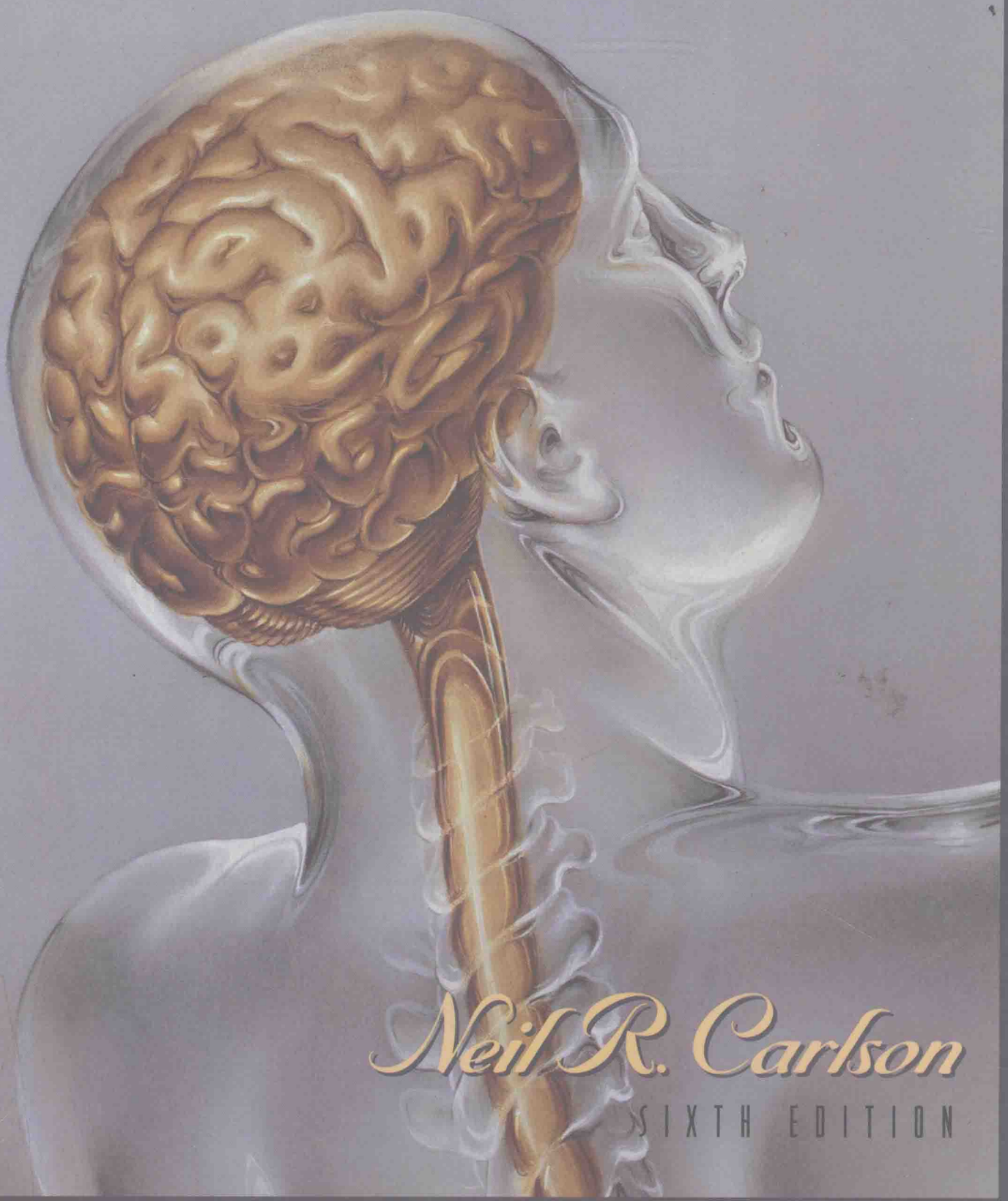
PHYSIOLOGY of BEHAVIOR



Neil R. Carlson

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Sixth Edition

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Physiology of Behavior

For Mary

Preface

I wrote the first edition of *Physiology of Behavior* a little over twenty years ago. The interesting work coming out of my colleagues' laboratories—a result of their creativity and hard work—has given me something new to say with each edition. Because there was so much for me to learn, I enjoyed writing this edition just as much as the first one. That is what makes writing new editions interesting—learning something new and then trying to find a way to convey the information to the reader.

In the preface to each of the previous editions I mentioned some of the new research methods that had recently been developed. Investigators are continuing to develop new methods—for example, new staining techniques for specific substances, new imaging methods, new recording methods, and the means for analyzing the release of neurotransmitters and neuromodulators in restricted regions of the brains of freely moving animals. The research reported in this edition reflects the enormous advances made in staining methods: new anterograde and retrograde tracers, dye-coupled antibodies for just about everything, in situ hybridization methods to localize messenger RNA, stains for Fos, single-photon and multiphoton laser scanning microscopy, targeted mutations ("knockouts") of just about any gene—and the list continues. Nowadays, as soon as a new method is developed in one laboratory, it is adopted by other laboratories and applied to a wide range of problems. And more and more, researchers are combining techniques that converge upon the solution to a problem. In the past, individuals tended to apply their particular research method to a problem; now they are more likely to use many methods, sometimes in collaboration with other laboratories.

You will notice that the book has a different look. Jay Alexander and I have worked together to redraw almost all of the anatomical art. Jay, an artist who also works as a technician in the Psychology Department at the University of Massachusetts, supplied the artistic talent. I think the result of our collaboration is a set of clear, consistent, and attractive illustrations.

In this edition, as in the previous ones, I have made some changes to the outline of the book, as a reader familiar with the previous edition will discover. Some of these changes were made in response to new directions in research efforts, and some were made in response to suggestions of students and colleagues concerning pedagogy. The two most frequent requests were to include full chapters on psychopharmacology and on the physiology of drug abuse, which I have done. Psychopharmacological methods have become increasingly important in recent years, and the identification of specific subclasses of receptors and the development of drugs that interact with them have contributed much to our understanding of neural mechanisms of behavior. The new chapter on the physiology of drug abuse complements the two chapters on mental disorders and with them illustrates the important role that the methods of neuroscience have come to play in the field of mental health.

The first part of the book is concerned with foundations: the history of the field, the structure and functions of neurons, neuroanatomy, psychopharmacology, and research methods. The second part is concerned with inputs and outputs: the sensory systems and the motor system. The third part deals with classes of species-typical behavior: sleep, reproduction, emotional behavior, and ingestion. The chapter on reproductive behavior includes maternal behavior as well as mating. The chapter on emotion includes a discussion of emotional reactions, communication of emotions, feelings of emotions, and aggression. As in the previous edition, ingestive behavior is covered in two chapters—one on drinking and one on eating.

The fourth part of the book deals with learning. The first learning chapter discusses research on synaptic plasticity and the neural mechanisms responsible for perceptual learning and stimulus–response learning (including classical and operant conditioning). The second learning chapter discusses human amnesia and the role of the hippocampal formation in relational learning. The final part of the book deals with verbal communication and mental

and behavioral disorders. The latter topic is now covered in three chapters; the first discusses schizophrenia and the affective disorders; the second discusses the anxiety disorders, autism, and stress; and, as I already mentioned, the third discusses drug abuse.

Besides updating my discussion of research, I have updated my writing. Writing is a difficult, time-consuming endeavor, and I find that I am still learning how to do it well. I have said this in the preface of every edition of this book, and it is still true. I have worked with copy editors who have ruthlessly marked up my manuscript, showing me how to do it better the next time. I keep thinking, "This time there will be nothing for the copy editor to do," but I am always proved wrong: each page contains notes showing me how to improve my prose. But I do think that each time the writing is better organized, smoother, and more coherent.

Good writing means including all steps of a logical discourse. My teaching experience has taught me that an entire lecture can be wasted if the students do not understand all of the "obvious" conclusions of a particular experiment before the next one is described. Unfortunately, puzzled students sometimes write notes feverishly, in an attempt to get the facts down so they can study them—and understand them—later. A roomful of busy, attentive students tends to reinforce the lecturer's behavior. I am sure all my colleagues have been dismayed by a question from a student that reveals a lack of understanding of details long since passed, accompanied by quizzical looks from other students that confirm that they too have the same question. Painful experiences such as these have taught me to examine the logical steps between the discussion of one experiment and the next and to make sure they are explicitly stated. A textbook writer must address the students who will read the book, not simply colleagues who are already acquainted with much of what he or she will say.

Because research on the physiology of behavior is an interdisciplinary effort, a textbook must provide the student with the background necessary for understanding a variety of approaches. I have been careful to provide enough biological background early in the book that students without a background in physiology can understand what is said later, while students with such a background can benefit from details that are familiar to them.

I designed this text for serious students who are willing to work. In return for their effort, I have endeavored to provide a solid foundation for further study. Those students who will not take subsequent courses in this or related fields should receive the satisfaction of a much better understanding of their own behavior. Also, they will have a greater appreciation for the forthcoming advances in medical practices related to disorders that affect a person's perception, mood, or behavior. I hope that students who carefully read this book will henceforth perceive human behavior in a new light.

Acknowledgments

Although I must accept the blame for any shortcomings of the book, I want to thank colleagues who helped me by sending reprints of their work, suggesting topics that I should cover, sending photographs that have been reproduced in this book, and pointing out deficiencies in the previous edition. I thank:

Peter Arnett, Gary Aston-Jones, Jeffrey Blaustein, Gemma Calvert, Edna Cohen, Geert DeVries, Nina Dronkers, Guinevere Eden, Mark George, Eugenia Gurevich, Marc Hauser, A.J. Hudspeth, Sarah Leibowitz, Deborah Mash, Julian Mercer, Jerrold Meyer, Shiro Minami, Mitchell Nobler, Steven Reppert, Randall Sakai, Dick Swaab, Simon Thornton, and Joe Tsien.

Before I began work on the book, my publisher sent a questionnaire to colleagues who were familiar with the previous edition. Their responses to this questionnaire helped me decide what changes to make in the revision. I thank:

A. Michael Anch, Anne Powell Anderson, Joyce Bishop, Joshua E. Blustein, John Broida, Edward Castaneda, Jess F. Deegun II, Linda Enloe, Paul Haerich, Jeremy Hall, Fred Heimstetter, Sandra Kelly, Michael Leon, Raymond Martinetti, June E. Millet, Antonio Nuñez, William Overman, Todd Schachtman, Ronald See, Rhea Steinpreis, Meg Waraczynski, Robert Webb, Frank Webbe, N. M. Weinberger, Margaret H. White, and Nancy J. Wolf.

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I also want to thank the people at Allyn and Bacon. Carolyn Merrill, my editor, provided assistance, support, and encouragement. Jennifer Normandin and Amy Goldmacher, editorial assistants, helped gather comments and suggestions from colleagues who have read the book. Mary Beth Finch, the production editor, assembled the team

that designed and produced the book. Barbara Gracia, of Woodstock Publisher's Services, demonstrated her masterful skills of organization in managing the book's production. She got everything done on time, despite an extremely tight schedule. Few people realize what a difficult, demanding, and time-consuming job a production editor has with a project such as this, with hundreds of illustrations and an author who tends to procrastinate, but I do, and I thank her for all she has done. Joyce Grandy and Barbara Willette served as copy editors. Their attention to detail surprised me again and again; they found inconsistencies in my terminology, awkwardness in my prose, and disjunctions in my logical discourse and gave me a chance to fix them before anyone else saw them in print.

I must also thank my wife Mary for her support. Writing is a lonely pursuit, because one must be alone with one's thoughts for many hours of the day. I thank her for giving me the time to read, reflect, and write without feeling that I was neglecting her too much. I also thank her and my daughter, Kerstin Carlson Le Floch, for the superb job they did preparing the study guide.

I was delighted to hear from many students and colleagues who read previous editions of my book, and I hope that the dialogue will continue. Please write to me and tell me what you like and dislike about the book. My address is: Department of Psychology, Tobin Hall, University of Massachusetts, Amherst, Massachusetts 01003. My e-mail is *nrc@psych.umass.edu*. When I write, I like to imagine that I am talking with you, the reader. If you write to me, we can make the conversation a two-way exchange.

Brief Contents

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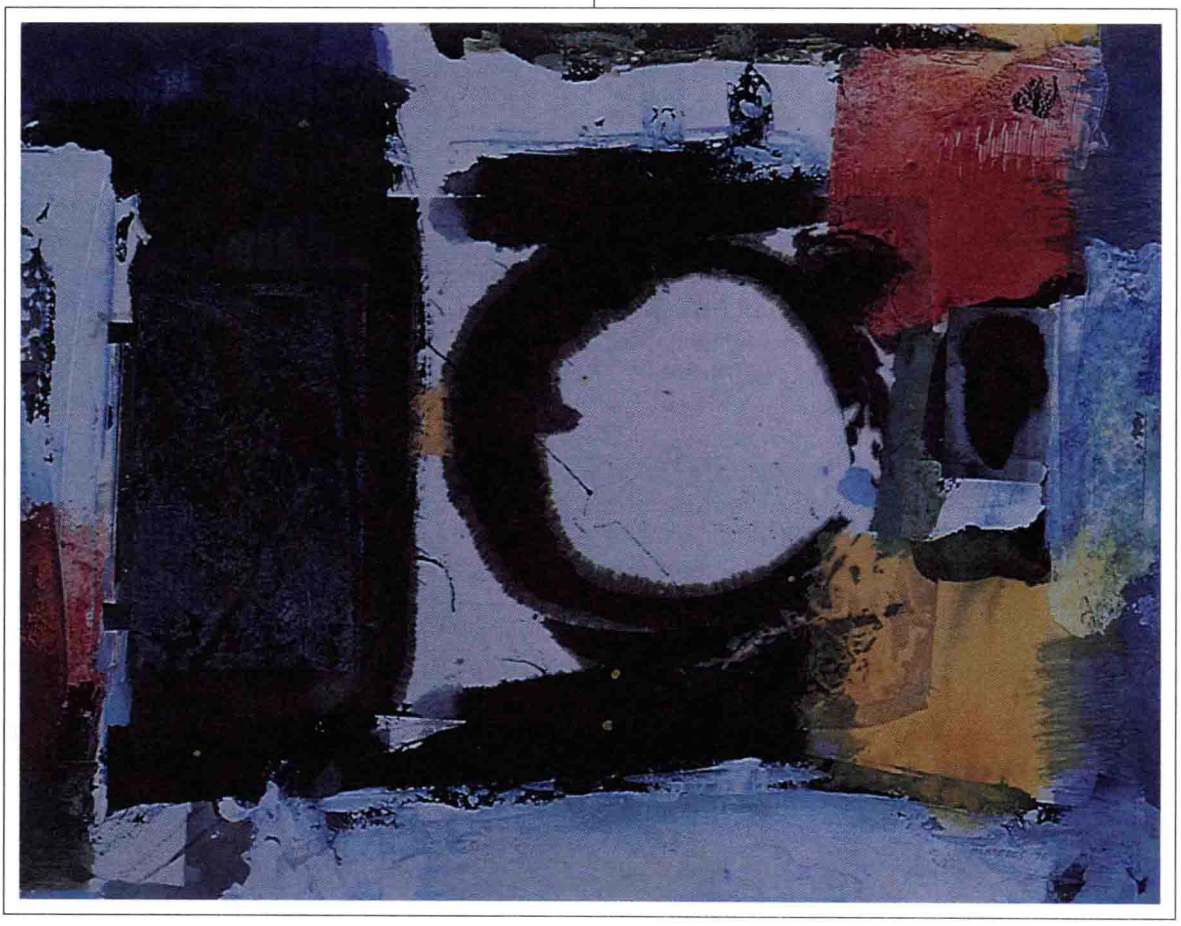
CHAPTER 1

Introduction



The Birth of Venus by Mercedes Nuñez. Courtesy of the artist.

The last frontier in this world—and perhaps the greatest one—lies within us. The human nervous system makes possible all that we can do, all that we can know, and all that we can experience. Its complexity is immense, and the task of studying it and understanding it dwarfs all previous explorations our species has undertaken.

One of the most universal of all human characteristics is curiosity. We want to explain what makes things happen. In ancient times, people believed that natural phenomena were caused by animating spirits. All moving objects—animals, the wind and tides, the sun, moon, and stars—were assumed to have spirits that caused them to move. For example, stones fell when they were dropped because their animating spirits wanted to be reunited with Mother Earth. As our ancestors became more sophisticated and learned more about nature, they abandoned this approach (which we call *animism*) in favor of physical explanations for inanimate moving objects. But they still used spirits to explain human behavior.

From the earliest historical times people have believed they possessed something intangible that animated them—a mind, or a soul, or a spirit. This belief stems from the fact that each of us is aware of his or her own existence. When we think or act, we feel as though something inside us is thinking or deciding to act. But what is the nature of the human mind? We have physical bodies, with muscles that move it and sensory organs such as eyes and ears that perceive information about the world around us. Within our bodies the nervous system plays a central role, receiving information from the sensory organs and controlling the movements of the muscles. But what role does the mind play? Does it *control* the nervous system? Is it a *part of* the nervous system? Is it physical and tangible, like the rest of the body, or is it a spirit that will always remain hidden?

This puzzle has historically been called the *mind–body question*. Philosophers have been trying to answer it for many centuries, and more recently scientists have taken up the task. Basically, people have followed two different approaches: dualism and monism. **Dualism** is a belief in the dual nature of reality. Mind and body are separate; the body is made of ordinary matter, but the mind is not. **Monism** is a belief that everything in the universe consists of matter and energy and that the mind is a phenomenon produced by the workings of the nervous system.

Mere speculation about the nature of the mind is futile. If we could answer the mind–body question simply by thinking about it, philosophers would have done so long ago. Physiological psychologists take an empirical, practical, and monistic approach to the study of human nature. Most of us believe that once we understand the workings of the human body—and, in particular, the workings of the nervous system—the mind–body problem will have been solved. We will be able to explain how we perceive, how we think, how we remember, and how we act. We will even be able to explain the nature of our own self-awareness. Of course, we are far from understanding the workings of the nervous system, so only time will tell whether this belief is justified.

UNDERSTANDING HUMAN CONSCIOUSNESS: A PHYSIOLOGICAL APPROACH

As you will learn from subsequent chapters, scientists have discovered much about the physiology of behavior: of perception, motivation, memory, and control of specific movements. But before addressing these problems, I want

dualism The belief that the body is physical but the mind (or soul) is not.

monism (***mahn*** *ism*) The belief that the world consists only of matter and energy and the mind is part of it.