教育部高等教育司推荐
国外优秀生命科学教学用书

Neuroscience

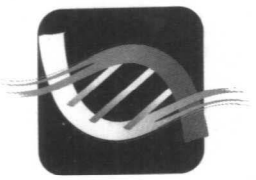
Exploring the Brain

神经科学 影印版

Second Edition

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

高等教育出版社
Higher Education Press



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出 版 前 言

随着克隆羊的问世和人类基因组计划的完成，生命科学成为21世纪名副其实的领头学科，生物高新技术产业逐步成为高科技产业的核心。生物科技和生物产业的发展对世界科技、经济、政治和社会发展等方面产生着深刻的影响，这也是我国赶超世界发达国家生产力水平最有前途和希望的领域。生命科学与技术全方位的发展呼唤高等教育培养更多高水平的复合型科技人才。

为此，教育部在《关于加强高等学校本科教学工作　提高教学质量的若干意见》[教高(2001)4号文件]中提出，高等学校要大力提倡编写、引进和使用先进教材，其中信息科学、生命科学等发展迅速、国际通用性强、可比性强的学科和专业可以直接引进先进的、能反映学科发展前沿的原版教材。教育部高等教育司还于2001年11月向全国主要大学和出版社下发了“关于开展‘国外生命科学类优秀教学用书’推荐工作的通知”，有力推动了生命科学类教材的引进工作。

高等教育出版社对国外生命科学教材进行了充分的调研，并委托教育部高等学校生物科学与工程教学指导委员会的专家教授开展了“引进国外优秀生命科学教材及其教学辅助材料专项研究”，并就国内外同类教材进行了比较，提出了具体的引进教材书目。经过版权谈判，目前我社已经购买了Pearson Education，McGraw－Hill，John Wiley & Sons，Blackwell Science，Thomson Learning，Cambridge University Press，Lippincott Williams & Wilkins等出版的13种教材的影印权，学科领域涉及生物化学、细胞生物学、遗传学、微生物学、生态学、免疫学、神经科学、发育生物学、解剖学与生理学、分子生物学、普通生物学等。这些教材具有以下特点：(1) 所选教材基本是近2年出版的，及时反映了学科发展的最新进展，在国际上使用广泛，具有权威性和时代感；(2) 内容简明，篇幅适中，结构合理，兼具一定的深度和广度，适用范围广；(3) 插图精美、丰富，既有很强的艺术性，又不失严谨的科学性，图文并茂，与正文相辅相成；(4) 语言简练、流畅，十分适合非英语国家的学生阅读。其中9种已入选教育部高等教育司推荐“国外优秀生命科学教学用书”。

考虑到中国国情，为了让学生买得起，同时又能让学生看到原版书彩色精美的插图，我们在引进学生用原版教材时，一方面采用黑白影印，最大限度地降低定价，另一方面随书附赠含有原书彩色插图的光盘，以充分体现原教材的风格、特色，为读者提供方便。

引进国外优秀生命科学教学用书是我社一项长期的重点工作，因此，我们衷心希望广大专家教授和同学提出宝贵的意见和建议，如有更好的教材值得引进，请与高等教育出版社生命科学分社联系，联系电话：010－68344002，E－mail地址：lifesciences－hep@x263.net。

高等教育出版社

2002年11月

to our parents

Naomi and Firman Bear
Rose and John Connors
Marie and Nicholas Paradiso

PREFACE

THE ORIGINS OF *NEUROSCIENCE: EXPLORING THE BRAIN*

For over twenty years, Brown University has offered a course called Neuroscience 1: An Introduction to the Nervous System. The course has been remarkably successful: Approximately one of every four Brown 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 will take in college.

The success of introductory neuroscience reflects the fascination and curiosity everyone has for how we sense, move, feel, and think. We believe, however, that the success of our course also derives from the way it is taught and what is emphasized. A cornerstone of our philosophy is that we assume only minimal prior knowledge of biology, physics, and chemistry. The fundamentals required for understanding neuroscience are covered as the course progresses. This approach ensures that we can work up to advanced concepts with confidence that students are on track. We also strive to show that science is interesting, exciting, and fun. To this end, we include liberal amounts of commonsense metaphors, real-world examples, humor, and anecdotes. Finally, our course does not survey all of neurobiology. Instead, we focus on mammalian brains and, whenever possible, the human brain. In this sense, the course closely resembles what is taught to most second-year medical students, but without prerequisites. 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 Neuroscience 1, incorporating the subject matter and philosophy that made introductory neuroscience successful here at Brown. It has been very gratifying to see that the book has gained popularity around the world, sometimes acting as the catalyst for new courses in introductory neuroscience. This enthusiastic response encouraged us to write a second edition. Not only have we updated the book with the latest discoveries in this fast-paced field, we have incorporated numerous suggestions for improvement from our students and colleagues.

NEW IN THE SECOND EDITION

Writing the second edition gave us the opportunity to review the research accomplishments of the past five years, and they are truly astonishing. Examples are the recent determination of the three-dimensional structure of a selectively permeable ion channel, important for understanding neuronal signaling, and the discovery of the hormone, leptin, which has revolutionized our understanding of how feeding behavior is regulated. The book has been revised to incorporate these and many other new findings. In addition to bringing the book up to date, we have expanded and added a number of new features.

More Connections With Real Life

A popular component of the first edition, *Of Special Interest* boxes illustrate how a knowledge of neuroscience can be applied. We have expanded this feature with an eye toward making more connections with real life, including substantially increased coverage of common nervous system disorders,

such as Alzheimer's disease and mental retardation. In addition, we incorporated more discussion of neurological disorders in the text of the chapters, where such coverage helps illustrate important principles—for example, in the control of voluntary movement.

More Anatomy

Over the years, our students have consistently indicated that they would like to have expanded coverage of nervous system anatomy to give them a better appreciation of how all the different components fit together. We have responded by including *An Illustrated Guide to Human Neuroanatomy*, new to the second edition as an appendix to Chapter 7. This illustrated appendix provides a preview of the structures students will encounter in specific functional contexts in later chapters. To help students learn the new terminology, a Self-Quiz with labeling exercises is also provided.

More Behavioral Neuroscience

Interesting topics in neuroscience far outnumber the chapters that are appropriate for an introductory text. Feedback from our colleagues at other institutions indicated, however, a need to expand coverage of behavioral neuroscience. Based on this valuable input, we added three exciting new chapters that connect the brain and behavior: Motivation (Chapter 16), Sex and the Brain (Chapter 17), and Mental Illness (Chapter 21).

More Brain Food

Our goal was to provide a book that anyone—regardless of his or her science background—could begin on the first page and understand all the way through. Of course, neuroscience is a rigorous, quantitative scientific discipline. In the first edition, we covered advanced concepts in cellular neurophysiology using *Brain Food* boxes. We have expanded this feature in the second edition, providing greater coverage of advanced concepts and new technologies. Isolating this material from the main text gives instructors flexibility in making reading assignments that are appropriate for students' backgrounds.

New Discoverers

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 new edition, with contributions from twenty-four esteemed scientists. Included in this illustrious group are three Nobel laureates: Erwin Neher, Torsten Wiesel, and Susumu Tonegawa. We are very grateful to the *Path of Discovery* authors for their time, effort, and enthusiasm.

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, mood, emotion, sleep, language, and attention. 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 levels, 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 we 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 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 used to study the chemistry of synaptic transmission. Later chapters do not assume an understanding of synaptic transmission at the depth of Chapter 6, however, so this 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 22.) We show that the specializations of the human brain are simple variations on the basic plan that applies to all mammals.

The Chapter 7 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 *Illustrated 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 an important part of everyday life that it is hard to imagine teaching introductory neuroscience without discussing them. The vestibular sense of balance is now also 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. We are well aware, however, 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 15–21)

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 explore 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 very 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, reinforcement and reward.

In Chapter 19, we explore 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 higher brain functions in Chapter 20 and of mental illness in Chapter 21.

Organization of Part IV: The Changing Brain (Chapters 22–24)

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

Chapter 22 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 explore 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 22 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 23 and 24 cover learning and memory. Chapter 23 focuses on the anatomy of memory, exploring how different parts of the brain contribute to storage of different types of information. Chapter 24 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 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, we include a brief set of questions for review. These 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 the Chapter 7 appendix, an extensive Self-Quiz is provided in the form of a workbook with labeling exercises.
- **References and Suggested Readings.** To guide study beyond the scope of the textbook, we provide selected readings 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 suggested readings 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 bar has been raised again, with many superb new illustrations for the second edition.

ACKNOWLEDGMENTS

First and foremost, we wish to thank four people who made extraordinary contributions to this edition of the book: Betsy Dilernia, Caitlin Duckwall, Jim McIlwain, and Suzanne Meagher. Betsy served as our development editor, once again keeping us in line with her purple pencil. We are especially grateful for the standard of excellence that she established and held us to. The clarity and consistency of the writing are due to her remarkable efforts. Caitlin produced the new art, and the results speak for themselves. Caitlin took our sometimes fuzzy concepts and made them a beautiful reality. Jim is a mentor, faculty colleague, and friend; he is also an award-winning professor of neuroscience. Jim read every word of our nascent manuscript and showed us how to improve it. 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!

We again would like to acknowledge the architects and current trustees of the undergraduate neuroscience curriculum at Brown University. We thank Mitchell Glickstein, Ford Ebner, James McIlwain, Leon Cooper, James Anderson, Leslie Smith, John Donoghue, and John Stein for all they did to make undergraduate neuroscience great at Brown. We thank the staff of Lippincott Williams & Wilkins for believing in this project and guiding it towards successful completion. We gratefully acknowledge the research support provided to us over the years by the National Institutes of Health, the Whitehall Foundation, the Alfred P. Sloan Foundation, the Klingenstein Foundation, the Charles A. Dana Foundation, the National Science Foundation, the Keck Foundation, the Human Frontiers Science Program, the Office of Naval Research, and the Howard Hughes Medical Institute. We thank our colleagues in the Brown University Department of Neuroscience for their support of this project and helpful advice. We thank the anonymous but very helpful colleagues at other institutions who gave us comments on the first edition and reviewed the first draft of our manuscript for the second. We gratefully acknowledge the scientists who provided us with figures illustrating their research results. In addition, many students and colleagues helped us to improve the new edition by informing us about recent research, pointing out errors in the first edition and suggesting better ways to describe or illustrate concepts. We thank them all, including (but not limited to) Yael Amitai, Teresa Audesirk, Michael Beierlein, Steve Chamberlin, Richard Cantin, Z. H. Cho, Geoffrey Gold, Jennifer Hahn, Richard Huganir, David Glanzman, Robert Malenka, John Morrison, Saundra Patrick, Robert Patrick, Erik Sklar, John Stein, Nelson Spruston, J. Michael Walker, and Wes Wallace.

We thank our loved ones for standing by us despite the countless weekends and evenings lost to preparing this book.

Last, but not least, we wish to thank the thousands of students to whom we have had the privilege to teach neuroscience over the past two decades.

国外优秀生命科学教学用书

（影印教材）

Biochemistry (2nd ed.)	生物化学
Cell and Molecular Biology (3rd ed.)	分子细胞生物学
Essentials of Genetics (4th ed.)	遗传学基础
Microbiology (5th ed.)	微生物学
Ecology: concepts and applications (2nd ed.)	生态学
Roitt's Essential Immunology (10th ed.)	Roitt 免疫学基础
Neuroscience：Exploring the Brain (2nd ed.)	神经科学
Essential Developmental Biology	发育生物学基础
Understanding Human Anatomy and Physiology (4th ed.)	人体解剖生理学
Gene Cloning and DNA Analysis (4th ed.)	基因克隆和 DNA 分析
Principles of Gene Manipulation (6th ed.)	基因操作原理
An Introduction to Genetic Engineering (2nd ed.)	遗传工程导论
Essential Biology	生物学导论

BRIEF CONTENTS

(continues)

PART IV THE CHANGING BRAIN

DETAILED CONTENTS

PART I FOUNDATIONS