

Fundamental Neuroscience



SECOND EDITION

Squire • Bloom • McConnell

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FUNDAMENTAL NEUROSCIENCE

SECOND EDITION

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FUNDAMENTAL NEUROSCIENCE

SECOND EDITION

Preface to the First Edition

To our students, from whom we learn much.

Fundamental Neuroscience began with an ambitious set of objectives. We wished to produce a textbook that would: (1) introduce graduate students coming from diverse backgrounds to the full range of neuroscience, from molecular biology to clinical science; (2) assist instructors in offering an in-depth course in neuroscience to advanced undergraduates; (3) permit a research-oriented approach to neuroscience for medical students and others preparing for a professional career in the health sciences; and (4) provide a current resource for all who wish to familiarize themselves with this rapidly changing area. We also wished to contribute to the educational process in another way—by providing direct financial support.

This book reviews most of the major issues in neuroscience and some of the minor ones as well. We have included a large number of illustrations, almost all of them newly drawn. In addition, we have described many experiments to illustrate how information is gathered and conclusions are drawn and have included boxes that provide greater details and clinical correlations. Although we have focused on vertebrate neurobiology, particularly that of mammals, we have included examples from studies of invertebrates when that information was thought particularly useful to our objectives. And we have added a number of ethics cases for your consideration to emphasize our belief that good science and responsible conduct are inseparable.

To accomplish all this, the senior editors identified a group of section editors with experience both as researchers and as educators. These individuals were then asked to draft a table of contents for their sections and to find appropriate authors. Finally, the authors were asked to take part in an experiment—to try to produce a textbook that had the wisdom of a collection of individual reviews written by experts in their field and the cohesiveness of a single-authored

volume. This required that the authors be willing to write material that would then be modified by others, often many others. We researchers don't like having our words—let alone our ideas—modified by anyone. And yet we assembled the team, and here, almost exactly six years after we began, our experiment has been completed.

The authors whom you will see listed under the titles of individual chapters and at the end of boxes are those people who accepted responsibility for preparing the initial drafts of material used in the textbook. In most cases they are listed in alphabetical order, although in some instances one individual played a substantially greater role than others and is listed first for that reason. There are instances in which the final chapter is very similar to that initially provided by the authors. In other cases a great deal of editing occurred. There are even chapters containing material taken from other chapters as well as chapters that were synthesized from several individual contributions. All this was done in an effort to provide you with the best possible textbook.

The Association of Neuroscience Departments and Programs (ANDP) was central to our efforts. The Council of the ANDP encouraged us to take on the task, and members of the ANDP provided critical input to the organization of the textbook. In particular, we thank the many individuals who commented on specific components of our project at various stages and thereby helped us to serve students and course instructors. These individuals include Yalchin Abdulaev, John Ashe, Jim Blankenship, John Bruno, Richard Burry, Dennis Choi, Avis Cohen, Gregory Cole, Ian Creese, Kathleen Dunlap, Gary Fiskum, Karen Gale, Glenn Hatton, John Hildebrand, John Kauer, James King, Kenneth Kratz, Richard Levine, Eve Marder, Alex Martin, Lorne Mendell, Ranney Mize, Sally Moody, Elisabeth Murray, Randolph Nudo, David Potter, Dale Purves, George Rebec, Nicholas Spitzer, Glenn Stanley, and Paula Tallal. One-third of the royalties generated by sales of this textbook will be contributed to the ANDP to support their educational projects.

A number of other neuroscientists also participated in the formulation of this project. Anthony Movshon played a major role in organizing the section on sensory systems and recruiting its authors. Dennis O'Leary was instrumental in formulating the section on development. In addition, Darcy Kelley, Tom Reese, Patricia Goldman-Rakic, Tom Carew, Paula Tallal, Karl Herrup, Joseph LeDoux, Nick Spitzer, Richard Thompson, and Stephen Waxman participated in early discussions concerning the book.

Many others should be acknowledged, as well. Perhaps chief among them is Bob Woolley, our illustrator. For two years this project was a central component of Bob's life as he struggled to convert authors' sketches into final products, sought their input, handled their feedback, and met our deadlines. We hope that the results of his efforts, and those of Patrick Hof, who collaborated on many of the illustrations, will enrich your reading of this textbook and, through the use of visual aids that we can provide, enrich the classroom experience as well.

Craig Panner, acquisitions editor, provided day-today (and year-to-year) coordination of the entire endeavor, working well beyond the call of professional duty to keep together the thousand pieces. Susan Giegel, working at the University of Pittsburgh, oversaw many aspects of the project, arranged conference calls and meetings, read and wrote memos, answered queries, and provided pleasant and effective encouragement to meet deadlines. Cindy MacDonald, editorial manager, orchestrated a team of developmental editors and moderated discussions with often fiercely independent authors to provide a consistent text. These outstanding editors, who challenged the authors to clarify and simplify and then clarify again, were Matt Lee, Arkady Mak, Philippa Solomon, Lee Young, and Patty Zimmerman. Jacqueline Garrett, desk editor, scheduled the final production of the book and then "made it happen." Debby Bicher provided the interface between the illustrators and the typesetters. Cathy Reynolds designed the book, inside and out. Suzanne Rogers developed the marketing designs that inspired the cover, while Karen Steele and Charlotte Brabants orchestrated the marketing and promotions. Jasna Markovac provided essential advice in the early stages of the project and continued encouragement throughout. Erika Conner provided assistance at the outset of this project, and Karen Dempsey provided key administrative help all along the way.

Finally, there is Graham Lees. It was Graham, neuroscientist by training, editor by profession, who provided the most essential ingredient for this project form the very beginning—faith. Graham did more than encourage us from the sidelines, he was an active participant, suggesting editors and authors, commissioning paragraphs and boxes, critiquing content and style—even approving expensive modifications (e.g., multicolor figures) when he felt it would help the students, and all the while sending out a cheery newsletter, *FuNews*. There would be no textbook without Graham.

We hope we have achieved our initial goal—a text-book that will be of value to virtually anyone interested in neuroscience. We invite all of you to join us in the adventure of studying the nervous system. Indeed, we hope you will be active participants in that adventure. Earlier in this preface we stated that our experiment had been completed. Of course, that is not entirely true. As you read this we are already beginning to prepare the next edition. And we hope that you will participate in the process by sending comments to us at FN@acad.com. You also are invited to stay in touch with us through our web site (www.academicpress.com/fun). Here we will post material to supplement the textbook, including study questions, updates, and corrections.

A story is told that Charles Darwin once received a letter from a student who was just beginning his studies as a naturalist. The student is said to have asked what advice Mr. Darwin might offer to someone just starting this career. Darwin wrote back, "Try to discover one new fact." This book contains many facts, along with unifying ideas and principles that reflect our current knowledge of the nervous system. But it is also true that there is still much, much more to understand and that in some cases we do not yet even know what the questions are. We hope—we believe—that from among those of you who use this book will come the next generation of neuroscientists, individuals who will take up Darwin's challenge to discover things about the brain that no one knew before. It is to you that we dedicate Fundamental Neuroscience.

> The Senior Editors La Jolla, California

Preface to the Second Edition

In this second edition of Fundamental Neuroscience, we have tried to improve on the first edition and to produce a volume that effectively introduces students to the full range of contemporary neuroscience. Neuroscience is a large field founded on the premise that all of behavior and all of mental life have their origin in the structure and function of the nervous system. Today, the need for a single-volume introduction to neuroscience is greater than ever. Toward the end of the 20th century, the study of the brain became a central part of biological and psychological science. The maturation of neuroscience has meant that individuals from diverse backgrounds-molecular biologists, computer scientists, and psychologists—are interested in learning about the structure and function of the brain, about how the brain works. In addition, new techniques and tools have become available to study the brain with ever-increasing precision and detail. In the last 10 years, new genetic methods have been introduced to study the molecular biology of cells, neural systems, behavior, and neuroimaging techniques such as functional magnetic resonance imaging have been developed that permit study of the living human brain while it is engaged in cognition.

This second edition attempts to capture the promise and excitement of this fast-moving discipline. The new edition is shorter than that the first one but covers the same comprehensive range of topics. The first section of the volume begins with a new opening chapter that provides an overview of the discipline. A second chapter presents fundamental information about the architecture and anatomy of nervous systems. The remainder of the volume (sections II–VIII) presents the major topics of neuroscience. The second section (Cellular and Molecular Neuroscience) considers the cellular and subcellular organization of neurons, the physiology of nerve cells, and how signaling occurs between neurons. The third section (Nervous System Development) includes discussions of neurogenesis,

migration, process outgrowth, and synapse formation. The fourth and fifth sections (Sensory Systems and Motor Systems) describe the neural organization of each sensory modality and the organization of the brain pathways and systems important for locomotion, voluntary action, and eye movements. The sixth section (Regulatory Systems) describes the variety of hypothalamic and extrahypothalamic systems that support motivation, reward, and internal regulation, including cardiovascular function, respiration, food and water intake, neuroendocrine function, circadian rhythms, and sleep and dreaming. The final section (Behavioral and Cognitive Neuroscience) describes the neural foundations of the so-called higher mental functions, including perception, attention, memory, language, and executive function. Each volume is accompanied by a CD of illustrations to increase the flexibility with which the material can be used.

Authors listed at the end of the chapters and boxes prepared drafts of their material, which were then edited by the senior editors. As in the first edition, the art program was under the excellent direction of Bob Woolley. We gratefully acknowledge the authors of the first edition for their valuable contributions, many of which served as the basis for chapters and boxes in the new edition. At Academic Press/Elsevier Science, the project was coordinated by Jasna Markovac (vice president and editorial director), and we are grateful to her for her vision, leadership, and advice throughout the project. In addition, Graham Lees helped produce the boxes, and Johannes Menzel and Lori Asbury very capably coordinated the production of the book.

The senior editors of *Fundamental Neuroscience*, all working neuroscientists, hope that users of this book, especially the students who will become the next generation of neuroscientists, find the subject matter of neuroscience as interesting and exciting as we do.

The Editors

Acknowledgments

The editors of the Second Edition would like to acknowledge the contributions of the section editors for the first edition: Thomas D. Albright, John H. Byrne, David R. Colman, Robert Y. Moore, Michael I. Posner, Edward M. Stricker, Larry W. Swanson, W. Thomas Thach, Leslie G. Ungerleider.

The editors and authors of the Second Edition also acknowledge those who contributed to chapters in the First Edition. Portions of this earlier material formed the basis for the revised chapters of the new edition, as indicated here.

Chapter 1.	Beth A Fischer and Story C. Landis
Chapter 2.	Thomas Lufkin and David R. Colman
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	and Mark Bennett
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	Jonathan Driver, Steven J. Luck, and
	Michael I. Posner
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	Terry J. Crow, Kevin S. LaBar,

Joseph E. LeDoux, and Richard F. Thompson

I ---- E Cabill Mark A Club

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