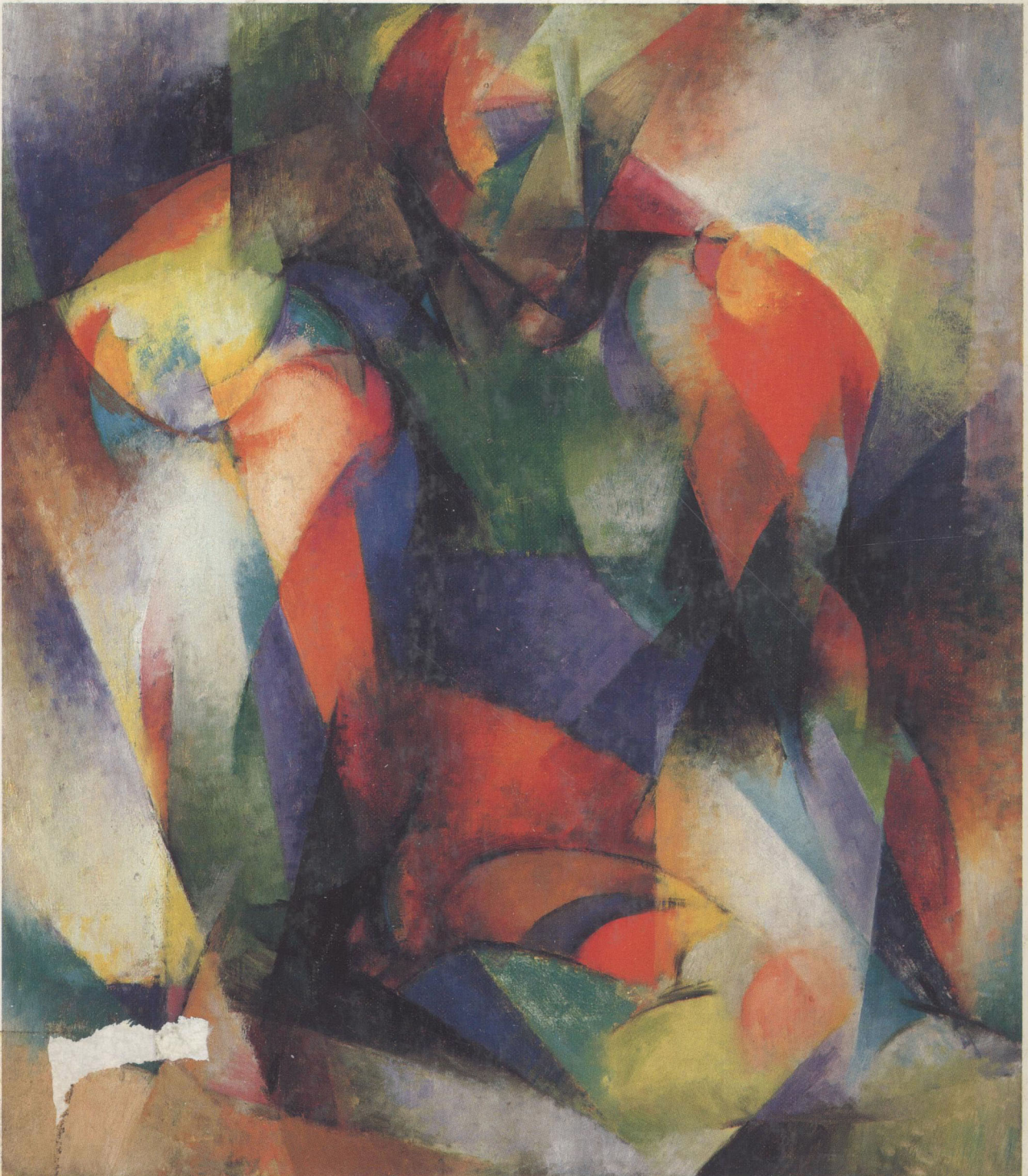


PHYSIOLOGY OF BEHAVIOR

THIRD EDITION

NEIL R. CARLSON

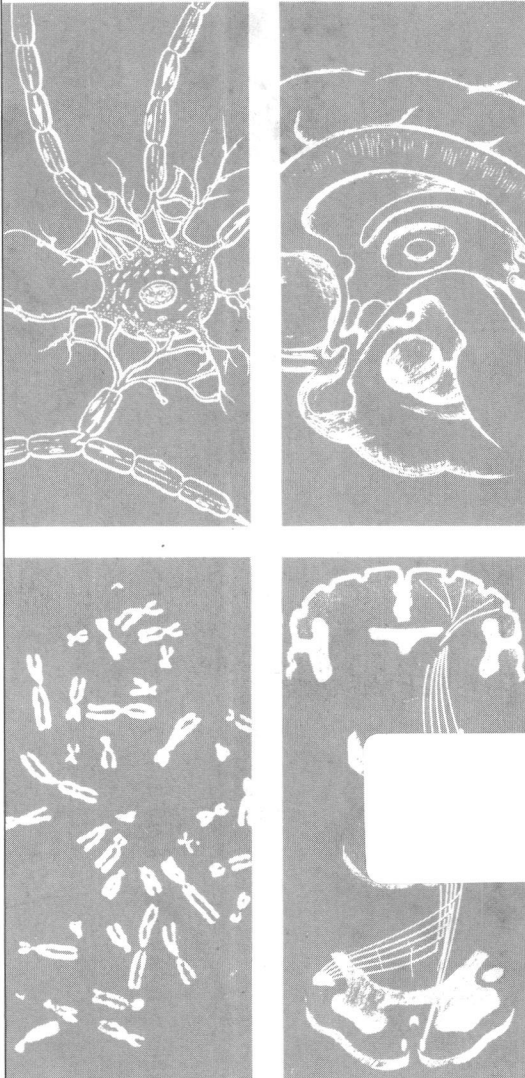


Physiology of Behavior

THIRD EDITION

Neil R. Carlson

University of Massachusetts



ALLEN AND BACON, INC.

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This book is dedicated to the memory of my mother,
Alice Janson Carlson,
1913 – 1984.



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Preface

The third edition of a book, I am told, often represents a watershed: does the writer still have the spark necessary to turn out a fresh piece of writing, or has the project gotten stale? Researchers have been very busy in their laboratories during the years since the previous edition of *Physiology of Behavior* came out. Thus, they have provided me with many new things to write about. If my writing still seems fresh, it is largely because of the efforts of these researchers. Their research reports gave me new facts and ideas to think about and write about.

In the preface to the second edition, I mentioned some of the new techniques, such as the horseradish peroxidase method, amino acid autoradiography, radioactive 2-DG autoradiography, and methods to assay receptors, that had been developed to help investigators study the physiology of behavior. These techniques, and many others, have become almost commonplace and have been fruitful, indeed. 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.

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 col-

leagues concerning pedagogy. The first part of the book is concerned with foundations: the history of the field, the structure and functions of neurons, neural communication, neuroanatomy, 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: reproduction, sleep, ingestion, and aggression. The fourth part deals with learning: reinforcement, the anatomy of learning, and the physiology and biochemistry of learning. The final part deals with human communication, both verbal and nonverbal, and mental disorders. Because I combined several pairs of small chapters, the book consists of seventeen chapters rather than twenty.

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 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: the amount of red pencil on each page remains constant. But I do think that each time the writing is better organized, smoother, and more coherent. If I have at least partly achieved my goal, readers will find that I have no particular writing "style," and yet they can understand what I have said and will remain interested in what they are reading. I agree with Graves and Hodge (1947), who say ". . . good English is a matter not merely of grammar and syntax and vocabulary, but also of sense: the structure of the sentences must hold together logically. . . . [Even] phrases which can be justified both grammatically and from the point of view of sense may give [the] reader a wrong first impression, or check his reading speed, tempting him to skip." "Readability" is not to

be determined by counting syllables in words or words in sentences; it is a function of the clarity of thought and expression.

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, and not simply address the 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 so 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 satisfac-

tion 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.

■ ACKNOWLEDGEMENTS

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:

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Leanna Standish and Elizabeth Swearenson, Department of Psychology, Smith College, have prepared a student workbook to accompany this text. We all know how important active participation is in the learning process, and this workbook provides an excellent framework for guiding the student's study behavior. Leanna and Elizabeth are fine teachers, and their combined experience has permitted them to make this edition of the workbook even better than the last one.

I also want to thank the people at Allyn and Bacon. Bill Barke, my editor, provided assistance, support, and encouragement. Lauren Whittaker, an editorial assistant, helped me gather comments and suggestions from col-

leagues who have read the book. Kazia Navas, the production editor, demonstrated her masterful skills of organization. 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. Nancy Newman was my copy editor. Her attention to detail surprised me again and again; she 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. Leslie Galton provided invaluable assistance with obtaining permissions to use figures previously published elsewhere. Mark Lefkowitz, medical illustrator; Vantage Art; and Horvath and Cuthbertson, Illustrators, did a superb job on the art, as you can easily see.

I must also thank my family for their assist-

ance. My daughter Kerstin helped me cut and paste illustrations and find references. My son Paul ran errands for me and patiently accepted that I was often busily engaged in reading or writing in my study. My wife Mary typed the entire second edition into my computer so I could use it to prepare this edition, found missing references, and prepared the author index. But even more important than this assistance was the moral support and encouragement that my family provided me.

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. 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.

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1



Introduction

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 - Monism**
- BIOLOGICAL ROOTS OF PHYSIOLOGICAL PSYCHOLOGY
 - Experimental Physiology**
 - Functionalism: Natural Selection and Evolution**
- CONTRIBUTIONS OF MODERN PSYCHOLOGY
 - The Goals of Research**
- ORGANIZATION OF THIS BOOK
 - Outline**
 - Some Mechanical Details**

Physiological psychologists, like other psychologists, try to explain behavior. What we know about the causes of behavior is certainly less than complete. The study of the physiology of behavior is thus very much an ongoing quest for answers. This book is much more a description of that quest than a list of answers. Its objective is to introduce you to what has been learned about the physiology of behavior and to describe the methods used to investigate this topic.

Investigation of the physiology of behavior has a long history, with roots in philosophy and biology. Philosophers asked how we perceive and understand reality and posed the mind-body question, which remains with us still. They also devised the scientific method—a set of rules that permits us to ask questions about the natural world with some assurance that we will receive reliable answers. Biologists devised experimental physiology, which provides the tools we use to investigate the workings of the body. They also developed the framework needed to integrate findings from diverse species—the principles of natural selection, evolution, and genetics.

Our knowledge about the physiology of behavior has been obtained through the efforts of psychologists, neurophysiologists, neurologists, cell physiologists, molecular biologists, biochemists, neuroanatomists, and endocrinologists. No single academic discipline can claim the field as solely its own, which accounts for the diversity of titles used to describe it. The names *physiological psychology*, *biological psychology*, *psychobiology*, *biopsychology*, *behavioral physiology*, and *behavioral neuroscience* all have approximately the same meaning.

■ PHILOSOPHICAL ROOTS OF PHYSIOLOGICAL PSYCHOLOGY

Philosophy (“love of wisdom”) originally concerned itself with the basis of human

knowledge and thought. Philosophers soon realized that in order to understand the basis of knowledge, they must understand the nature of reality, which led them to develop “natural philosophy,” the predecessor of modern physical and biological science.

One of the most universal human characteristics is a need to *explain* things. In ancient times, natural phenomena were commonly explained as being the results of 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 *animism* in favor of physical explanations for inanimate moving objects. But they still used spirits to explain human—and sometimes animal—behavior.

From the earliest historical times, people have believed they possess souls. This belief stems from the fact that each person is aware of his or her own existence. When we think or act, we feel as if something inside us is thinking or deciding to act. It is natural to assume that other people have similar experiences—that *they* feel something inside them, too. Because we cannot directly examine these “things” people have inside them, we conclude that they are made of something different from that of our physical bodies.

Dualism

Early philosophers believed that reality was divided into two categories: the material and the spiritual. According to this belief, humans had physical bodies and nonphysical spirits, or souls. The belief that humans possess both mind and body is called *dualism*. But if the physical and spiritual aspects of our nature are independent, as this model suggests, then

what is the purpose of having both, or in what way are they related? If the body functions independently of the soul, then what does the soul do?

The concept of soul is the cornerstone of religion; philosophers were therefore unwilling to dispense with it. Instead, they suggested that the soul controls the body. The soul and body interact: hence the term *interactionism*. Because the eyes and ears—the primary windows to the soul—are located in the head, the probable location of the soul was presumed to be the brain. Moreover, damage to the head can lead to unconsciousness or paralysis, which suggested that the soul moved the body by controlling the operations of the brain.

In the seventeenth century, the French philosopher and mathematician René Descartes attempted to explain how the soul could control the body. (See **Figure 1.1**.) Descartes believed that animals other than humans were machines. If we could understand how their parts were put together, we should be able to understand them completely. The *bodies* of humans were also machines and operated on exactly the same principles. However, unlike other animals, we had a God-given soul. The soul received information about the world through the body's senses, thought about what it perceived, and made decisions about actions. When it wanted to move the body, it did so by acting on the brain, which in turn moved the muscles.

Descartes formulated the first physiological model of behavior. He based his model on the mechanism that activated the statues in the Royal Gardens. As a young man, he was fascinated by the hidden mechanisms that would cause the statues to move and dance when people visiting the gardens stepped on hidden plates. The statues were moved by hydraulic cylinders powered by water pressure. Descartes believed that the muscles of the body also worked hydraulically. When we



FIGURE 1.1
René Descartes (1596–1650), French philosopher and mathematician, at the court of Queen Christina of Sweden. Descartes's particular form of dualism (interactionism) stimulated interest in the relation between mind and body. (Courtesy of the Granger Collection.)

exert a force with our limbs, our muscles appear to get larger. Descartes concluded that this enlargement occurs because fluid is pumped into the muscles through the nerves. When nerves are cut, a liquid oozes out; hence, the nerves must be hollow.

What is the source of the fluid that gets pumped into the muscles? According to Descartes, it was the *cerebral ventricles*—the hollow, fluid-filled chambers of the brain. He concluded that the mechanism that directed the pressurized fluid into the appropriate nerves was the *pineal body*, a small organ situated on top of the brain stem. The pineal

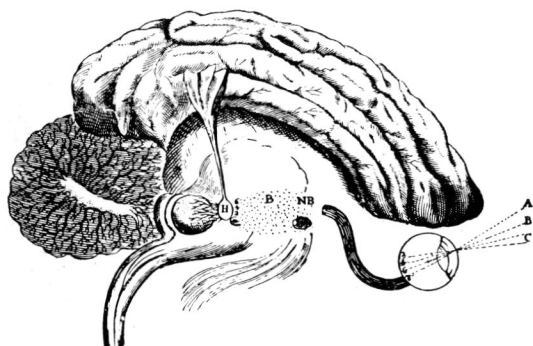


FIGURE 1.2
Descartes believed that the soul controlled the movements of the muscles through its influence on the pineal body. His explanation is modeled on the mechanism that animated statues in the Royal Gardens. More recent attempts to explain the physiology of behavior are modeled on newer devices, such as computers. (Courtesy of Historical Pictures Service, Chicago.)

body acted like a little joystick: when it was tilted slightly in various directions, it opened pores that permitted fluid to enter the nerves and inflate the muscles. (See **Figure 1.2.**)

Because animals lacked souls, Descartes believed that this model completely explained their behavior. Of course, the details would have to be worked out through further study. Humans, however, possessed souls as well as bodies. The pineal gland, which controlled the movements of the pressurized fluids through the nerves to the muscles, provided the place for the soul to interact with the body. When the soul desired a particular action, it tilted the pineal gland appropriately, and the muscles needed to carry out the action became inflated.

As philosophers have subsequently noted, Descartes's theory, like all interactionistic theories, contains a built-in contradiction. If the soul or mind is conceived as nonmaterial, then it cannot (by definition) exert a force

that moves physical objects. Thus, it cannot interact with matter. If the soul or mind possesses material properties that permit it to interact with the body, then it, like the body, is physical. Of course, we could conclude that no contradiction exists, but the issue is beyond human understanding.

However, the spirit of human inquiry is not so easily stifled. Some philosophers after Descartes concluded that his conception of the body as a physical machine was correct as far as it went — but that it should go further. For example, the nineteenth-century British philosopher James Mill agreed that the body was a machine but concluded that the mind was simply a part of the machine. As such, it was subject to the same physical laws as the rest of nature.

Monism

The belief that reality consists of a unified whole — and thus that the mind is a phenomenon produced by the workings of the body — is called *monism*. Modern scientists take a monistic approach to studying the physiology of behavior. That is, we believe that the physiological basis of behavior will be completely understood once we know all the details of the working of the body, especially of the nervous system. Of course, a complete understanding of behavior also requires an analysis of the environment and its effects on the organism. But the reality we deal with is entirely physical in nature. When we study the causes of behavior, we consider only physical events in the environment and in the organism's physiology. What we call “mind” is a consequence of the functioning of the body and its interactions with the environment. The mind-body problem thus exists only as an abstraction.

What can a physiological psychologist say