PRINCIPLES OF NEURAL SCIENCE

Fifth Edition

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Cover image: This image is a lithograph by F. Schima from a drawing by Sigmund Freud of the spinal ganglion of the lamprey *Petromyzon.* Before he discovered the unconscious, Freud had a promising career as a neural scientist. The cover thus recognizes that, a century after Freud's discovery, progress in the study of cognition has reemphasized the importance of unconscious mental processes for perception and action. (Reproduced, with permission, from Sigmund Freud, "Über Spinalganglien und Rückenmark der Petromyzon," *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften,* LXXVIII. Band I. Abtheilung, 1878, copyright New York Academy of Medicine.)

PRINCIPLES OF NEURAL SCIENCE

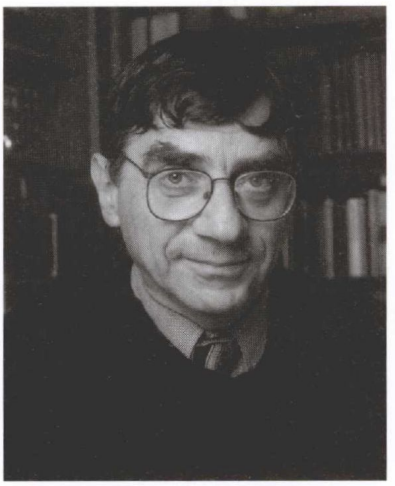
Columns II (left) and IV (right) of the Edwin Smith Surgical Papyrus

This papyrus, transcribed in the Seventeenth Century B.C., is a medical treatise that contains the earliest reference to the brain anywhere in human records. According to James Breasted, who translated and published the document in 1930, the word brain occurs only 8 times in ancient Egyptian, 6 of them on these pages. The papyrus describes here the symptoms, diagnosis, and prognosis of two patients with compound fractures of the skull, and compares the surface of the brain to "those ripples that happen in copper through smelting, with a thing in it that throbs and flutters under your fingers like the weak spot of the crown of a boy before it becomes whole for him." The red ink highlights the patients' ailments and their prognoses. (Reproduced, with permission, from the New York Academy of Medicine Library.)

Men ought to know that from the brain, and from the brain only, arise our pleasures, joys, laughter and jests, as well as our sorrows, pains, griefs and tears. Through it, in particular, we think, see, hear, and distinguish the ugly from the beautiful, the bad from the good, the pleasant from the unpleasant. . . . It is the same thing which makes us mad or delirious, inspires us with dread and fear, whether by night or by day, brings sleeplessness, inopportune mistakes, aimless anxieties, absent-mindedness, and acts that are contrary to habit. These things that we suffer all come from the brain, when it is not healthy, but becomes abnormally hot, cold, moist, or dry, or suffers any other unnatural affection to which it was not accustomed. Madness comes from its moistness. When the brain is abnormally moist, of necessity it moves, and when it moves neither sight nor hearing are still, but we see or hear now one thing and now another, and the tongue speaks in accordance with the things seen and heard on any occasion. But when the brain is still, a man can think properly.

attributed to Hippocrates
Fifth Century, B.C.

Reproduced, with permission, from The Sacred Disease, in *Hippocrates,* Vol. 2, page 175, translated by W.H.S. Jones, London and New York: William Heinemann and Harvard University Press. 1923.



James H. Schwartz
1933–2006

WE WISH TO DEDICATE THIS FIFTH EDITION of *Principles of Neural Science* to our friend and colleague, James H. Schwartz, one of the founding editors who died on March 13, 2006. Jimmy was an outstanding neuroscientist and scholar. His talent for science and his extraordinary erudition were evident from his days as a medical student at New York University. While at NYU he worked with Werner Maas in the microbiology department and carried out an important set of studies on feedback inhibition in bacterial metabolism. This work was so impressive that upon completing medical school, Jimmy was nominated for the highly selective graduate program in biology that had just been established at The Rockefeller University by Detlev Bronk. By the time Jimmy obtained his Ph.D. in Fritz Lippman's laboratory and graduated from Rockefeller in 1964, he had established himself as an outstanding biochemist. He was therefore eagerly recruited back to NYU in 1965 as an Assistant Professor in the Department of Microbiology.

There Jimmy turned to studying the nerve cells of the snail *Aplysia*, which were so large and uniquely identifiable that they seemed likely candidates for a study of neuronal biochemical identity. The immediate success of his initial studies encouraged him to devote himself completely to the nervous system. He rapidly became one of the leading biochemists on the nervous system and one of the leading thinkers regarding the relationship of brain to behavior.

The idea of going from molecules to behavior was the organizing theme of the first edition of *Principles of Neural Science,* which Jimmy co-edited. He simply loved working on *Principles*. A superb writer, he demanded precision in language both in himself and in others. This made him an exceptional editor. He read and avidly edited every chapter. In addition, Jimmy contributed his sense of historical scholarship. It was his idea to open *Principles* with the images of hieroglyphics from the Egyptian papyrus, the earliest reference to the brain in human record, which we include as the opening images in this edition as well. But perhaps most importantly, Jimmy championed the idea that this book should delineate fundamental principles rather than serve as an encyclopedia of facts. Thus, Jimmy's vision and editorial skill greatly enriched each of the five editions. In his absence we have striven to make the final product an edition that will continue to meet the high standards of readability and scholarship he set for all of us.

Notice

Medicine is an ever-changing science. As new research and clinical experience broaden our knowledge, changes in treatment and drug therapy are required. The authors and the publisher of this work have checked with sources believed to be reliable in their efforts to provide information that is complete and generally in accord with the standards accepted at the time of publication. However, in view of the possibility of human error or changes in medical sciences, neither the authors nor the publisher nor any other party who has been involved in the preparation or publication of this work warrants that the information contained herein is in every respect accurate or complete, and they disclaim all responsibility for any errors or omissions or for the results obtained from use of the information contained in this work. Readers are encouraged to confirm the information contained herein with other sources. For example and in particular, readers are advised to check the product information sheet included in the package of each drug they plan to administer to be certain that the information contained in this work is accurate and that changes have not been made in the recommended dose or in the contraindications for administration. This recommendation is of particular importance in connection with new or infrequently used drugs.

Preface

The ultimate goal of neural science is to understand how the flow of electrical signals through neural circuits gives rise to mind—to how we perceive, act, think, learn, and remember. Although we are still many decades away from achieving this level of understanding, neuroscientists have made significant progress in gaining insight into the neural mechanisms underlying behavior, the observable output of the nervous systems of humans and other organisms. We are also beginning to understand the disorders of behavior associated with neurological and psychiatric disease. As in the earlier editions of this book, we emphasize in this edition that behavior can be examined in terms of the electrical activity of both individual neurons and systems of nerve cells by seeking answers to five basic questions. How does the brain develop? How do nerve cells in the brain communicate with one another? How do different patterns of interconnections give rise to different perceptions and motor acts? How is the communication between neurons modified by experience? How is that communication altered by disease?

When we published the first edition of this book in 1981, these questions could be addressed only in terms of cellular biology. By the fourth edition in 2000 the same problems were being studied at the molecular level. In the decade intervening between the fourth and the present edition, molecular biology has continued to enlighten the analysis of neurobiological problems. Molecular biology has made it possible to probe the pathogenesis of many neurological diseases, including several devastating genetic disorders: muscular dystrophy, retinoblastoma, neurofibromatosis, Huntington disease, and certain forms of Alzheimer disease. Molecular biology also has greatly expanded our understanding of how the brain develops. Genetically modified worms, flies, and mice have allowed us to relate single genes, including the mutant genes underlying neurological disease, to signaling in nerve cells and to an organism's behavior. At the same time new molecular and optical tools have made it possible to image the activity of individual neurons in the intact brain and to manipulate the electrical activity of neurons and neural circuits to alter behavior. Such experiments have made it possible to examine the molecular dynamics of nerve cells in the circuits responsible for cognitive processes.

Every disease that affects the nervous system has some inherited component. Now that the 20,000 genes of the human genome have been sequenced, it is possible to identify which genes make us susceptible to certain disorders and thus to predict an individual's predisposition to a particular illness. This knowledge of the human genome is beginning to transform the practice of medicine. An individual genome scan can quantify the personal risk for neurological and psychiatric disorders at levels of increasing detail and complexity. We therefore again stress vigorously our view—advocated since the first edition—that the future of clinical neurology and psychiatry depends on the progress of neural science.

Despite the power of molecular biology to elucidate molecular mechanisms of neural function and disease, any detailed understanding of how neurons act to generate complex behaviors requires an analysis of the circuitry in which the neurons participate. Thus, key questions in neuroscience include: How are neuronal assemblies formed during development? What are the computations performed by those neural circuits and how does this activity generate behavior? How are circuits modified during learning and memory? What are the changes in neural circuits that give rise to neurological and psychiatric disease? Although the cellular and molecular biological approaches emphasized in the previous editions will certainly continue to yield important information, knowledge of the function of assemblies of neurons in defined circuits must be attained to arrive at a comprehensive cognitive neuroscience.

To study how we perceive, act, think, learn, and remember, we must develop new approaches and conceptual schemes for understanding the behavior of systems that range from single nerve cells to the substrate of cognition. As a result, in this edition we discuss more fully how the cognitive and behavioral functions of the sensory and motor systems expand our treatment of cognitive processes, and incorporate into our discussion the increasing power and importance of computational neural science. Our ability to record the electrical activity and visualize functional changes in the brain during normal and abnormal mental activity permits even complex cognitive processes to be studied directly. No longer are we constrained simply to infer mental functions from observable behavior. Indeed, a new appreciation of Freud's original insight about the importance of unconscious processes—one of the major new themes to emerge in cognitive neural science—re-emphasizes the great limitation of restricting our analysis of mind to observable behaviors. As a result of its progress in describing unconscious mental processes, neural science may soon develop the tools needed to probe the deepest of biological mysteries—the biological basis of consciousness and free will.

The intuitive insights that guided thinking about the mind at the time of our first edition in 1981 are proving inadequate in the 21st century. To give but one example, we intuitively sense that we perceive an object before interacting with it and we therefore fully expect that the brain acts in this sequential way. But recent studies indicate that at the highest levels the motor and sensory systems act in parallel, not in series, and that the motor system has considerable cognitive capability.

As a result of this progress, it has become easier to write a coherent introduction to the nervous system for students of behavior, biology, and medicine. Indeed, we think such a coherent summary is even more necessary now than it was with the first edition. Today neurobiology is central to the biological sciences—and indeed to science as a whole. Students of biology increasingly want to become familiar with neural science, and most students of psychology consider themselves to be studying the biological basis of behavior. At the same time progress in neural science is providing clearer guidance to clinicians, particularly in the treatment of psychiatric disorders. In fact, perhaps the most significant change in the clinical landscape since the first edition is the realization that psychiatry can be a clinical neural science, that the progress of psychotherapy can be assessed quantitively using brain imaging. We therefore believe it is particularly important to clarify the major principles and mechanisms governing the functions of the nervous system in health and disease without becoming lost in details.

This book provides the detail necessary to meet the interests and requirements of students in particular fields but is organized in such a way that excursions into special topics are not necessary for grasping the major principles of neural science. Toward that end we have continued to refine the illustrations in the book to allow students to understand the fundamental concepts of neural science.

Throughout this book we document the central principle that all behavior is an expression of neural activity and illustrate the insights into behavior that neural science provides. With this fifth edition we again hope to encourage the next generation of undergraduate, graduate, and medical students to approach the study of behavior in a way that unites its biological and social dimensions. From ancient times, understanding human behavior has been central to civilized cultures. Engraved at the entrance to the Temple of Apollo at Delphi was the famous maxim "Know thyself." For us, the study of mind and consciousness defines the frontier of biology.

Eric R. Kandel
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Acknowledgments

We were fortunate to have had the creative editorial assistance of Howard Beckman once again, who worked on the ongoing revisions of the fifth edition of *Principles of Neural Science* with the same characteristic demand for clarity of style and logic of argument that he has brought to previous editions. Without his assistance this edition would be a pale reflection of its previous editions.

Working on the other side of Manhattan at The Rockefeller University, away from the other editors at Columbia, Jim Hudspeth was responsible for the sections on Perception and Movement. In this lonely task Amy Miller, who cheerfully and accurately corrected the preliminary drafts of the relevant chapters, assisted him.

We owe a special debt to Sarah Mack who once again reinvented the entire art program. With her remarkable insight into science and detail, she produced remarkably clear, didactic, and artistically pleasing diagrams and images. We would like to thank our colleague Jane Dodd as well as Charles Lam, Becky Oles, and Terri Hamer for their help with the art program, and particularly Ann Canapary for her artistic contribution to the illustrations. We appreciate the generous help that Neil McMillan, Jackie Stewart, and Mariah Widman provided with the figures.

A great debt is also owed to Clayton Eccard who managed the editorial project with intelligence and diligence, allowing us to bring the book to fruition.

We thank Millie Pellan, Kathy MacArthur, and especially Maria Palileo at Columbia University, who typed the many versions of the manuscript through the various editorial stages.

We are indebted to our colleagues at McGraw-Hill, Harriet Lebowitz, Eve Siegel, and Ann Sydor, for their invaluable help in the production of this edition and grateful for the assistance of Rajni Pisharody in the composition of the book.

Many other colleagues have helped the editors by critically reading many chapters of the book. We are especially indebted to John Krakauer and John Koester for their efforts, which proved to be invaluable. Most importantly we owe the greatest debt to the contributing authors of this edition.

We finally thank our spouses and families for their support and forbearance during the editorial process.

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