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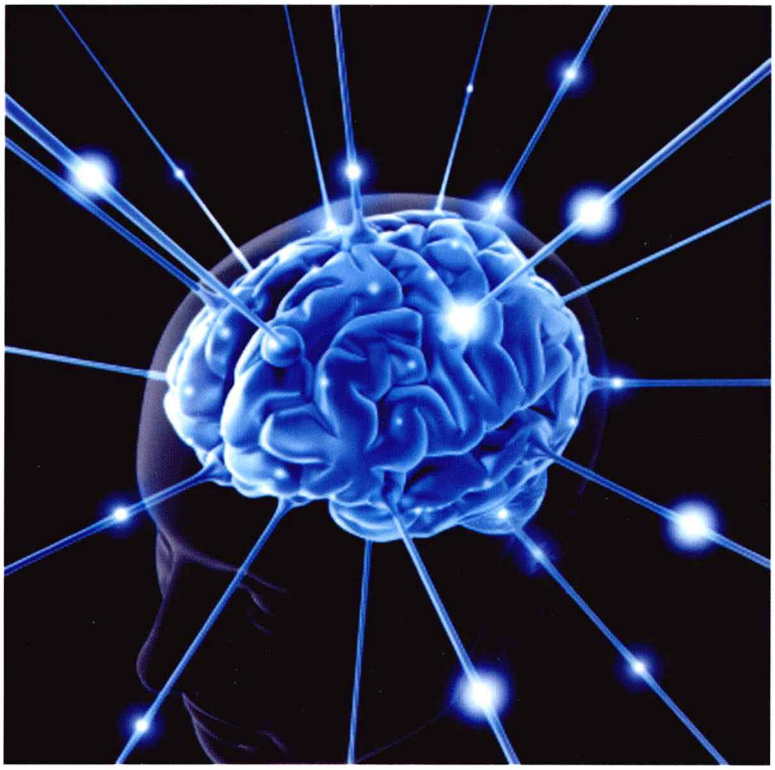

神经科学

——探索脑（第3版）（影印版）

NEUROSCIENCE

Exploring the Brain *Third Edition*

Mark F. Bear
Barry W. Connors
Michael A. Paradiso

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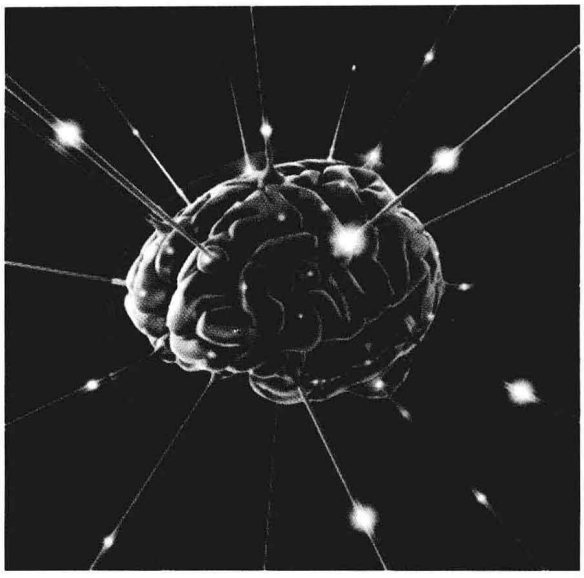

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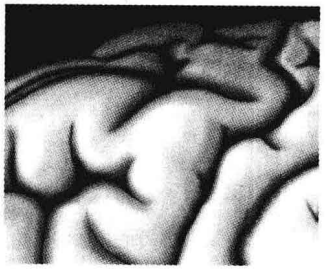
Exploring the Brain

THIRD EDITION



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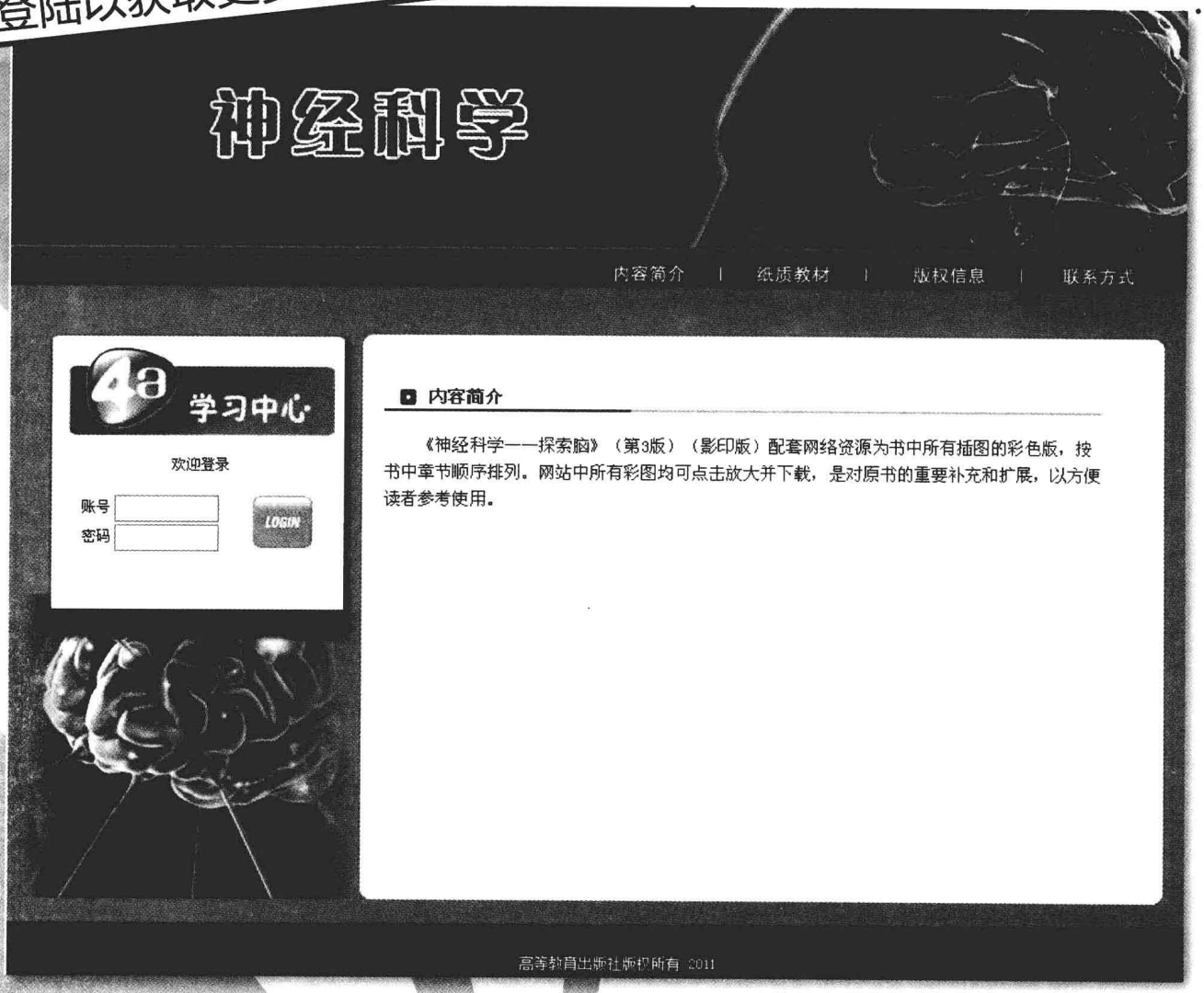

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to Terry, Ashley, and Kendall -mfb

to Rebecca, Maia, and Nina -bwc

to Wendy, Bear, and Luca Boo -map

Preface

THE ORIGINS OF *NEUROSCIENCE: EXPLORING THE BRAIN*

For over 25 years, we have taught a course called Neuroscience 1: An Introduction to the Nervous System. The course has been remarkably successful—at Brown University, where the course originated, approximately one out of every four undergraduates takes it. For a few students, this is the beginning of a career in neuroscience; for others, it is the only science course he or she takes in college.

The success of introductory neuroscience reflects the fascination and curiosity everyone has for how we sense, move, feel, and think. However, the success of our course also derives from the way it is taught and what is emphasized. First, there are no prerequisites, so the elements of biology, chemistry, and physics required for understanding neuroscience are covered as the course progresses. This approach ensures that no students are left behind as the course progresses. Second, liberal use of commonsense metaphors, real-world examples, humor, and anecdotes remind students that science is interesting, approachable, exciting, and fun. Third, the course does not survey all of neurobiology. Instead, the focus is on mammalian brains and, whenever possible, the human brain. In this sense, the course closely resembles what is taught to most beginning medical students. Similar courses are now offered at many colleges and universities by psychology, biology, and neuroscience departments.

The first edition of *Neuroscience: Exploring the Brain* was written to provide a suitable textbook for Neuro 1, incorporating the subject matter and philosophy that made this course successful. Based on feedback from our students and colleagues at other universities, we expanded the second edition to include more topics in behavioral neuroscience and some new features to help students understand the structure of the brain. We must have gotten it right, because the book now ranks as one of the most popular introductory neuroscience books in the world. It has been particularly gratifying to see our book used as a catalyst for the creation of new courses in introductory neuroscience.

NEW IN THE THIRD EDITION

Our main goals for the third edition were to incorporate the many discoveries of the past five years without increasing the length of the text, to shorten chapters when possible by emphasizing principles more and details less, and to make the book even more user-friendly by improving the layout and clarity of the illustrations.

Writing the third edition gave us the opportunity to review the research accomplishments of the past five years, and they are truly astonishing. Perhaps the most significant development has been the sequencing of the human genome, suggesting new avenues for understanding the neural basis of individuality, as well as neurological and psychiatric diseases. The book has been revised to incorporate these and many other new findings.

We authors are all active neuroscientists, and we want our readers to understand the allure of research. A unique feature of our book is the *Path of Discovery* boxes, in which famous neuroscientists tell stories about their own research. These essays serve several purposes: to give a flavor of the thrill of discovery; to show the importance of hard work and patience, as well as serendipity and intuition; to reveal the human side of science; and to entertain and amuse. We have continued this tradition in the third edition, with new contributions from 24 esteemed scientists. Included in this illustrious group are recent Nobel laureates Roderick MacKinnon and Arvid Carlsson.

AN OVERVIEW OF THE BOOK

Neuroscience: Exploring the Brain surveys the organization and function of the human nervous system. We present material at the cutting edge of neuroscience, in a way that is accessible to both science and nonscience students alike. The level of the material is comparable to an introductory college text in general biology.

The book is divided into four parts: Part I, Foundations; Part II, Sensory and Motor Systems; Part III, The Brain and Behavior; and Part IV, The Changing Brain. We begin Part I by introducing the modern field of neuroscience and tracing some of its historical antecedents. Then we take a close look at the structure and function of individual neurons, how they communicate chemically, and how these building blocks are arranged to form a nervous system. In Part II, we go inside the brain to examine the structure and function of the systems that serve the senses and command voluntary movements. In Part III, we explore the neurobiology of human behavior, including motivation, sex, emotion, sleep, language, attention, and mental illness. Finally, in Part IV, we look at how the environment modifies the brain, both during development and in adult learning and memory.

The human nervous system is examined at several different scales, ranging from the molecules that determine the functional properties of neurons to the large systems in the brain that underlie cognition and behavior. Many disorders of the human nervous system are introduced as the book progresses, usually within the context of the specific neural system under discussion. Indeed, many insights into the normal functions of neural systems have come from the study of diseases that cause specific malfunctions of these systems. In addition, we discuss the actions of drugs and toxins on the brain, using this information to illustrate how different brain systems contribute to behavior and how drugs may alter brain function.

Organization of Part I: Foundations (Chapters 1–7)

The goal of Part I is to build a strong base of general knowledge in neurobiology. The chapters should be covered sequentially, although Chapters 1 and 6 can be skipped without a loss of continuity.

In Chapter 1, we use a historical approach to review some basic principles of nervous system function and then turn to the topic of how neuroscience research is conducted today. We directly confront the ethics of neuroscience research, particularly that which involves animals.

In Chapter 2, we focus mainly on the cell biology of the neuron. This is essential information for students inexperienced in biology, and we find that even those with a strong biology background find this review helpful. After touring the cell and its organelles, we go on to discuss the structural features that make neurons and their supporting cells unique, emphasizing the correlation of structure and function.

Chapters 3 and 4 are devoted to the physiology of the neuronal membrane. We cover the essential chemical, physical, and molecular properties that enable neurons to conduct electrical signals. Throughout, we appeal to students' intuition by using a commonsense approach, with a liberal use of metaphors and real-life analogies.

Chapters 5 and 6 cover interneuronal communication, particularly chemical synaptic transmission. Chapter 5 presents the general principles of chemical synaptic transmission, and Chapter 6 discusses the neurotransmitters and their modes of action in greater detail. We also describe many of the modern methods for studying the chemistry of synaptic transmission. Later chapters do not assume an understanding of synaptic transmission at the depth of Chapter 6, however, so this chapter can be skipped at the instructor's discretion. Most coverage of psychopharmacology appears in Chapter 15, after the general organization of the brain and its sensory and motor systems has been presented. In our experience, students wish to know where, in addition to how, drugs act on the nervous system and behavior.

Chapter 7 covers the gross anatomy of the nervous system. Here we focus on the common organizational plan of the mammalian nervous system by tracing the brain's embryological development. (Cellular aspects of development are covered in Chapter 23.) We show that the specializations of the human brain are simple variations on the basic plan that applies to all mammals.

Chapter 7's appendix, An Illustrated Guide to Human Neuroanatomy, covers the surface and cross-sectional anatomy of the brain, the spinal cord, the autonomic nervous system, the cranial nerves, and the blood supply. A self-quiz will help students learn the terminology. We recommend that students become familiar with the anatomy in the Guide before moving on to Part II.

Organization of Part II: Sensory and Motor Systems (Chapters 8–14)

Part II surveys the systems within the brain that control conscious sensation and voluntary movement. In general, these chapters do not need to be covered sequentially, except for Chapters 9 and 10 on vision and Chapters 13 and 14 on the control of movement.

We chose to begin Part II with a discussion of the chemical senses—smell and taste—in Chapter 8. These are good systems for illustrating the general principles and problems in the encoding of sensory information, and the transduction mechanisms have strong parallels with other systems.

Chapters 9 and 10 cover the visual system, an essential topic for all introductory neuroscience courses. Many details of visual system organization are presented, illustrating not only the depth of current knowledge, but also the principles that apply across sensory systems.

Chapter 11 explores the auditory system, and Chapter 12 introduces the somatic sensory system. Audition and somatic sensation are such important parts of everyday life, it is hard to imagine teaching introductory neuroscience without discussing them. The vestibular sense of balance is covered in a separate section of Chapter 11. This placement offers instructors the option to skip the vestibular system at their discretion.

In Chapters 13 and 14, we discuss the motor systems of the brain. Considering how much of the brain is devoted to the control of movement, this more extensive treatment is clearly justified. However, we are well aware that the complexities of the motor systems are daunting to students and instructors alike. We have tried to keep our discussion sharply focused, using numerous examples to connect with personal experience.

Organization of Part III: The Brain and Behavior (Chapters 15–22)

Part III explores how different neural systems contribute to different behaviors, focusing on the systems where the connection between the brain and behavior can be made most strongly. We cover the systems that control visceral function and homeostasis, simple motivated behaviors (such as eating and drinking), sex, mood, emotion, sleep, consciousness, language, and attention. Finally, we discuss what happens when these systems fail during mental illness.

Chapters 15–19 describe a number of neural systems that orchestrate widespread responses throughout the brain and the body. In Chapter 15, we focus on three systems that are characterized by their broad influence and their interesting neurotransmitter chemistry: the secretory hypothalamus, the autonomic nervous system, and the diffuse modulatory systems of the brain. We discuss how the behavioral manifestations of various drugs may result from disruptions of these systems.

In Chapter 16, we look at the physiological factors that motivate specific behaviors, focusing mainly on recent research on the control of eating habits. Chapter 17 investigates the influence of sex on the brain and the influence of the brain on sexual behavior. Chapter 18 examines the neural systems believed to underlie emotional experience and expression, specifically emphasizing fear and anxiety, anger and aggression.

In Chapter 19, we investigate the systems that give rise to the rhythms of the brain, ranging from the rapid electrical rhythms of the brain during sleep and wakefulness to the slow circadian rhythms controlling hormones, temperature, alertness, and metabolism. Part III ends with a discussion of the neuroscience of language and attention in Chapters 20 and 21 and of mental illness in Chapter 22.

Organization of Part IV: The Changing Brain (Chapters 23–25)

Part IV explores the cellular and molecular basis of brain development, and learning and memory. These subjects represent two of the most exciting frontiers of modern neuroscience.

Chapter 23 examines the mechanisms used during brain development to ensure that the correct connections are made between neurons. The cellular aspects of development are discussed here rather than in Part I for several reasons. First, by this point in the book, students fully appreciate that normal brain function depends on its precise wiring. Because we use the visual system as a concrete example, the chapter also must follow a discussion of the visual pathways in Part II. Second, we survey aspects of experience-dependent development of the visual system that are regulated by the diffuse modulatory systems of the brain, so this chapter is placed after the early chapters of Part III. Finally, an exploration of the role of the sensory environment in brain development in Chapter 23 is followed in the next two chapters by discussions of how experience-dependent modifications of the brain form the basis for learning and memory. We see that many of the mechanisms are similar, illustrating the unity of biology.

Chapters 24 and 25 cover learning and memory. Chapter 24 focuses on the anatomy of memory, exploring how different parts of the brain contribute to the storage of different types of information. Chapter 25 takes a deeper look into the molecular and cellular mechanisms of learning and memory, focusing on changes in synaptic connections.

HELPING STUDENTS LEARN

Neuroscience: Exploring the Brain is not an exhaustive study. It is intended to be a readable textbook that communicates to students the important principles of neuroscience clearly and effectively. To help students learn neuroscience, we include a number of features designed to enhance comprehension:

- **Chapter Outlines, and Introductory and Concluding Remarks.** These elements preview the organization of each chapter, set the stage, and place the material into broader perspective.
- **Key Terms and Glossary.** Neuroscience has a language of its own, and to comprehend it, one must learn the vocabulary. In the text of each chapter, important terms are highlighted in boldface type. To facilitate review, these terms appear in a list at the end of each chapter, in the order in which they appeared in the text, along with page references. The same terms are assembled at the end of the book, with definitions, in a glossary.
- **Review Questions.** At the end of each chapter, a brief set of questions for review are specifically designed to provoke thought and help students integrate the material.
- **Internal Reviews of Neuroanatomical Terms.** In Chapter 7, where nervous system anatomy is discussed, the narrative is interrupted periodically with brief self-quiz vocabulary reviews to enhance understanding. In Chapter 7's appendix, an extensive self-quiz is provided in the form of a workbook with labeling exercises.
- **Further Reading.** New to the third edition, we include a list of several recent review articles at the end of each chapter to guide study beyond the scope of the textbook.
- **References and Resources.** At the end of the book, we provide selected readings and online resources that will lead students into the research literature associated with each chapter. Rather than including citations in the body of the chapters, where they would compromise the readability of the text, we have organized the references and resources by chapter and listed them at the end of the book.
- **Full-Color Illustrations.** We believe in the power of illustrations—not those that "speak a thousand words," but those that each make a single point. The first edition of this book set a new standard for illustrations in a neuroscience text. The third edition reflects improvements in the pedagogical design of many figures from earlier editions and includes many superb new illustrations as well.

User's Guide

This User's Guide shows you how to put the features of *Neuroscience: Exploring the Brain* to work for you.

Chapter Outline
This serves as your "roadmap" to the chapter content.

CHAPTER 6

Neurotransmitter Systems

Box 3.2 BRAIN FOOD

The Nernst Equation

The equilibrium potential for an ion can be calculated using the Nernst equation:

$$E_{ion} = 2.303 \frac{RT}{zF} \log \frac{[ion]_o}{[ion]_i}$$

where

E_{ion} = ionic equilibrium potential
R = gas constant
T = absolute temperature
z = charge of the ion
F = Faraday's constant
log = base 10 logarithm
$[ion]_o$ = ionic concentration outside the cell
$[ion]_i$ = ionic concentration inside the cell

The Nernst equation can be derived from the basic principles of physical chemistry. Let's see if we can make some sense of it.

Remember that equilibrium is the balance of two influences: diffusion, which pushes an ion down its concentration gradient, and electricity, which causes an ion to be attracted to opposite charges and repelled by like charges. Increasing the thermal energy of each particle increases diffusion and will therefore increase the potential difference achieved at equilibrium. Thus, E_{ion} is proportional to T. On the other hand, increasing the electrical charge of each particle will decrease the potential difference needed to balance diffusion. Therefore, E_{ion} is inversely proportional to the charge of the ion (z). We need not worry about R and F in the Nernst equation because they are constants.

At body temperature (37°C), the Nernst equation for the important ions—K^+, Na^+, Cl^-, and Ca^{2+}—simplifies to:

$$E_K = 61.54 \text{ mV} \log \frac{[K^+]_o}{[K^+]_i}$$

$$E_{Na} = 61.54 \text{ mV} \log \frac{[Na^+]_o}{[Na^+]_i}$$

$$E_{Cl} = -61.54 \text{ mV} \log \frac{[Cl^-]_o}{[Cl^-]_i}$$

$$E_{Ca} = 30.77 \text{ mV} \log \frac{[Ca^{2+}]_o}{[Ca^{2+}]_i}$$

Therefore, in order to calculate the equilibrium potential for a certain type of ion at body temperature, all we need to know is the ionic concentrations on either side of the membrane. For instance, in the example we used in Figure 3.12, we stipulated that K^+ was twentyfold more concentrated inside the cell:

If $$\frac{[K^+]_o}{[K^+]_i} = \frac{1}{20}$$

and $$\log \frac{1}{20} = -1.3$$

then $$E_K = 61.54 \text{ mV} \times -1.3$$
$$= -80 \text{ mV}.$$

Notice that there is no term in the Nernst equation for permeability or ionic conductance. Thus, calculating the value of E_{ion} does not require knowledge of the selectivity or the permeability of the membrane for the ion. There is an equilibrium potential for each ion in the intracellular and extracellular fluid. E_{ion} is the membrane potential that would just balance the ion's concentration gradient, so that no net ionic current would flow if the membrane were permeable to that ion.

Brain Food Boxes
These boxes highlight optional advanced material, allowing for flexibility in the classroom.

Box 17.1 OF SPECIAL INTEREST

Bird Songs and Bird Brains

To our ears, the singing of birds may be simply a pleasant harbinger of spring, but for birds, it is part of the serious business of sex and reproduction. Singing is strictly a male function for many species, performed for the purpose of attracting and keeping a mate and for warning off potential rivals. Studies of two bird species with different habits of reproduction and singing have revealed some fascinating clues about the control and diversity of sexual dimorphisms in the brain.

Zebra finches are popular pets, but their wild habitat is the harsh Australian desert. To breed successfully, birds require dependable sources of food, but in the desert, food comes only with sporadic and unpredictable rains. Zebra finches must therefore be ready and willing to breed whenever food and a mate are available, in any season. Wild canaries, on the other hand, live in the more predictable environment of the Azores and (where else!) the Canary Islands. They breed seasonally during spring and summer, and do not reproduce during fall and winter. The males of both species are passionate singers, but they differ greatly in the size of their repertoires. Zebra finches belt out one simple ditty all their lives, and cannot learn new ones. Canaries learn many elaborate songs, and they add new ones each spring. The different behaviors of zebra finches and canaries require different mechanisms of neural control.

The birds' sexually dimorphic behavior— singing—is generated by dramatically dimorphic neural structures. Birds sing by forcing air past a special muscularized organ called the syrinx, which encircles the air passage. The muscles of the syrinx are activated by motor neurons of the nucleus of cranial nerve XII, which are in turn controlled by a set of higher nuclei collectively called the *vocal control regions*, or *VCRs* (Figure A). In zebra finches and canaries, VCR size is five or more times larger in males than in females.

The development of VCRs and singing behavior is under the control of steroid hormones. However, the very different seasonal requirements of zebra finches and canaries are paralleled by distinctly different modes of steroidal control. Zebra finches apparently require early doses of steroids to *organize* their VCRs, and later androgens to *activate* them. If a hatchling female zebra finch is exposed to testosterone or estradiol, its VCRs will be larger than those of normal females when it reaches adulthood. If the masculinized female is given more testosterone as an adult, its VCRs will grow larger still, and she will then sing like a male. Females that are not exposed to steroids when young are unresponsive to testosterone as adults.

By contrast, the song system in canaries seems to be independent of early steroid exposure, yet it bursts into full service each spring. If female canaries are given androgens for the first time as adults, they will begin singing within a few weeks. The androgens of males surge naturally each spring; their VCRs double in size as neurons grow larger dendrites and more synapses, and singing commences. Remarkably, *neurogenesis*, the birth of neurons, continues throughout adulthood in songbird brains, further contributing to the VCR circuitry during the mating season. By fall, male androgen levels drop, and the canary song system shrinks in size as his singing abates. In a sense, the male canary rebuilds much of his song control system anew each year as courtship begins. This may enable him to learn new songs more easily and, with his enlarged repertoire, gain some advantage in attracting a mate.

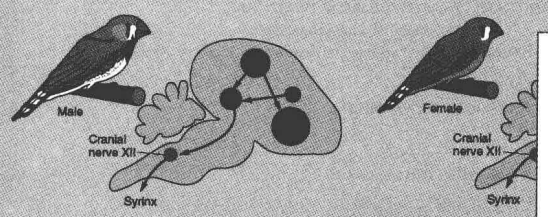


FIGURE A
Blue circles represent the vocal control regions in male and female zebra finches.

Of Special Interest Boxes
This content complements the text by enhancing the connection between neuroscience and real life, with discussion of brain disorders, human case studies, drugs, new technology, and more.

Box 3.4 PATH OF DISCOVERY

The Atomic Structure of a Potassium Channel

by Roderick MacKinnon

It should never be too late to follow a new idea. That is what I told myself when, at nearly thirty years old, I abandoned my career as a medical doctor, realizing I would be happier as a scientist. In Chris Miller's laboratory at Brandeis University, I was introduced to potassium channels. That was the beginning of an exciting adventure for me—a mixture of "chance and design," to use Alan Hodgkin's words. I think in my case it was mostly chance.

The year was 1986, when biophysicists imagined ion channels to be membrane pores with selectivity filters and gates. This essentially correct view had been deduced by Clay Armstrong, Bertil Hille, and others through thoughtful analysis of electrophysiological recordings. But ion channels were not quite "molecular." In the same way biochemists viewed enzymes. No one had ever visualized a potassium channel protein. In fact, potassium channel genes had not yet been identified, so even their amino acid sequences were a mystery. I began to study what are known as high-conductance Ca^{2+}-activated potassium channels, which we isolated from mammalian skeletal muscle and reconstituted into lipid membranes. My question was a humble one: How does a scorpion toxin inhibit these potassium channels? Admittedly, this was not a very hot topic. In fact you might say it was cold, but that made no difference to me. I was having fun learning channel biophysics, and I found the mechanism of toxin inhibition interesting, even if it seemed unimportant. It became clear to me that the toxin functions as a plug on the pore, and it interacts with ions inside the pore. I spent long hours trying to imagine what the channel might look like, and how it could selectively conduct ions at such a high rate.

About a year into my toxin studies, the potassium channel field got a huge boost when the laboratories of Lily and Yuh Nung Jan, Mark Tanouye, and Olaf Pongs reported the cloning of the *Shaker* channel from *Drosophila*. As luck would have it, I found during a late night experiment at a Cold Spring Harbor course that the *Shaker* channel was sensitive to scorpion toxins. I knew immediately that I could use scorpion toxins together with site-directed mutagenesis to identify which amino acids form the ion conduction pore. That would be valuable information because the amino acid sequence had no assigned function. The toxin led me directly to the pore and to other interesting aspects of potassium channels, such as how many subunits they have. After a few years at Harvard Medical School, where I had taken a faculty position, my laboratory defined which amino acids form the selectivity filter of the *Shaker* channel. Conservation of these amino acids in different potassium channels seemed to underscore the fact that nature had arrived at a single solution for selective K^+ conduction across the cell membrane. I began to realize then that I would not understand nature's solution without actually seeing the atomic structure (Figure A).

I needed to become a membrane protein biochemist and X-ray crystallographer. I abandoned my nicely advancing career as an electrophysiologist at Harvard and moved to Rockefeller University to concentrate on learning the new techniques. I was told that I was committing career suicide because of the difficulty with membrane proteins and my complete lack of experience. But it made little difference to me. My reasoning was simple: I would rather crash and burn trying to solve the problem than not try at all. Though the lab was initially small, we were very determined. It was a thrilling time because we knew we were working on a good problem, and we were passionate about it. Through hard work, perseverance, and more than a little luck, a very beautiful piece of nature slowly revealed itself to us. It was in fact more beautiful than I ever could have imagined.

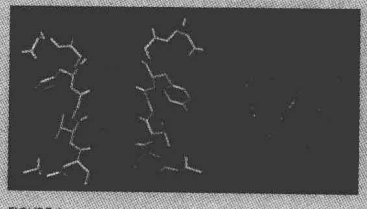


FIGURE A
The protein structure of the potassium channel selectivity filter (from two of four subunits) is yellow; oxygen atoms are red spheres. Electron density (blue mesh) shows K^+ ions (green spheres) lined up along the pore. Inside the filter, each K^+ ion binding site is surrounded by eight oxygen atoms, which appear to mimic the water molecules surrounding the hydrated K^+ ion below the filter. (Courtesy of Dr. Roderick MacKinnon.)

Path of Discovery Boxes
24 new boxes, written by leading neuroscience researchers, highlight current discoveries and achievements of individuals in the field of neuroscience. Path of Discovery boxes from the previous two editions are available on the Instructor's Resource CD and online at http://connection.lww.com/go/bear.

spinal cord runs anterior to posterior. The top side of the spinal cord is the dorsal side, and the bottom side is the ventral side.

If we look down on the nervous system, we see that it may be divided into two equal halves (Figure 7.2b). The right side of the brain and spinal cord is the mirror image of the left side. This characteristic is known as *bilateral symmetry*. With just a few exceptions, most structures within the nervous system come in pairs, one on the right side and the other on the ft. The invisible line running down the middle of the nervous system is lled the **midline**, and this gives us another way to describe anatomical ferences. Structures closer to the midline are **medial**; structures farther way from the midline are **lateral**. In other words, the nose is medial to e eyes, the eyes are medial to the ears, and so on. In addition, two struc- res that are on the same side are said to be **ipsilateral** to each other; for ample, the right ear is ipsilateral to the right eye. If the structures are on pposite sides of the midline, they are said to be **contralateral** to each her; the right ear is contralateral to the left ear.

To view the internal structure of the brain, it is usually necessary to slice up. In the language of anatomists, a slice is called a *section*; to slice is *to ction*. Although one could imagine an infinite number of ways we might ut into the brain, the standard approach is to make cuts parallel to one of e three *anatomical planes of section*. The plane of the section resulting from plitting the brain into equal right and left halves is called the **midsagittal lane** (Figure 7.3a). Sections parallel to the midsagittal plane are in the **agittal plane**.

The two other anatomical planes are perpendicular to the sagittal plane and one another. The **horizontal plane** is parallel to the ground (Figure 3b). A single section in this plane could pass through both the eyes and e ears. Thus, horizontal sections split the brain into dorsal and ventral arts. The **coronal plane** is perpendicular to the ground and to the sagit- l plane (Figure 7.3c). A single section in this plane could pass through oth eyes or both ears, but not through all four at the same time. Thus, the oronal plane splits the brain into anterior and posterior parts.

The Golgi Stain

The Nissl stain, however, does not tell the whole story. A Nissl-stained neuron looks like little more than a lump of protoplasm containing a nucleus. Neurons are much more than that, but how much more was not recognized until the publication of the work of Italian histologist Camillo Golgi (Figure 2.2). In 1873, Golgi discovered that by soaking brain tissue in a silver chromate solution, now called the **Golgi stain**, a small percentage of neurons became darkly colored in their entirety (Figure 2.3). This revealed that the neuronal cell body, the region of the neuron around the nucleus that is shown with the Nissl stain, is actually only a small fraction of the total structure of the neuron. Notice in Figures 2.1 and 2.3 how different histological stains can provide strikingly different views of the same tissue. Today, neurohistology remains an active field in neuroscience, along with its credo: "The gain in brain is mainly in the stain."

The Gólgi stain shows that neurons have at least two distinguishable parts: a central region that contains the cell nucleus, and numerous thin tubes that radiate away from the central region. The swollen region containing the cell nucleus has several names that are used interchangeably: **cell body**, **soma** (plural: somata), and **perikaryon** (plural: perikarya). The thin tubes that radiate away from the soma are called **neurites** and are of two types: **axons** and **dendrites** (Figure 2.4).

The cell body usually gives rise to a single axon. The axon is of uniform diameter throughout its length, and if it branches, the branches generally extend at right angles. Because axons can travel over great distances in the body (a meter or more), it was immediately recognized by the histologists of the day that axons must act like "wires" that carry the output of the neurons. Dendrites, on the other hand, rarely extend more than 2 mm in

KEY TERMS

Types of Memory and Amnesia
learning (p. 726)
memory (p. 726)
declarative memory (p. 726)
nondeclarative memory (p. 726)
procedural memory (p. 726)
long-term memory (p. 727)
short-term memory (p. 729)
memory consolidation (p. 729)
working memory (p. 729)
amnesia (p. 729)
retrograde amnesia (p. 730)
anterograde amnesia (p. 730)

The Search for the Engram
engram (p. 731)
cell assembly (p. 733)

The Temporal Lobes and Declarative Memory
hippocampus (p. 740)
entorhinal cortex (p. 741)
perirhinal cortex (p. 741)
parahippocampal cortex (p. 741)
fornix (p. 741)
delayed non-match to sample (DNMS) (p. 741)
recognition memory (p. 742)
Korsakoff's syndrome (p. 744)
Morris water maze (p. 746)
place cell (p. 747)
relational memory (p. 749)

The Striatum and Procedural Memory
striatum (p. 751)

The Neocortex and Working Memory
prefrontal cortex (p. 754)
lateral intraparietal cortex (area LIP) (p. 757)

Key Terms
Appearing in bold throughout the text, key terms are also listed at the end of each chapter and defined in the glossary.

REVIEW QUESTIONS

1. If you try to recall how many windows there are in your house by mentally walking from room to room, are you using declarative memory, procedural memory, or both?
2. What evidence is there that declarative and nondeclarative memory use distinct circuits?
3. What abilities and disabilities do you think a person completely lacking working memory would have?
4. Why did Lashley conclude that all cortical areas contribute equally to learning and memory? Why was this conclusion later called into question?
5. What evidence indicates that long-term memories are stored in neocortex?
6. If you were using a microelectrode to record from the brain and you suspected that a neuron you encountered was involved in storing long-term memories, how would you test that hypothesis?
7. If a neuron in visual cortex responds to faces, how could you determine whether it is involved in perception or storing memories for faces?
8. What are place cells, and where are they found? In what ways are the response characteristics of place cells different from the receptive fields of sensory neurons?
9. What role does the hippocampus play in spatial memory, working memory, and relational memory?
10. What is working memory, and in what brain areas have neural correlates of working memory been observed?

Review Questions
Chapter review questions provoke thought and help students test their comprehension of each chapter's major concepts.

FURTHER READING

Baddeley A. 2003. Working memory: looking back and looking forward. *Nature Reviews Neuroscience* 4:829–839.

Corkin S. 2002. What's new with the amnesic patient H.M.? *Nature Reviews Neuroscience* 3:153–160.

Eichenbaum H. 2000. A cortical-hippocampal system for declarative memory. *Nature Reviews Neuroscience* 1:41–50.

Haxby JV, Petit L, Ungerleider LG, Courtney SM. 2000. Distinguishing the functional roles of multiple regions in distributed neural systems for visual working memory. *Neuroimage* 11:380–391.

Passingham D, Sakai K. 2004. The prefrontal cortex and working memory: physiology and brain imaging. *Current Opinion in Neurobiology* 14:163–168.

Squire LR, Stark CEL, Clark RE. 2004. The medial temporal lobe. *Annual Review of Neuroscience* 27:279–306.

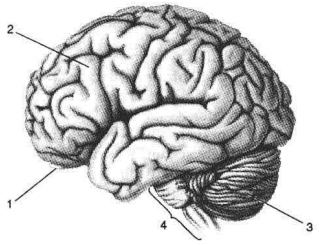
Further Reading
Recent review articles are identified at the end of each chapter to guide further study.

▼ SELF-QUIZ

This review workbook is designed to help you learn the neuroanatomy that has been presented. Here we have reproduced the images from the Guide; instead of labels, however, numbered leader lines (arranged clockwise) point to the structures of interest. Test your knowledge by filling in the appropriate names in the spaces provided. To review what you have learned, quiz yourself by putting your hand over the names. This technique greatly facilitates the learning and retention of anatomical terms. Mastery of the vocabulary of neuroanatomy will serve you well as you learn about the functional organization of the brain in the remainder of the book.

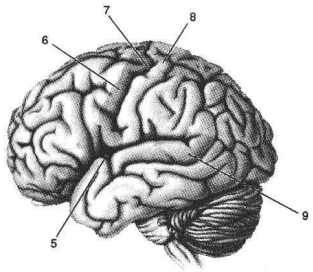
THE LATERAL SURFACE OF THE BRAIN

(a) Gross Features



1. _____
2. _____
3. _____

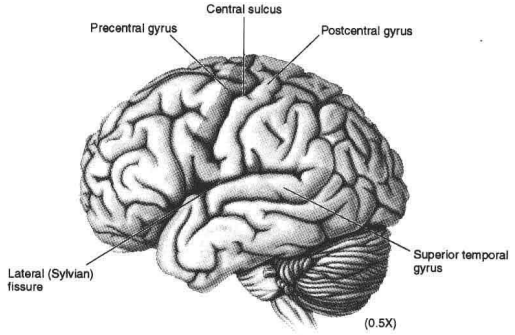
(b) Selected Gyri, Sulci, and Fissures



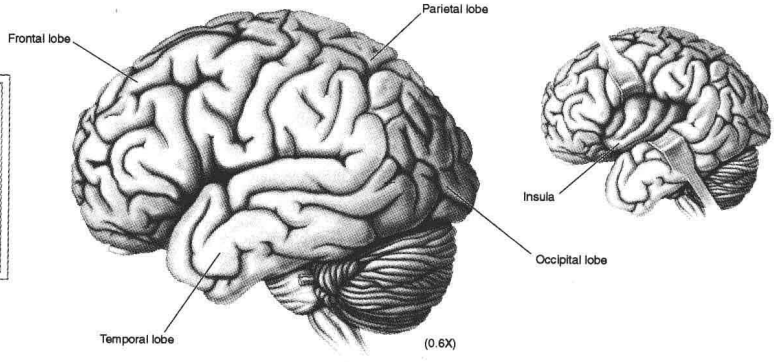
An Illustrated Guide to Human Neuroanatomy

This exceptional appendix to Chapter 7 includes an extensive self-quiz with labeling exercises that enable students to assess their knowledge of neuroanatomy.

(b) Selected Gyri, Sulci, and Fissures. The cerebrum is noteworthy for its convoluted surface. The bumps are called gyri, and the grooves are called sulci or, if they are especially deep, fissures. The precise pattern of gyri and sulci can vary considerably from individual to individual, but many features are common to all human brains. Some of the important landmarks are labeled here. The postcentral gyrus lies immediately posterior to the central sulcus, and the precentral gyrus lies immediately anterior to the central sulcus. The neurons of the postcentral gyrus are involved in somatic sensation (touch; Chapter 12), and those of the precentral gyrus control voluntary movement (Chapter 14). Neurons in the superior temporal gyrus are involved in audition (hearing; Chapter 11).



(c) Cerebral Lobes and the Insula. By convention, the cerebrum is subdivided into lobes named after the bones of the skull that lie over them. The central sulcus divides the frontal lobe from the parietal lobe. The temporal lobe lies immediately ventral to the deep lateral (Sylvian) fissure. The occipital lobe lies at the very back of the cerebrum, bordering both parietal and temporal lobes. A buried piece of the cerebral cortex, called the insula (Latin for "island"), is revealed if the margins of the lateral fissure are gently pulled apart (inset). The insula borders and separates the temporal and frontal lobes.



Self-Quiz

These brief vocabulary reviews found in Chapter 7 enhance students' understanding of nervous system anatomy.

▼ SELF-QUIZ

Take a few moments right now and be sure you understand the meaning of these terms:

anterior	ventral	contralateral
rostral	midline	midsagittal plane
posterior	medial	sagittal plane
caudal	lateral	horizontal plane
dorsal	ipsilateral	coronal plane

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Exceptional artwork engages readers and illuminates content.

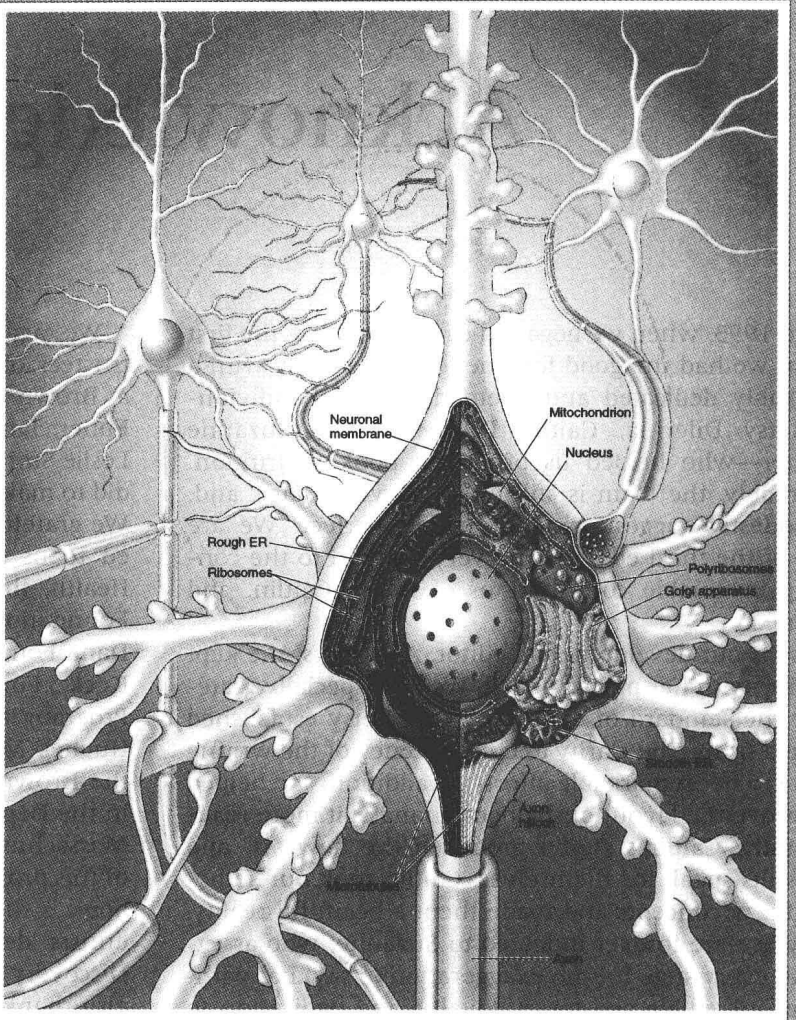

FIGURE 2.7
The internal structure of a typical neuron.

Acknowledgments

Back in 1993, when we began in earnest to write the first edition, we had the good fortune to work closely with a remarkably dedicated and talented group of individuals—Betsy Dilernia, Caitlin Duckwall, and Suzanne Meagher—who helped us bring the book to fruition. Remarkably, the team is still intact 12 years later, and, we modestly suggest, practice makes perfect. We are proud of the third edition, and very grateful to the continuing invaluable contributions of Betsy, Caitlin, and Suzanne.

Betsy is our developmental editor. As always, she kept us in line with her purple pencil. We are especially grateful for the standard of excellence that Betsy established and held us to. The clarity and consistency of the writing are due to her remarkable efforts. In addition, she helped us improve the layout of the book to make it more reader-friendly. Caitlin's studio produced the new art, and the results speak for themselves. Caitlin took our sometimes fuzzy concepts and made them a beautiful reality. Finally, we are forever indebted to Suzanne, who assisted us at every step. It is no exaggeration to say that without her incredible assistance, loyalty, and dedication to this project, the book would never have been completed. Suzanne, you are the best!

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In the publishing industry, editors seem to come and go with alarming frequency. Yet two senior editors at Lippincott Williams & Wilkins have stayed the course and been unwavering advocates for our project: Nancy Evans and Susan Katz. Thanks to you and the entire staff under your direction. It has been a pleasure working with you.

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