrate across chapters rather than treating them as stand-alone modules, and to encourage students to see the connections among the topics. For example, connections are made between glutamate as a chemical messenger, its role in learning, the effects of psychoactive drugs on glutamate, its role in psychosis, and its importance to the causes and treatments of stroke and epilepsy.

Pedagogical Features

We realize that a course in behavioral neuroscience can be challenging for many students, particularly those who are underprepared for science courses. To make the process of mastering behavioral neuroscience concepts easier, we have included the following features:

- **Accessible Writing Style** Many textbooks are classified by "level," but it is my opinion that the most complex topics can be mastered by students across a wide range of preparation if the writing style is clear. Students and instructors from the community college through the top R1 universities have kindly complimented me on the accessible writing style used in this textbook. The textbook is also widely adopted in non-English-speaking countries, which suggests that the writing style is manageable for those for whom English is not a first language.
- **Clear, Large, Carefully Labeled Illustrations** Our medical-quality anatomical illustrations help students visualize the structures and processes discussed in each part of the textbook. Behavioral neuroscience is similar to geography in its highly visual nature, and both fields require more visual aids than most other courses. The illustrations in the textbook are augmented by a set of online animations that help the student grasp processes over time, such as the propagation of action potentials down the length of an axon.
- **Learning Objectives and Chapter Outlines** Each chapter begins with a concise set of learning objectives designed to tap into higher levels of Bloom's taxonomy as well as an outline of the chapter's content. These features assist students in planning their learning and in becoming familiar with main terms and concepts to be covered.
- **Margin Glossaries** We regularly provide marginal definitions for many difficult terms. Unlike many textbooks, we do not restrict margin definitions to key terms only. In the electronic forms of the book, these take the form of pop-up definitions.
- **Key Terms** We provide a concise list of key terms to help students focus their learning. Behavioral neuroscience can often seem more like a foreign language course than a science course, and students benefit from guidance regarding which terms should be prioritized.
- **Interim Summaries** Each chapter features two to three interim summaries where students can catch their breath and check their mastery of the material before proceeding. These summaries feature summary points keyed to the learning objectives listed at the beginning of each chapter as well as review questions. Most interim summaries also include a helpful table that pulls together key concepts from the previous section in one convenient place.
- **Chapter Integration** To emphasize how the material fits together and to promote elaborative rehearsal, we make references to other chapters relevant to the topic at hand.
- **Chapter Review** At the end of each chapter, the student will find some thought questions that can also serve as essay or discussion prompts. The Chapter Reviews also include the list of key terms.
- **Practice Tests** In the electronic version of the textbook (see the description of Infuse), practice tests will be available for each main heading with a comprehensive practice test at the end of each chapter.

Additional Features

Students have told me that the narrative of the textbook is "packed" and that skimming paragraphs is usually a recipe for disaster, as each sentence counts. In defense, I respond that we have so much to say and so little room to say it in that there is little space for fluff. At the same time, psychological science shows that spaced learning is superior to massed learning, so it is a good idea to provide regular breaks in the narrative to allow students to catch their breath and digest what they have read. We like to think of these breaks as cool stepping-stones in the flow of lava.

One type of break that we used in the previous editions and continue here in the fifth is the use of interim summaries that include section summary points and review questions. Most also feature tables that pull together chunks of material in a way that makes it easy to learn. Any complex field like the neurosciences entails a bit of simple, rote memorization to form a foundation for later analysis and critical thinking. The more quickly we can bring students up to speed on the basics, the faster we can move on to higher levels of discussion. Chapter summaries include thought questions designed to push students to think more actively and deeply about what they have read.

In addition to the interim and chapter summaries, each chapter includes four types of features. We recognize that "boxing" material often encourages students to overlook content unless expressly instructed to read the boxes, but we trust instructors to use these in ways consistent with their personal style. Obviously, we hope that the content is sufficiently engaging that students will read the material regardless of "what's on the test."

- **Thinking Ethically** features introduce controversial, contemporary questions that require the students to use the information in the chapter in critical ways. Our students will graduate to become community leaders, and they need to be able to think ethically about future cultural choices related to the neurosciences. For example, this feature in Chapter 5: Genetics and the Development of the Human Brain asks when adolescents can be held legally responsible for their actions. Chapter 10: Sexual Behavior discusses timely issues of gender and sport. In Chapter 16: Psychopathology, we consider the file drawer problem and ask how we know whether a medication actually works.
- **Connecting to Research** features highlight either classic or very contemporary single studies in behavioral neuroscience. This provides students with a "soft" segue into the scholarly literature, which might otherwise seem somewhat intimidating. Each feature models the organization of published research by including an introduction, the research question, summaries of the methods and results, and an overview of the conclusions. The feature emphasizes the type of critical thinking and creativity required to advance science. For example, this feature in Chapter 1 explores Covid-19 relevant research demonstrating that how you think about your level of social connectivity influences your immune system to gear up to battle either viruses or bacteria.
- **Behavioral Neuroscience Goes to Work** features expose students to some of the many real-world career paths that relate to behavioral neuroscience. In my experience, many students are unaware of a number of these options. They love the material but have no idea how they can meld this passion with their need to find employment. In this feature in Chapter 5, we describe the role of the genetics counselor, whose insights will be increasingly important as the public obtains more information about personal genotypes. As a bridge between biological sciences and the counseling professions, this career has become increasingly popular with my students. At least a dozen who are now enrolled or who have completed genetics counseling master's degrees attribute their career choice to my "selling" this concept in class.
- **Neuroscience in Everyday Life** features provide an additional opportunity for students to think critically about behavioral neuroscience in the context of relatable life experiences. Students learn strategies for reducing loneliness, consider the efficacy of smartphone sleep apps, debate whether brain training is an effective strategy, and find out whether they qualify as a super-recognizer.

New Content for the Fifth Edition

This new edition contains hundreds of new citations to reflect the advances in the field that have occurred since the previous edition went to press. Textbook authors are often challenged by colleagues with questions about "why do you need a new edition?" In behavioral neuroscience, this question is easy to answer: we have so much new, exciting research to share.

All terminology and descriptions of mental disorders were updated to reflect the publication of *DSM-5-TR* in 2022. Illustrations have also been updated to reflect the new content. Because space is so precious, illustrations are viewed as "teachable moments" that expand on or further explain the narrative rather than redundant, "pretty" placeholders. We are especially proud of our medical-quality anatomical illustrations, which have been the source of much positive feedback through the previous editions. Be on the lookout for illustrations attributed to Karla Freberg, my youngest daughter. Karla has autism spectrum disorder and takes great pleasure in producing illustrations for my books.

Space does not permit me to provide an exhaustive list of the updates, but here are some of the more extensive chapter-by-chapter highlights:

Chapter 1 What Is Behavioral Neuroscience?

- Included new Connecting to Research topic: The effects of loneliness on the immune system.
- Added descriptions of applied areas of forensic and consumer neuroscience.
- Introduced organizing principles for evaluating methods: invasiveness, spatial resolution, and temporal resolution.
- Added section on peripheral methods, including facial electromyography, heart rate variance, skin conductance, eye tracking, and pupil dilation. Related the

use of these technologies to applied fields, such as consumer neuroscience.

- Added descriptions of functional near-infrared spectrometry (fNIRS), hyperscanning, EEG microstates, transcranial electrical stimulation (tES), and functional magnetic resonance spectrometry (fMRS).
- Added section on Open Science related to neuroscience, including discussion of power and fMRI studies.

Chapter 2 Functional Neuroanatomy and the Evolution of the Nervous System

- Covered careers in neurosurgery in Behavioral Psychology Goes to Work feature.
- Covered the prediction of "dangerousness" in Thinking Ethically feature.
- Covered strategies for improving heart rate variability (HRV) in Neuroscience in Everyday Life feature.
- Updated Connecting to Research feature with latest work on the brain-immune system interface.
- Updated information on a number of specific structures, including reticular formation, basal ganglia, and the cingulate cortex.
- Updated section on neural networks.
- Added further information on heart rate variability to the section on the autonomic nervous system.
- Updated information on the enteric nervous system and the gut-brain axis.

Chapter 3 Neurophysiology: The Structure and Function of the Cells of the Nervous System

- Added material on reactive astrocytes.
- Updated terminology related to cytoskeleton to include intermediate filaments.
- Updated section on kiss and run.
- Clarified ligand-gated and chemically-gated terminology.
- New Connecting to Research feature based on the relationship between synapse size and strength.
- New Neuroscience in Everyday Life feature on prebiotics and probiotics.
- Revised Behavioral Neuroscience Goes to Work feature on how EEG works.

Chapter 4 Psychopharmacology

- Updated discussion of gasotransmitters.
- Updated discussion of reserpine's effects on mood.
- Updated placebo section to include nocebo controls.
- Updated/expanded section on addiction.
- Updated nicotine section with information about e-cigarettes.
- Added discussion of the opioid epidemic.
- Updated section on cannabis and psychosis.
- Expanded section on hallucinogens.
- Updated discussion of alcohol j-curve.
- New Neuroscience in Everyday Life feature on using hallucinogens in therapy.

Chapter 5 Genetics and the Development of the Human Brain

- Updated/expanded section on transgenerational epigenetics.
- Updated/expanded section on neurogenesis.
- Updated/expanded cellular migration section.
- Revised sections on cellular differentiation and synapse formation.
- Updated/expanded section on apoptosis.
- Revised sections on synapse elimination and myelination.
- Revised plasticity section, including discussion of critical periods.
- Added encephalocele to neural tube disorders.
- Updated fetal alcohol and FASD discussion.
- Updated and revised adolescent development.
- Revised section on the healthy adult brain.

Chapter 6 Vision

- Deleted section on protecting the eye.
- Updated discussion of bipolar cell types and ganglion cells.
- Further clarified discussion of receptive fields (although this is always tough).
- Refreshed Thinking Ethically feature with discussion of inclusive web design.
- Refreshed Neuroscience in Everyday Life with discussion of super-recognizers.

Chapter 7 Nonvisual Sensation and Perception

- Updated section on hearing disorders.
- Updated terminology and functions of mechanoreceptors.
- Included the female homunculus.
- Updated section on pain, gustatory receptors, and synaesthesia.

- Corrected information on supertasters (number of papillae is no longer considered relevant).
- Refreshed Thinking Ethically feature with discussion of sonic weapons.
- Revised Neuroscience in Everyday Life feature about earbuds and hearing loss.

Chapter 8 Movement

- Updated section on aging and muscles.
- Updated discussion of central pattern generators.
- Revised section on basal ganglia.
- Updated section on initiation of movement.
- Reworked section on mirror neurons and mirror systems.
- Updated discussion of myasthenia gravis, polio, spinal cord injury, amyotrophic lateral sclerosis (ALS), and Parkinson disease.
- Updated Thinking Ethically feature on gene doping.
- Refreshed Connecting to Research feature with a discussion of the intention to move and free will.
- Refreshed Neuroscience in Everyday Life feature with new information on CRISPR.

Chapter 9 Homeostasis, Motivation, and Reward

- Expanded discussion of thermoreceptors.
- Updated discussion of water intoxication/hyponatremia.
- Updated/expanded discussion of neurochemicals and hunger/satiety.
- Updated discussion of obesity.
- Updated section on the causes of eating disorders.
- Expanded/updated section on pleasure and reward.
- Refreshed the Neuroscience in Everyday Life feature to discuss Covid-19 and fever.
- Refreshed the Connecting to Research feature to cover classic work by Olds and Milner.
- Refreshed Behavioral Neuroscience Goes to Work feature to cover nutritional neuroscience.
- Refreshed the Thinking Ethically feature to cover the concept of "Fat But Fit."

Chapter 10 Sexual Behavior

- Added Trisomy X syndrome.
- Updated discussion of 2D:4D ratio and otoacoustic emissions.
- Updated discussion of sexual dimorphism in the nervous system.
- Added material on gender identity and gender-conforming behavior.
- Expanded discussion of transgender and non-binary identities.
- Updated cognitive differences between men and women to include data from individuals with CAH or IGD.
- Added section on empathy and aggression.
- Updated/expanded section on sex, gender, and psychological disorders.
- Updated discussion of sexual orientation.
- Updated discussion of peripartum depression.
- Updated discussion of sexual interest.
- Updated discussion of symmetry and "averageness" in physical attraction.
- Updated discussion of MHC and attraction.
- Updated discussion of oxytocin.
- Updated section on sexual dysfunction.
- Refreshed Thinking Ethically feature with a discussion of gender and sport.

Chapter 11 Biorhythms

- Added discussion of the role of astrocytes in SCN activity.
- Updated section on the cellular clocks.
- Added discussion of mu waves.
- Updated discussion of NREM to use the now generally accepted Stage 3, combining Stage 3 and 4.
- Added discussion of sharp-wave ripples.
- Revised sections on the default mode network, REM eye movements, and REM brain activity.
- Revised the memory and sleep section and the dreaming section.
- Added section on circadian disorders.
- Discussed controversies regarding major depressive disorder with seasonal pattern, formerly known as seasonal affective disorder (SAD).

Chapter 12 Learning and Memory

- Added material on social learning
- Expanded and clarified discussion of long-term potentiation (LTP)
- Updated spatial learning and LTP section.
- Revised section on memory updating.
- Added information on engram cells.
- Updated sections on systems supporting different types of learning and memory.
- Separated sections on the effects of stress and healthy aging on memory.
- Updated the discussion of stress effects on memory.

- Updated Behavioral Neuroscience Goes to Work feature on neuroeducation.
- Revised Neuroscience in Everyday Life feature to ask whether brain training really works.

Chapter 13 Cognitive Neuroscience

- Added introductory section on consciousness and disorders of consciousness.
- Updated section on lateralization, including development, emotion, music, and gender.
- Added information about language and self-domestication.
- Updated information about genetics and the origins of language.
- Updated sections on language models, multilingualism, dyslexia, and stuttering.
- Updated section on intelligence, including network neuroscience and artificial intelligence.
- Updated section on decision making.
- Refreshed Neuroscience in Everyday Life to cover consumer neuroscience.

Chapter 14 Social and Affective Neuroscience

- Changed the title to reflect current terminology in neuroscience.
- Simplified coverage of classic emotion models and added discussion of primal versus constructed emotion and emotion versus reason.
- Updated discussion of universal emotions and cultural contributions to emotion.
- Updated emotion regulation section.
- Expanded section of aggression and violence to distinguish more clearly between proactive and reactive aggression.
- Updated biochemistry of aggression section to include cortisol/testosterone interactions.
- Added new section on social neuroscience, with subsections on social cognition and empathy, prejudice, and loneliness.
- Refreshed Behavioral Neuroscience Goes to Work feature with information on forensic neuropsychology.
- Refreshed Neuroscience in Everyday Life feature with information on reducing loneliness.

Chapter 15 Neuropsychology

- Updated all sections using terminology and content from *DSM-5-TR*.
- Added section on frontotemporal neurocognitive disorder.
- Added section on neurocognitive disorder with Lewy bodies.
- Updated sections on neuropsychological assessment.
- Discussed controversies over the amyloid hypothesis of Alzheimer disease.
- Updated genetics, cellular correlates, and network effects of Alzheimer disease.
- Updated section on treatment of stroke.
- Updated traumatic brain injury (TBI) section, especially material on military blast TBI, repeated TBI (chronic traumatic encephalopathy), and treatments of TBI.
- Updated section on neurocysticercosis.
- Added section on cognitive outcomes of SARS-CoV-2.
- Updated section on multiple sclerosis.
- Distinguished between functional and structural neuroplasticity in rehabilitation.
- Distinguished between near and far transfer in rehabilitation.
- Refreshed Thinking Ethically feature to cover the amyloid hypothesis in Alzheimer disease.
- Refreshed Connecting to Research feature with key prion paper by Stanley Prusiner.

Chapter 16 Psychopathology

- Updated all terminology and content based on *DSM-5-TR*.
- Expanded discussion of mental disorder terminology to include disorder, disability, disease, and difference.
- Distinguished between familial heritability and SNP-based heritability.
- Expanded general discussion of anxiety.
- Refreshed Connecting to Research feature to cover the androgynous brain and mental health (one of the top-rated papers of 2021).
- Refreshed Thinking Ethically feature to discuss how we know when medications work.
- Refreshed the Neurscience in Everyday Life feature with a discussion of the gut microbiota and mental disorders.

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I view this text as a work in progress. Please take a moment to share your thoughts and suggestions with me: lfreberg@calpoly.edu. You can also find me on Facebook, on Twitter as @biopsych, and on my blog: http://www.laurafreberg.com/blog. I am happy to Zoom in to classrooms to help with a lecture or two (Vision seems to be one topic faculty are happy to hand off). I can also share my own recorded lectures for my students.

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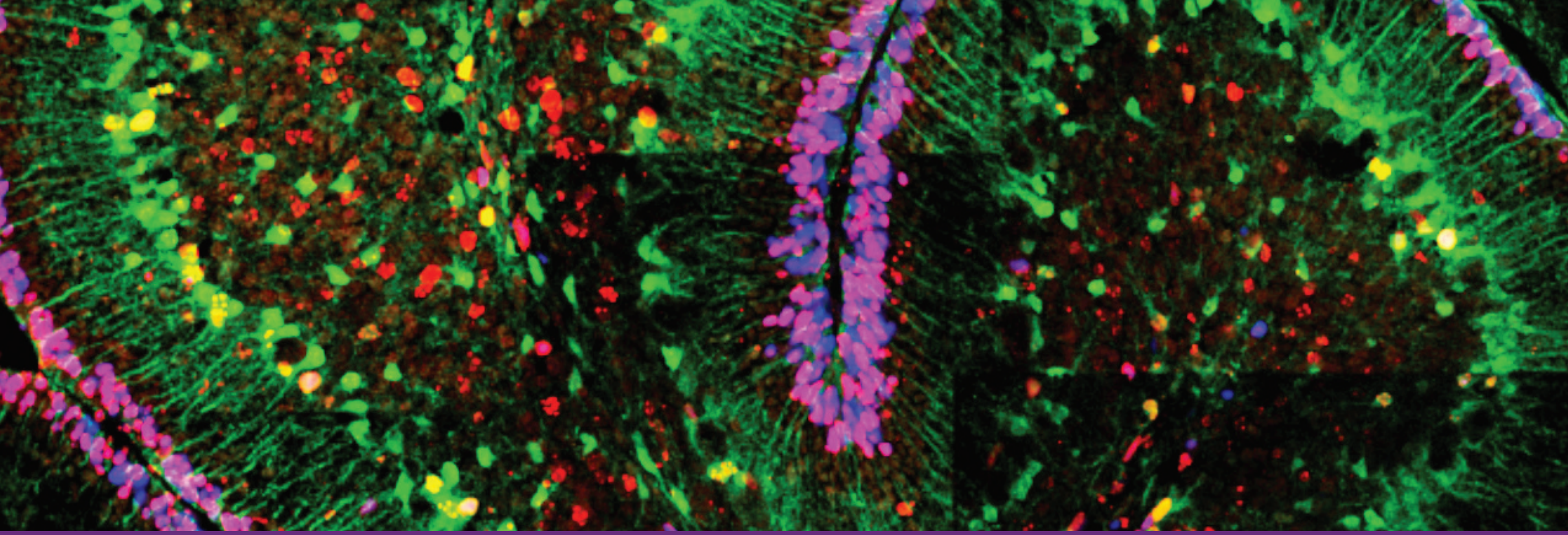


Chapter 1

What Is Behavioral Neuroscience?

Learning Objectives

L01 Classify the subfields of neuroscience and explain how behavioral neuroscience fits within the field.

L02 Interpret the significance of the major historical highlights in the study of the nervous system.

L03 Differentiate the brain imaging technologies, including CT, PET, SPECT, MRI, fMRI, fNIRS, and DTI.

L04 Assess the use of microscopic, peripheral, recording, hyperscanning, stimulation, optogenetic, lesion, and biochemical methods in behavioral neuroscience.

L05 Analyze the relative strengths and weaknesses of twin studies, adoption studies, and molecular genetics for understanding behavior.

L06 Evaluate the contributions of open science approaches and ethical research practices to progress in behavioral neuroscience.

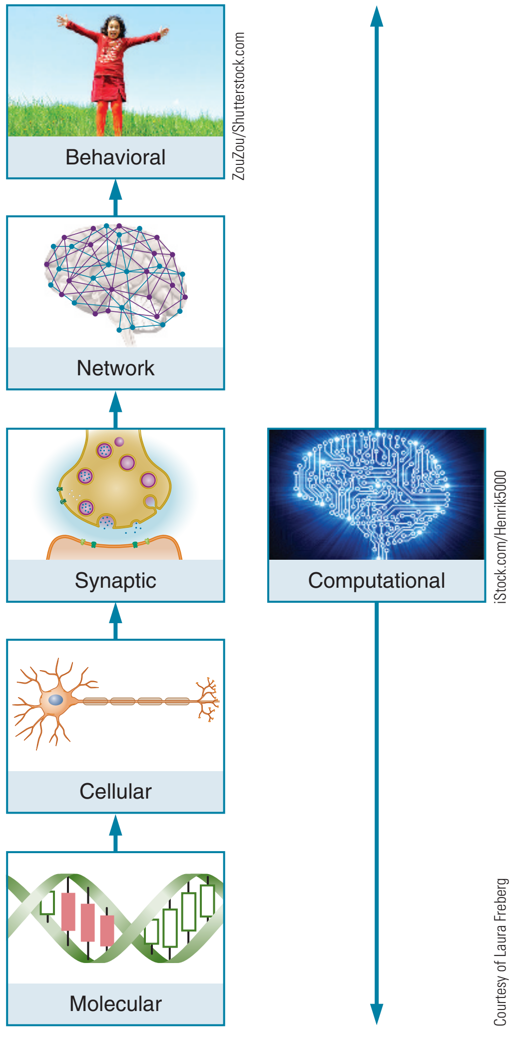
Chapter Outline

Neuroscience as an Interdisciplinary Field

Neuroscience is the interdisciplinary study of the nervous system, whose ultimate goal is to understand brain and nervous system function and neurological disease at many levels (UCLA, 2021). The term "neuroscience" was coined by Francis O. Schmitt, who established MIT's Neurosciences Research Program in 1962.

Neuroscientists strive to understand the functions of the brain and nervous system across several levels of analysis, using molecular, cellular, synaptic, network, computational, and behavioral approaches (refer to Figure 1.1). You might think of this field as analogous to Google Earth. We can zoom in to observe the tiniest details and then zoom back out again to get the "big picture."

Figure 1.1 The Neurosciences: Building from Molecule to Behavior



Beginning at the most microscopic stage, the molecular neuroscientist explores the nervous system at the level of the molecules that serve as its building blocks. We will cover their work in our chapters on neural cell physiology (Chapter 3), psychopharmacology (Chapter 4), and genetics (Chapter 5). Starting with DNA, RNA, and the proteins resulting from gene expression, the molecular neuroscientist attempts to understand the chemicals that build the system and make neural functioning possible.

Zooming out just a bit from the molecular level of analysis, we find the cellular neuroscientist hard at work outlining the structure, physiological properties, and functions of single cells found within the nervous system. These isolated cells would be of no use unless they could forge connections, which they do at junctions we call synapses. Synaptic neuroscience examines the strength and flexibility of neural connections, which underlie complex processes such as learning and memory.

Beyond the single synapse, we find that interconnected neurons form pathways or networks. In contemporary neuroscience, we are experiencing a move away from the idea that "this structure engages in this function" to ideas that more accurately reflect neural networks. We are more likely to say that "this structure participates in a network connecting these other structures to engage in this type of processing."

Zooming out to perhaps the most global point of view, we find **behavioral neuroscience**, also known as **biological psychology**, which is the primary focus of this textbook. Behavioral neuroscientists use all the previous levels of analysis, from the molecular up through the network, in their efforts to understand the biological correlates of behavior. The relationship between biology and behavior is reciprocal—biology can impact our behavior, and behavior, including your thoughts and emotions, impacts biology. The experiment described in the Connecting to Research feature illustrates this reciprocal relationship. The way you think about your degree of social connection to others can influence your immune system's response to viruses and bacteria.

Like the neurosciences in general, behavioral neuroscience looks at the activity of the nervous system in health and in cases of illness, injury, and psychological disorder. Subspecialties within behavioral neuroscience include cognitive neuroscience, or the study of the biological correlates of information processing, learning and memory, decision making, and reasoning. We investigate these topics in depth in the chapters on sensation and perception

neuroscience The interdisciplinary study of the nervous system, whose ultimate goal is to understand brain and nervous system function and neurological disease at many levels.

behavioral neuroscience/biological psychology The study of the biological correlates of behavior, emotions, and mental processes.

Connecting to Research

Thinking About Yourself as Lonely or Socially Connected Can Influence Your Immune System

One of the key aspects of behavioral neuroscience that we introduce in this chapter is the reciprocal nature of the relationship between biology and behavior. Most of us are quite familiar and comfortable with the idea that our biology can influence our behavior, but the influence of behavior on biology is perhaps less obvious. Cole et al. (2015) describe the remarkable influence our perception of social isolation has on the actions of our immune system.

Before we explore this research, please consider the following questions and rate them on a scale from 1 (never) to 4 (often). How often do you:

1. Feel that you lack companionship?
2. Feel left out?
3. Feel isolated from others?

Your total score should be somewhere between 3 and 12, with 10 being the cut-off for high loneliness (Hughes et al., 2004). If your score is on the high side, please note that high loneliness is typical among young adults. Also note that loneliness is a perception of isolation, not necessarily reality. Some people surrounded by friends and loved ones can still feel lonely while others are content with a pet.

Azndc/Getty Images

Figure 1.2 Biology and Behavior Form Reciprocal Relationships. Feeling lonely changes the way your immune system behaves.

The Question: Does loneliness affect the functions of the immune system?

Method

The researchers took blood samples and administered standard assessments of loneliness to 108 older adults. The blood samples were used to analyze relative expression of immune system genes.

Results

Once loneliness is perceived, it begins a cascade of responses, many of which are well below the threshold of conscious awareness. Cole et al. (2015) established that people responded to loneliness by downgrading their immune responses to viruses while gearing up their responses to bacteria.

Conclusions

As we know all too well from the Covid-19 pandemic, viruses love close contact. This means that socially connected people are at greater risk from viruses. In contrast, among our hunter-gatherer ancestors, isolated humans were more exposed to predators and hostile humans, putting them at greater risk from bacteria entering the body through cuts and scrapes. Over the millennia, our perceptions of our social connectivity acquired the ability to signal our immune systems to address the greater threat.

It is ironic that the very same preventive measures used during the Covid-19 pandemic, such as social distancing, stay-at-home, and lockdowns, could have reduced our immune system's ability to fight the virus by increasing loneliness. If your loneliness score was on the high side, do not despair. Many steps can be taken to reduce loneliness, such as initiating small conversations with people you meet every day, like the barista who makes your coffee. A number of these small interactions can provide the same sense of human connectivity as one or two deep connections.

(Chapters 6 and 7), learning and memory (Chapter 12), and cognition (Chapter 13). Social and affective neuroscience, covered in Chapter 14, explores the interactions between the nervous system, emotions, and our human social environment and behavior.

In addition to basic laboratory research, behavioral neuroscience also features many practical applications. Chapters 15 and 16 explore the assessment and treatment of neurological and psychological disorders from the neuroscience perspective. Forensic neuroscience applies neuroscience principles to the understanding and management of criminal behavior. Neuroeducation attempts to improve the educational experience based on our understanding of how the brain learns. Consumer neuroscience and neuroeconomics focus on the biological correlates of choice. Organizational neuroscience seeks to illuminate the biological underpinnings of group performance and leadership. Health neuroscience incorporates the "mind" into the overall understanding of physical health. Finally, behavioral neuroscience has enjoyed a productive and exciting relationship with robotics and artificial intelligence.

Computational neuroscience runs parallel to the types of neuroscience described so far, but it draws from computer science, electrical engineering, mathematics, and physics to produce models of the nervous system from the molecular level up through the behavioral level of analysis. The predictions from these computational models can then be tested against living systems, forming a cooperative symbiosis with researchers in other areas of neuroscience. One of the practical applications of computational neuroscience is the use of neural decoding, or the use of neural activity to estimate what the brain is doing, in the development of sophisticated prosthetic devices. These devices can use neural activity to figure out the brain's intentions to move in certain ways or perceive certain types of input as touch.

These various levels of analysis complement rather than compete with one another. Because of the diversity of skills needed to pursue each of these approaches, neuroscience is an interdisciplinary field of study, reaching across the traditional academic departments of biology, chemistry, psychology, medicine, mathematics, physics, engineering, statistics, and computer science.

The need for a better understanding of the nervous system has never been greater. In 2017, about 200 million Americans (about 60% of the population) experienced at least one neurological condition, ranging from tension headaches and migraines to strokes and dementia (GBD 2017 US Neurological Disorders Collaborators, 2021). The cost of these conditions in terms of health care and lost productivity is close to $800 billion (Gooch et al., 2017). Connections between biology and behavior are not just relevant to neurological disease. They also inform our understanding of health in general. Compared to 100 years ago, when most people died from infectious diseases, today's killers (cancer, diabetes, heart disease) are tightly linked to behavior. Reflecting the recognition

Behavioral Neuroscience Goes to Work

What Can I Do with a Degree in Neuroscience?

One of the pleasures of teaching courses in behavioral neuroscience occurs when a student suddenly falls in love with the field. "This is for me," the student might say, but the question that usually follows is, "But how can I make a living doing this?" The answers to this question are as diverse as the field. Because neuroscience is so broad, opportunities can be found down many different paths.

Like many other fields, neuroscience has more opportunities for people with more education. Many practicing neuroscientists have medical degrees, PhDs, or both. This does not mean that jobs are unavailable for people with undergraduate degrees, however. People with undergraduate degrees can be employed as research assistants in pharmaceutical firms, universities, and government agencies. Some neuroscience graduates work in substance abuse counseling or in mental health facilities. Neuroscience is used in some unexpected places as well. A growing trend in advertising agencies is to use brain imaging and other technologies to gauge public reactions to advertising. Web and application designers use eye-tracking technology to evaluate the user experience (UX), such as whether a person processes the important features of a webpage and has an enjoyable time while doing so.

The ongoing burst in neuroscience technologies is likely to continue to shape the field, and additional opportunities are likely to emerge. In the meantime, any student interested in neuroscience would benefit from gaining the best possible skills in general science, research methods, mathematics, and statistics.

MONOPOLY919/Shutterstock.com

Figure 1.3 Consumer Neuroscience One of the possible careers associated with neuroscience is the application of neuroscience principles and methods to understanding purchase choices made by consumers. This augmented reality technology might help retailers predict the effects of product display on consumer attention and action.

of the role of behavior in illness, the standardized Medical College Admission Test (MCAT) for medical school applicants now contains a sizable number of questions about psychology and behavioral neuroscience.

Illness is only part of the human equation. We also need to understand how the nervous system responds in typical ways to promote well-being, including better relationships, better parenting, better child development, and better thinking and learning. Through improved understanding of the nervous system and its interactions with behavior, scientists and practitioners will be more thoroughly prepared to tackle the significant challenges to health and well-being faced by contemporary world populations.

Historical Highlights in Neuroscience

The history of neuroscience parallels the development of tools for studying the nervous system. Early thinkers made progress despite limited scientific methods and technologies.

Ancient Milestones in Understanding the Nervous System

Our earliest ancestors had at least a rudimentary understanding about the brain's essential role in maintaining life. Archaeological evidence of brain surgery suggests that as many as 7,000 years ago, people tried to cure others by drilling holes in the skull, a process known as trephining or trepanation (refer to Figure 1.4). Because some skulls have been located that show evidence of healing following the drilling procedure, we can assume that the patient lived through the procedure and that this was not a postmortem ritual. What is less clear is the intent of such surgeries. Possibly, these early surgeons hoped to release demons or relieve feelings of pressure (Clower & Finger, 2001).

Figure 1.4 Prehistoric Brain Surgery

As far back in history as 7,000 years ago, people used trepanation (trephining), or the drilling of holes in the skull, perhaps to cure "afflictions" such as demonic possession. Regrowth around some of the holes indicates that at least some of the patients survived the procedure. More recently, trephining has resurfaced as a DIY (do it yourself) process, possibly as a type of self-injurious behavior.

The *Edwin Smith Surgical Papyrus* (about 1600 BCE) represents the oldest known medical writing in history, yet it features many sophisticated observations (Breasted, 1930). The Egyptian author of the *Papyrus* clearly understood that paralysis and a lack of sensation in the body resulted from nervous system damage. Cases of nervous system damage were usually classified as "an ailment not to be treated," indicating the author's understanding of the relatively permanent damage involved.

Building on the knowledge taken from ancient Egypt, the Greek scholars of the fourth century BCE proposed that the brain was the organ of sensation. Hippocrates (460–379 BCE) correctly identified epilepsy as originating in the brain, although the most obvious outward signs of the disorder were muscular convulsions (refer to Chapter 15). Galen (130–200 CE), a Greek physician serving the Roman Empire, made careful dissections of animals (and we suspect of the mortally wounded gladiators in his care as well). Galen believed erroneously that the ventricles played an important role in transmitting messages to and from the brain, an error that influenced thinking about the nervous system for another 1,500 years (Aronson, 2007).

The Dawn of Scientific Reasoning

The French philosopher René Descartes (1596–1650) argued in favor of mind–body dualism. For Descartes and other dualists, the mind is neither physical nor accessible to study through the natural sciences. In contrast, the modern neurosciences are based on monism rather than dualism. The monism perspective proposes that the mind is the result of activity in the brain, which can be studied scientifically. Descartes's ideas were very influential, and even today, some people struggle with the idea that factors such as personality, memory, and logic simply represent the activity of neurons in the brain. Later in the chapter, our discussion of research ethics presents another legacy of Descartes's ideas. Because many shared his view of animals as mechanical, not sentient, beings, experiments were carried out on animals that seem barbaric to many modern thinkers. In 1865, Claude Bernard (1813–1878) wrote that "the science of life is a superb and dazzlingly lighted hall which may be reached only by passing through a long and ghastly kitchen" (Bernard, 1865/1927, p. 15).

Between 1500 and 1800, scientists made considerable progress in describing the structure and function of the nervous system. The invention of the light microscope by Anton van Leeuwenhoek in 1674 opened a whole new level of analysis. Work by Luigi Galvani and

Emil du Bois-Reymond established electricity as the mode of communication used by the nervous system (refer to Figure 1.5). British physiologist Charles Bell (1774–1842) and French physiologist François Magendie (1783–1855) demonstrated that information travels in one direction, not two, within sensory and motor nerves.

Modern Neuroscience Begins

As late as the beginning of the twentieth century, many scientists, including Italian researcher Camillo Golgi, continued to support the concept of the nervous system as a vast, interconnected network of continuous fibers. Others, including the Spanish anatomist Santiago Ramón y Cajal, argued that the nervous system was composed of an array of separate, independent cells, like the one he illustrated in Figure 1.6. Cajal's concept is known as the Neuron Doctrine. Golgi and Cajal shared the Nobel Prize for their work in 1906. Ironically, Cajal used a stain invented by Golgi to prove that Golgi was incorrect.

The road to our current understanding of the nervous system has not been without its odd turns and dead ends. The notion that specific body functions are controlled by certain areas of the brain, called localization of function, began with an idea proposed by Franz Josef Gall (1758–1828) and elaborated on by Johann Gasper Spurzheim (1776–1832). These otherwise respectable scientists proposed a "science" of phrenology that maintained that the structure of people's skulls could be correlated with their individual personality characteristics and abilities. A phrenologist could "read" a person's character by comparing the bumps on that person's skull to a bust showing the supposed location of each trait (refer to Figure 1.7). Although misguided, Gall and Spurzheim's work did move us away from the metaphysical, nonlocalized view of the brain that had persisted from the time of Descartes. Instead, Gall and Spurzheim proposed a more modern view of the brain as the organ of the mind, composed of interconnected, cooperative, yet relatively independent functional units.

Further evidence in support of the localization of function in the brain began to accumulate. In the mid-1800s, a French physician named Paul Broca correlated the damage he observed in patients with their behavior and concluded that language functions were localized in the brain (refer to Chapter 13). Incidentally, it was also Broca who brought the practice of trepanation, described earlier in this chapter, to the attention of the scientific community (Clower & Finger, 2001). In 1870, Gustav Theodor Fritsch (1838–1927) and Eduard Hitzig (1838–1907) described how electrically stimulating the cortex of a rabbit and a dog produced movement on the opposite side of the body. The localization of function in the brain became a generally accepted concept.

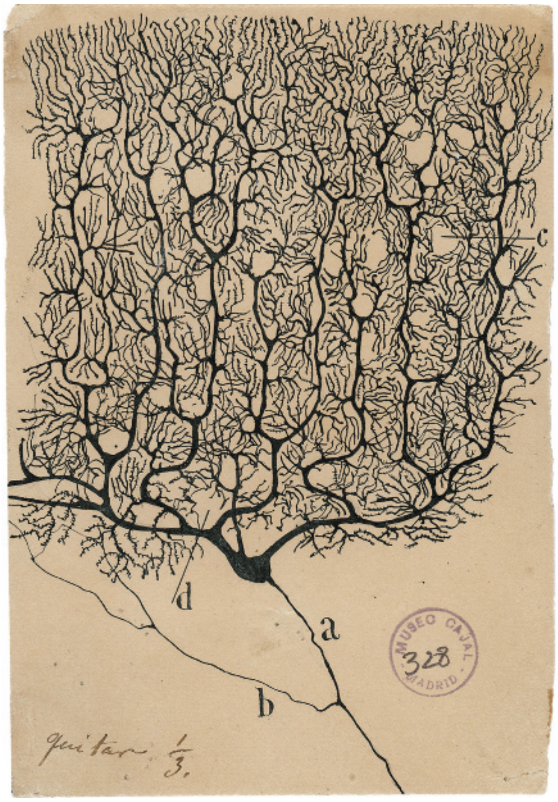
Figure 1.5 Luigi Galvani Demonstrated a Role for Electricity in Neural Communication

Luigi Galvani and his wife Lucia Galeazzi Galvani discovered that electrical stimulation would contract the leg muscles of frogs. Their experiments not only established an understanding of the electrical nature of neural communication but also inspired Mary Shelley to write *Frankenstein*.

The Print Collector/Heritage Images/Alamy Stock Photo

Figure 1.6 Improvements in Microscopic Methods Opened a New World

Santiago Ramón y Cajal used microscopic stains developed by his rival, Camillo Golgi, to view single nerve cells. These observations supported Cajal's Neuron Doctrine, which states that the nervous system is made from individual cells, like the one illustrated in Cajal's beautiful drawing of a Purkinje cell from the human cerebellum.



Santiago Ramón y Cajal/Wikimedia Commons

More support for the mind's physical, nonmystical nature was provided by physiologists and psychophysicists (refer to Chapters 6 and 7). Hermann von Helmholtz (1821–1894) demonstrated that the mind has a physical basis by asking participants to push a button as soon as they felt a touch. The participants reacted faster when their thigh was touched than when their toe was touched because the more distant signal from the toe would take more time to reach the brain.

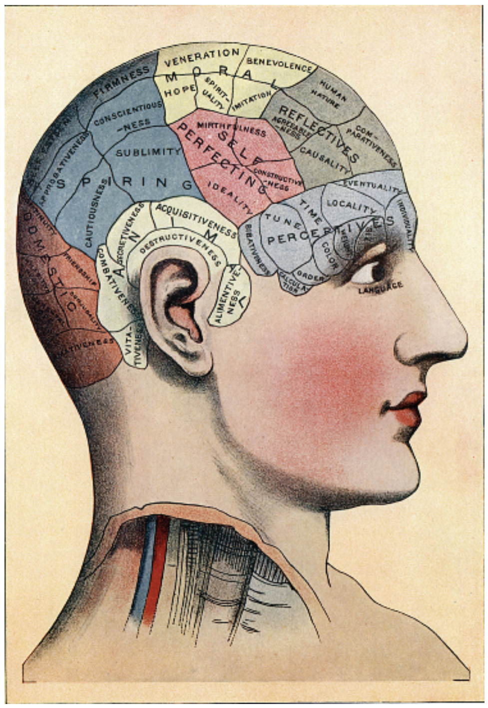
The founding of modern neuroscience has often been attributed to the British neurologist John Hughlings Jackson (1835–1911). Hughlings Jackson proposed that the nervous system was organized as a hierarchy, with simpler processing carried out by lower levels and more sophisticated processing carried out by higher levels, such as the cerebral cortex. For example, we normally inhibit aggressive behaviors, associated with activity in lower levels of the brain, by engaging our higher cortical executive functions. When a person consumes alcohol, however, the cortical inhibition might fail, leaving the lower parts of the brain to initiate a bar fight. We will meet Hughlings Jackson again in Chapter 15, in which his contributions to the understanding of epilepsy will be discussed.

Progress in the neurosciences over the past 100 years accelerated rapidly as new methods became available for studying the nervous system. Charles Sherrington not only coined the term *synapse* (defined as the point of communication between two neurons) but also conducted extensive research on reflexes and the motor systems of the brain (refer to Chapter 8). Otto Loewi demonstrated chemical signaling at the synapse (refer to Chapter 3) using an elegant research design that he claims came to him while asleep. Sir John Eccles, Bernard Katz, Andrew Huxley, and Alan Hodgkin furthered our understanding of neural communication. You will meet many more contemporary neuroscientists as you read the remainder of this text.

The ranks of neuroscientists continue to grow, with membership in the Society for Neuroscience expanding from 500 members in 1969 to approximately 36,000 members in 95 countries as of 2022 (Society for Neuroscience, 2022).

Figure 1.7 Phrenology Bust

Franz Josef Gall and his followers used maps like this one to identify traits located under different parts of the skull. Bumps on the skull were believed to indicate that the underlying trait had been "exercised." Although Gall's system was an example of bad science, the underlying principle that functions could be localized in the brain turned out to be valuable.



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Interim Summary 1.1

Summary Points 1.1

1. Neuroscience is the field that explores the structures, functions, and development of the nervous system in illness and in health. Behavioral neuroscience is the branch of the neurosciences that studies the correlations between the structures and functions of the nervous system and behavior. **(LO1)**
2. Although some periods of enlightenment regarding the relationship between the nervous system and behavior emerged among the Egyptians and Greeks, the major advances in behavioral neuroscience required technological innovation and have been relatively modern. **(LO2)**
3. Highlights in the neuroscience timeline include discoveries regarding the electrical and chemical nature of neural communication, the control of sensation and motor functions by separate nerves, the role of single cells as building blocks for the nervous system, and the localization of functions in the brain. **(LO2)**

Review Questions 1.1

1. How would you describe the goals and methods of the interdisciplinary field of neuroscience?
2. What historical discoveries contributed to our modern understanding of the brain and behavior? Which concepts actually led us in the wrong direction?

Summary Table 1.1: Highlights in the Neuroscience Timeline

Historical Period	Significant Highlights and Contributions
Ca. 3000 BCE	• Egyptians discard brain during mummification process; however, published case studies indicate accurate observations of neural disorders.
Ca. 400 BCE–200 CE	• Hippocrates recognizes that epilepsy is a brain disease. • Galen makes accurate observations from dissection; however, he believed erroneously that fluids transmitted messages.
1600–1800	• René Descartes suggests mind-body dualism. • Anton van Leeuwenhoek invents the light microscope. • Galvani and du Bois-Reymond discover that electricity transmits messages in the nervous system.
1800–1900	• Bell and Magendie determine that neurons communicate in one direction and that sensation and movement are controlled by separate pathways. • Gall and Spurzheim make inaccurate claims about phrenology, but their notion of the localization of function in the nervous system is accurate. • Paul Broca discovers the localization of speech production. • Fritsch and Hitzig identify the localization of motor function in the cerebral cortex.
1900–Present	• Ramón y Cajal declares that the nervous system is composed of separate cells; he shares the 1906 Nobel Prize with Camillo Golgi. • John Hughlings Jackson explains brain functions as a hierarchy, with more complicated functions carried out by higher levels of the brain. • Charles Sherrington coins the term *synapse*; he wins the Nobel Prize in 1932. • Otto Loewi demonstrates chemical signaling at the synapse; he wins the Nobel Prize in 1936. • Sir John Eccles, Andrew Huxley, and Alan Hodgkin share the 1963 Nobel Prize for their work in advancing our understanding of the way neurons communicate. • Bernard Katz receives the 1970 Nobel Prize for his work on chemical transmission at the synapse. • Society for Neuroscience counts about 36,000 members in 2022.

Behavioral Neuroscience Research Methods

The methods described in this section have helped neuroscientists discover the structure, connections, and functions of the nervous system and its components. From the level of single molecules to the operation of large parts of the nervous system, we now can make detailed observations that would likely astonish the early pioneers of neuroscience. The choice of methods depends very much on the goals and research questions of the neuroscientist. Each method has its share of strengths and weaknesses, but the use of multiple methods to answer a single research question can usually compensate for any gaps in a particular method.

Neuroscience methods differ along several dimensions (refer to Figure 1.8). First, we evaluate methods based on **invasiveness**, or the amount of harm associated with a method. A method that requires surgery, for example, is more invasive than one that does not. Methods also vary in the quality of their spatial and temporal resolution. A method with good **spatial resolution** will provide detailed structural images, while a method with good **temporal resolution** will provide information without delay. These factors are especially important in behavioral neuroscience as we often want to correlate a localized neural response with a stimulus.

Microscopic Methods

Microscopic, or histological, methods provide the means for observing the structure, organization, and connections of individual cells.

The naked eye can perceive objects that are at least 0.2 mm in size. To see anything smaller requires magnification (refer to Figure 1.9). Magnification alone does not guarantee a clear image, however, as you probably have noticed when you've zoomed in on an image on your computer. You just get the same blurry image with bigger pixels. Our ability to see small structures also depends on spatial resolution, or the ability to tell two points of light apart. Overcoming the natural scatter of light within the tissue being observed, which makes the image look blurry, is the main challenge of all microscopic technologies.

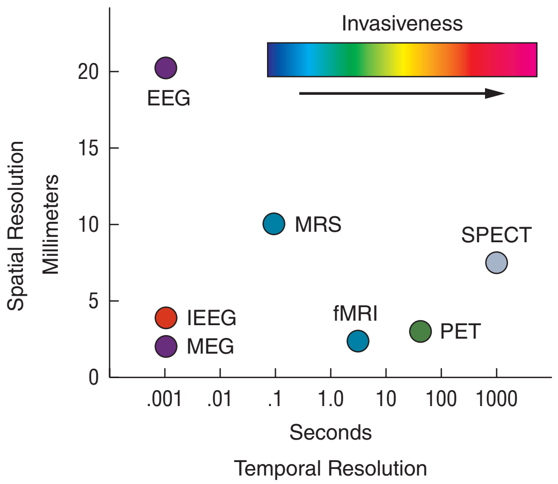
Today's light microscope can magnify an image 1,000 times while maintaining adequate spatial resolution, allowing scientists to observe a feature as small as a synapse. Because of the way our visual systems process visible light, discussed in Chapter 6, using a light microscope to magnify images beyond about 1,000 times compromises resolution to an unacceptable degree. Fortunately, other methods have been discovered that maintain both high levels of magnification and resolution. Electron microscopy can resolve images at the level of the nanoscopic scale, or between 1–100 nanometers. A nanometer is one billionth of a meter. In other words, these methods are about one million times more powerful than the naked eye.

Before using either light or electron microscopy, tissue must be prepared for viewing in a series of steps. Tissue must be thin enough to allow light (or electrons) to pass through it without too much scatter. Brain tissue is fragile and somewhat watery, which makes the production of thin enough slices impossible without further treatment. To solve this problem, the first step in the histological process is to "fix" the tissue, either by freezing it, dehydrating it, or treating it with formalin, a liquid containing the gas formaldehyde. Formalin not only hardens the tissue, making it possible to produce thin slices, but it also preserves the tissue from breakdown by enzymes or bacteria. Freezing the tissue accomplishes these objectives as well. The resulting samples can be embedded in gelatin, paraffin wax, or plastic to provide further stability and ease of slicing.

Once tissue is fixed, it is sliced or "sectioned" by a special machine known as a microtome (refer to Figure 1.10). Some microtomes look and work like a miniature version of the meat slicers found in most delicatessens. The tissue is pushed forward while a sliding blade moves back and forth across the tissue, producing slices. Other microtomes use a vibrating knife, similar to your electric toothbrush. These are particularly useful when sectioning tissue that is not frozen. For viewing tissue under the light microscope, tissue slices between 10 and 80 μm (micrometers) thick are prepared. A micrometer is one one-millionth of a meter or one

Figure 1.8 Comparing Neuroscience Methods

We can compare neuroscience methods along the dimensions of invasiveness, spatial resolution, and temporal resolution to find the best choice for our research question. Invasiveness refers to the amount of harm associated with a method. Intracranial electroencephalograms (IEEG) require surgery, so they are at the higher end of invasiveness. In contrast, electroencephalograms, taken with surface electrodes, are non-invasive. Methods with good spatial resolution (lower numbers of millimeters between dots that can be distinguished) provide better detail. Methods with good temporal resolution (fewer seconds between a neural event and its recording) allow researchers to more easily correlate neural events with their recordings in time.



Source: MIT http://web.mit.edu/kitmitmeg/whatis.html Figure 5

invasiveness A measure of the degree of harm involved with a method.

spatial resolution The ability to see fine detail in an image.

temporal resolution The ability to obtain information without delay.