

AN INTRODUCTION TO
BRAIN AND BEHAVIOR

BRYAN KOLB
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Brain and Behavior



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Preface

In the past decades, scientific understanding of the brain and human behavior has grown exponentially. In this book we have tried to communicate the excitement of recent breakthroughs in brain science and some of our own experiences in studying the brain over the past 30 years. We have tackled this story by imagining ourselves as students taking this first brain-science course, and we have tried to make sense of it by structuring the text around the key questions we ask about the brain, both as students and as neuroscientists: Why do we have a brain? How is it organized? How do drugs affect our behavior? How does the brain learn? How does it think? Emphasizing these and other basic questions about the brain will help to make clear our reasons for covering the information we do in this book. For example, if the reader realizes that we are ultimately interested in how the brain understands language or music, the functioning of the ear becomes more relevant because the ear is where auditory information enters the brain. And asking fundamental questions about the brain has another important benefit: It piques students' interest in the subject they are studying and challenges them to join us on the journey of discovery that is brain science.

Learning Aids That Distinguish This Book

Scientific Background Provided

We have tried to describe this journey in a way that students just beginning to study the brain and behavior will be able to understand. We have found that this course can sometimes be quite daunting, largely because information from all of the basic sciences is needed to understand brain function. This can be both a surprise and a shock to introductory students, who often come to the course lacking the necessary background. Many books provide their readers with little assistance in acquiring this background, assuming that students can simply jump right into the fray. But often that is not possible or appropriate. This book takes a different approach to dealing with the problem. It provides all the background students require to understand an introduction to brain science. For example, we provide the philosophical background needed to understand modern evolutionary theory, and we offer a short introduction to chemistry before describing the chemical activities of the brain. Similarly, we briefly discuss electricity before exploring the brain's electrical activity. In these ways the student is able to tackle brain science with greater confidence.

Teaching Through Metaphors, Examples, and Principles

We've tried to develop this book in a style that students will enjoy, for if a textbook is not enjoyed, it has little chance of teaching well. We have heightened student interest in the material they are reading particularly through abundant use of metaphors and examples. We have also facilitated learning by reemphasizing main points, and by distilling out sets of principles about brain function that can serve as frameworks to guide students' thinking. For instance, Chapter 2 contains a discussion of eight key principles explaining how the various parts of the nervous system work together. This set of principles forms the basis of many later discussions in the book. Similarly, Chapter 15 provides a summary of major points extracted from the previous 14 core chapters of the book. Students will find that reading and rereading this summary can help them

understand and remember the broader themes and messages of the book. This summary will also help students put the key information in each chapter into a meaningful context.

Abundant Chapter Pedagogy

In addition to the innovative teaching devices just described, you will find numerous other pedagogical aids in every chapter. For instance, each chapter begins with both an outline and an opening vignette that connects the world of brain and behavior to some concrete experience. Within the chapters there are end-of-section reviews that help students remember the major points, marginal pictures that add visual illustration of concepts, and a marginal glossary that highlights and reinforces the definitions of important terms. Each chapter ends with a chapter summary organized around key questions, a list of additional questions to aid in review and preparation for tests, and a number of provocative questions for further thought that explore interesting implications of chapter content. At the end of every chapter there is also a list of key terms (with the page numbers on which those terms are defined in the book), an annotated list of recommended readings, and a list of on-line sources that can broaden a student's understanding of chapter topics.

Unique Illustration Program

Our most important learning aid you'll be able to see by simply paging through this book. We have developed an expansive and, we believe, exceptional set of illustrations which, hand in hand with our words, describe and illuminate the world of the brain. In addition, the illustrations in every chapter are consistent and reinforce each other. For example, in every picture we use the same color code for each aspect of the neuron, and we often include an electronmicrograph image to show what a particular structure actually looks like when viewed through a microscope. You will also find these images on our Powerpoint presentations and integrated as labeling exercises in our study guide and testing materials.

Our Integration of Certain Topics

Clinical Information

Instructors will find that the placement of some topics is novel relative to traditional treatments. For example, we include brief descriptions of brain diseases close to discussions of basic processes that may involve those diseases. This placement is intended to help the first-time student repeatedly see the close links between what they are learning and real-life problems. The integration of real-life problems, especially behavioral disorders, into every chapter is further accomplished by our many Focus on Disorders boxes. These boxes typically employ interesting case studies to highlight specific disorders that are related to a chapter's content. We cover more than sixty disorders from addiction to Tourette's syndrome (a complete list of these discussions is presented in Table 15-2 on page 586). Our capstone Chapter 15 includes in-depth coverage of schizophrenia and affective disorders, along with a discussion of treatments, causes, and classifications of abnormal behavior.

The Relationship of the Brain to Behavior

We feature the relationship between the brain and behavior in every chapter. For example, when we first describe how neurons communicate, we also describe how plasticity in connections between neurons can serve as the basis of learning. Later, in the chapter directed to the question of how we learn, we explore how interactions between different parts of the brain enable our more complex behaviors, a topic that is usually reserved for a discussion of cognitive processes.

Research Methods

Some instructors may be surprised that we have not included a separate chapter on research methods. The reason is that the subject of research methods has also been integrated throughout the book. We believe that research methods are best understood in the context of what they are used for. We've included coverage of more than twenty methods (for a complete list, see Table 15-1 on page 585), many of which are accompanied by an illustration in the text and an animation on the accompanying CD-ROM. For instance, in describing how a neuron works, we explore how scientists record the electrical activity of the neuron. When we discuss how humans think, we examine the techniques of medical imaging that researchers use to see the brain in the act of thinking. And when answering the question of what motivates behavior, we delve into the research methods of producing brain lesions or electrically stimulating the brain. In these ways the uses of a particular method are made more meaningful to students.

Areas of Emphasis

Big-Picture Issues

One of the challenges in writing an introductory book on any topic is to decide what to include and what to exclude. We have organized discussions so as to focus on the bigger picture. A prime example is the discussion of general principles of nervous system function contained in Chapter 2. Although such a set of principles may be a bit arbitrary, it nevertheless gives students a useful framework for understanding the brain's activities. Similarly, in later chapters of this text we tackle topics in a more general way than most contemporary books do. For instance, in Chapter 11 we revisit the experiments and ideas of the 1960s as we try to understand why animals behave the way they do, after which we consider behaviors as diverse as drinking and anxiety attacks. Another example of our focus on the larger picture is our discussion of learning and memory, which occurs alongside a discussion of recovery from brain damage. We believe that such a broader focus helps students appreciate the larger problems that behavioral neuroscience is all about. Of course, broadening our focus has required us to leave out some of the details that might be found in other texts. But for us, discussions of larger problems and issues in the study of brain and behavior are more interesting for, and more likely to be remembered by, the student who is new to this field.

The Relevance of Neuroscience

Throughout this book we have repeatedly emphasized that neuroscience is a human science — that everything in this book is relevant to our lives. Neuroscience helps us understand how we learn, how we develop, and how we can help people who suffer from sometimes deadly and destructive brain and behavioral disorders. We have found that emphasizing the clinical aspects of neuroscience is especially useful in motivating introductory students and in demonstrating to them the relevance of our field. Clinical material helps to make neurobiology particularly relevant to those who are going on to careers in psychology, social work, or other mental-health-related professions, as well as to students pursuing careers in the biological sciences. That is why we have not only integrated clinical information throughout this text and featured it in our Focus on Disorders boxes, but have also expanded upon it in our final chapter (Chapter 15).

The Biological Basis of Behavior

Another area of emphasis in this book is a focus on questions that relate to the biological basis of behavior. For us, the excitement of neuroscience is in understanding how the brain explains what we do, whether it be talking, sleeping, seeing, or learning.

Readers will therefore find nearly as many illustrations about behavior as there are illustrations about the brain. This emphasis on explaining behavior is another reason why we have included three boxes on neurological disorders in every chapter.

Evolution, Genetics, and Psychopharmacology

We wanted to make sure that this book reflected the excitement of current neuroscience, as we understand it as active researchers. Therefore, we have given emphasis to coverage of evolution, genetic research, contemporary research methods, and psychopharmacology. We cover the evolution of the brain in depth in Chapters 1 and 2 and return to this perspective in almost every chapter. The foundations of genetic research is introduced in depth in Chapter 3, but we discuss genetics in many other places in the text. You'll find the newest research methods throughout the book, with PET in Chapter 9, fMRI in Chapters 11 and 14, TMS in Chapter 14, and ERP in Chapter 4. We have an entire chapter on drugs and behavior (Chapter 6), but we return to the topic in many chapters, with coverage of drugs and information transfer in Chapter 4, drugs and cellular communication in Chapter 5, drugs and motivation in Chapter 11, drugs and sleep disorders in Chapter 12, and cellular changes with drug use in Chapter 13.

COVERAGE OF THE EVOLUTION OF THE BRAIN

Evolution of the neuron, the brain, and hominids	Chapter 1
Evolution of the human brain	Chapter 2
Evolution of the synapse	Chapter 5
Evolution of geniculostriate and tectopulvinar pathways	Chapter 8
Evolution of thought and language	Chapter 9
Evolutionary and environmental influences on thought and language	Chapter 11
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COVERAGE OF GENETICS

Genes, cells, and behavior	Chapter 3
Metabotropic receptors and DNA	Chapter 5
Learning and genes	Chapter 5
Genes and drug action	Chapter 6
Genes and development	Chapter 7
Genetics of color vision	Chapter 8
Genetics of sleep disorders	Chapter 12

Current Research

Finally, in this book we emphasize the findings of current research. You will not, however, find a great many citations embedded in the chapter discussions. We feel that numerous citations can sometimes disrupt the flow of a text and distract students from the task of mastering what they read. We have consequently been selective in our citation of the truly massive literature on the brain and behavior. We provide citations to classic works by including the names of the researchers, and sometimes their pictures, and by mentioning where the research was performed. In areas where there is controversy or new breakthroughs, we also include more detailed citations to current papers, citing papers from the year 2000 when possible. A reference list to all of the literature used in developing this text is provided at the end of the book.

Supplements

A number of student and instructor materials are available to supplement our book.

You'll find the innovative *Foundations of Behavioral Neuroscience CD-ROM* inside the back cover of this book. Created by Uri Hasson from the Weizmann Institute in Israel and Yehuda Shavit from Hebrew University of Jerusalem and produced by the Open University of Israel, this CD includes five modules: Research Methods, Neural Communication, Vision, Movement, and the Central Nervous System. References to this CD (and to the book's Web site, described below) appear in the margins of each

chapter, pointing to places where the text discussion is enhanced by a video clip or an animation. The CD features rotating 3-D models of the human brain and eye, more than twenty-five video clips, animations of key physiological mechanisms, and interactive examples of new neuroimaging technology. It also includes multiple-choice questions for each chapter of the text.

A **Web site**, found at www.worthpublishers.com/kolb, with material provided by Keith Trujillio of California State University at San Marcos, offers a variety of simulations, video clips, tutorials, and quizzes. It is updated periodically with new links, exercises, and developments in neuroscience. For the instructor, the site offers on-line testing, a syllabus posting service, Web site building service, Powerpoint presentation files, and access to electronic versions of the artwork from the book.

The **Instructor's Manual**, written by Debora Baldwin of the University of Tennessee, Knoxville, contains lecture suggestions, lab activities, and handouts for student projects. Course planning suggestions, ideas for term projects, and a guide to videos and Internet resources are also included.

A battery of more than 2000 test questions is available in a **Test Bank** written by Robert Sainsbury of the University of Calgary. The Test Bank provides true/false, multiple-choice, short-answer, and essay questions, as well as labeling exercises tied to the art in the text. Each question is keyed to a learning objective and page-referenced to the textbook. The Test Bank is also available on a dual-platform CD-ROM, which allows instructors to quickly add, edit, re-format, and re-sequence questions. The CD is also the access point for Diploma On-line Testing, which allows instructors to create and administer secure exams over a network and over the Internet.

The **Student Study Guide**, written by Terry Bazzett of the State University of New York at Geneseo, is a carefully crafted guide with multiple tools for learning and retaining text material. Each chapter includes a review of key concepts, terms, practice tests, short-answer questions, illustrations for labeling and identification, Internet activities, CD-ROM questions, and crossword puzzles.

Other helpful supplements for instructors include the **transparency package**, available as traditional acetates as well as on-line in our Web site. There is also a library of **videos**, including a collection of Scientific American Frontiers segments on the brain and behavior featuring the work of Irene Pepperberg, Steve Pinker, and Linda Bartoshuk, as well as the revised second editions of both *The Brain* and *The Mind* Video Teaching Modules, updated by Frank Vattano and his colleagues at Colorado State University.

Acknowledgments

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Bryan Kolb and Ian Q. Whishaw

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Twelve years ago, I survived a serious head injury. In the second it took for my car to crash head-on, my life was permanently changed, and I became another statistic in what has been called "the silent epidemic."

During the next months, my family and I began to understand something of the reality of the experience of head injury. I had begun the painful task of recognizing and accepting my physical, mental, and emotional deficits. I couldn't taste or smell. I couldn't read even the simplest sentence without forgetting the beginning before I got to the end. I had a hair-trigger temper that could ignite instantly into rage over the most trivial incident.

During the first year, I could not take too much stimulation from other people. My brain would simply overload, and I would have to go off into my room to get away. Noise was hard for me to take, and I wanted the place to be kept quiet, which was an impossibility in a small house with three youngsters in it. I remember laying down some impossible rules for all of us. For example, I made rules that everybody had to be in bed by 9:30 PM, that all lights had to be out, and that no noise of any kind was permitted after that time. No TV, radios, or talking was allowed. Eventually the whole family was in an uproar.

Two years after my injury, I wrote a short article: "What Does It Feel Like to Be Brain Damaged?" At that time, I was still intensely focusing on myself and my own struggle. (Every head-injured survivor I have met seems to go through this stage of narcissistic preoccupation, which creates a necessary shield to protect them from the painful realities of the situation until they have a chance to heal.) I had very little sense of anything beyond the material world and could only write about things that could be described in factual terms. I wrote, for example, about my various impairments and how I learned to compensate for them by a variety of methods.

At this point in my life, I began to involve myself with other brain-damaged people. This came about in part after the publication of my article. To my surprise, it was reprinted in many different publications, copied, and handed out to thousands of survivors and families. It brought me an enormous outpouring of letters, phone calls, and personal visits that continue to this day. Many were struggling as I had struggled, with no diagnosis, no planning, no rehabilitation, and most of all, no hope.

The far-ranging effects of head injury on the survivor's life and that of his or her family cannot be overemphasized. In my own case I realize that it was for me the single most

significant event of my lifetime. The catastrophic effect of my injury was such that I was shattered and then remolded by the experience, and I emerged from it a profoundly different person with a different set of convictions, values, and priorities. Above all, I have learned that there is no limit to the power of faith, hope, and love. With these, I made the journey out of the shadows into a larger, brighter world than the one I had left behind before my injury. (Linge, 1990)

This description of what it is like to be brain injured was written by Fred Linge, a clinical psychologist with a degree in brain research. (For an explanation of how the brain can be injured in an accident, see "Closed Head Injury" on page 2.) In the years after his injury, Linge made an immense journey. He traveled from a time before the car crash, when he gave less thought to the relation between his brain and his behavior than he did to the way in which he dressed. At the end of the journey, thoughts about his brain and his behavior dominated his life. He became a consultant and advisor to many people who also had suffered brain injury.

Most of you are like Fred Linge before he took that journey. Your brain does its work so efficiently and unobtrusively that you hardly give it any thought. You may be unaware that the human brain has hundreds of parts, each of which participates in certain tasks. You may have no knowledge that the brain changes as you age, as you undergo major life events, and even as you engage in seemingly trivial behaviors, such as reading the words on this page. In learning about the origins of the universe, the world, and human beings, you may have encountered no mention of the brain and its relation to behavior. Yet, if you ever had first-hand experience with brain damage, you, too, would be confronted with the workings of this most wonderful and complex machine.

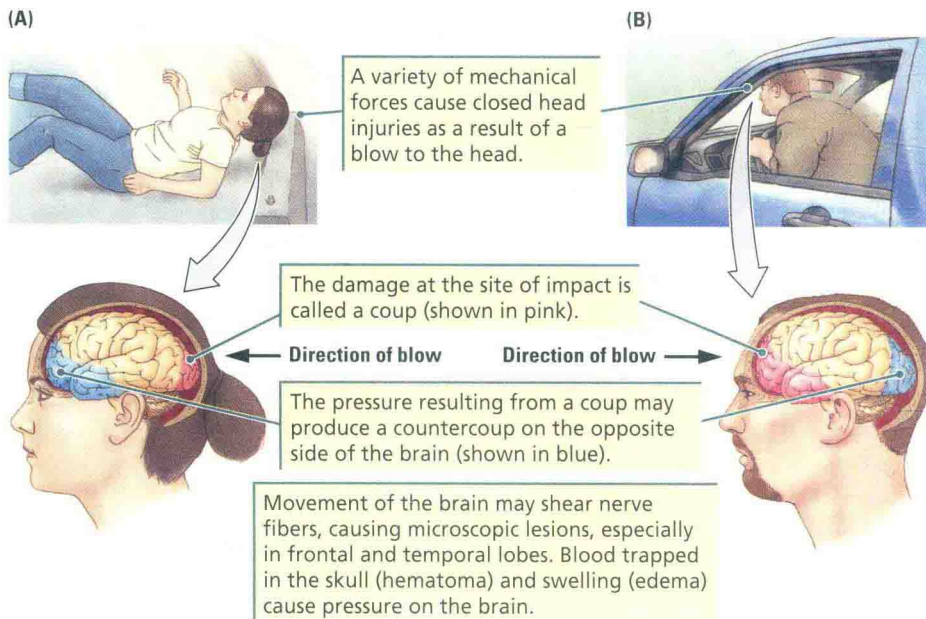
The purpose of this book is to take you on a journey not unlike the one that Fred Linge took. Through it you, too, will come to understand the link between brain and behavior. Of course, we do not ask that you experience brain damage to undertake this journey. The road that we offer is simply one of information and discovery. Yet, along

Closed Head Injury

Focus on Disorders

Closed head injury results from a blow to the head that subjects the brain to a variety of forces. First, the force exerted on the skull at the site of the blow causes bruising (contusion) known as a “coup.” Second, the blow may force the brain against the opposite side of the skull, producing an additional bruise called a “countercoup” (see the accompanying illustration). Third, the movement of the brain may cause a twisting or shearing of nerve fibers, causing microscopic lesions. Such lesions may be found throughout the brain, but they are most common in the frontal and temporal lobes. Fourth, the bruises and strains caused by the impact may produce bleeding (hemorrhage). Because the blood is trapped within the skull, it acts as a growing mass (hematoma), which exerts pressure on surrounding brain regions. Finally, like blows to other parts of the body, blows to the brain produce swelling (edema). This swelling, which is a collection of fluid in and around damaged tissue, is another source of pressure on the brain.

People who sustain closed head injury often lose consciousness because the injury affects fibers in lower parts of the brain that are associated with waking. The severity of coma can indicate the severity of the injury. Closed head injuries resulting from motor vehicle accidents are particularly



Shading (pink and blue) indicates regions of the brain most frequently damaged in closed head injury. A blow can produce a contusion both at the site of impact and at the opposite side of the brain owing to compression of the brain against the front (A) or back (B) of the skull.

severe because the head is moving when the blow is struck, thereby increasing the velocity of the impact.

The diffuse effects of closed head injuries make diagnosis very difficult, which is why these kinds of injuries have been collectively called a “silent epidemic.” Victims of severe closed head injury can suffer serious repercussions in their everyday lives. Like Fred Linge, many have difficulty returning to their former levels of functioning, including carrying out their previous jobs.

it, you will find that much of the evidence that we have about the brain and behavior comes from the study of changes in people who have suffered brain injury. At the same time, we are also learning more and more about how the brain works when we are healthy. This emerging knowledge is changing how we think about ourselves, how we structure education and our social interactions, and how we aid those with brain injury.

In this chapter, we answer the question, What are the origins of brain and behavior? We begin by defining both the brain and behavior and outlining the nervous system’s basic structure. We then look at how people through history have viewed the relation between brain and behavior, starting with the mentalistic perspective of Aristotle and progressing to the biological perspective of today. With this background in mind, we explore the evolution of