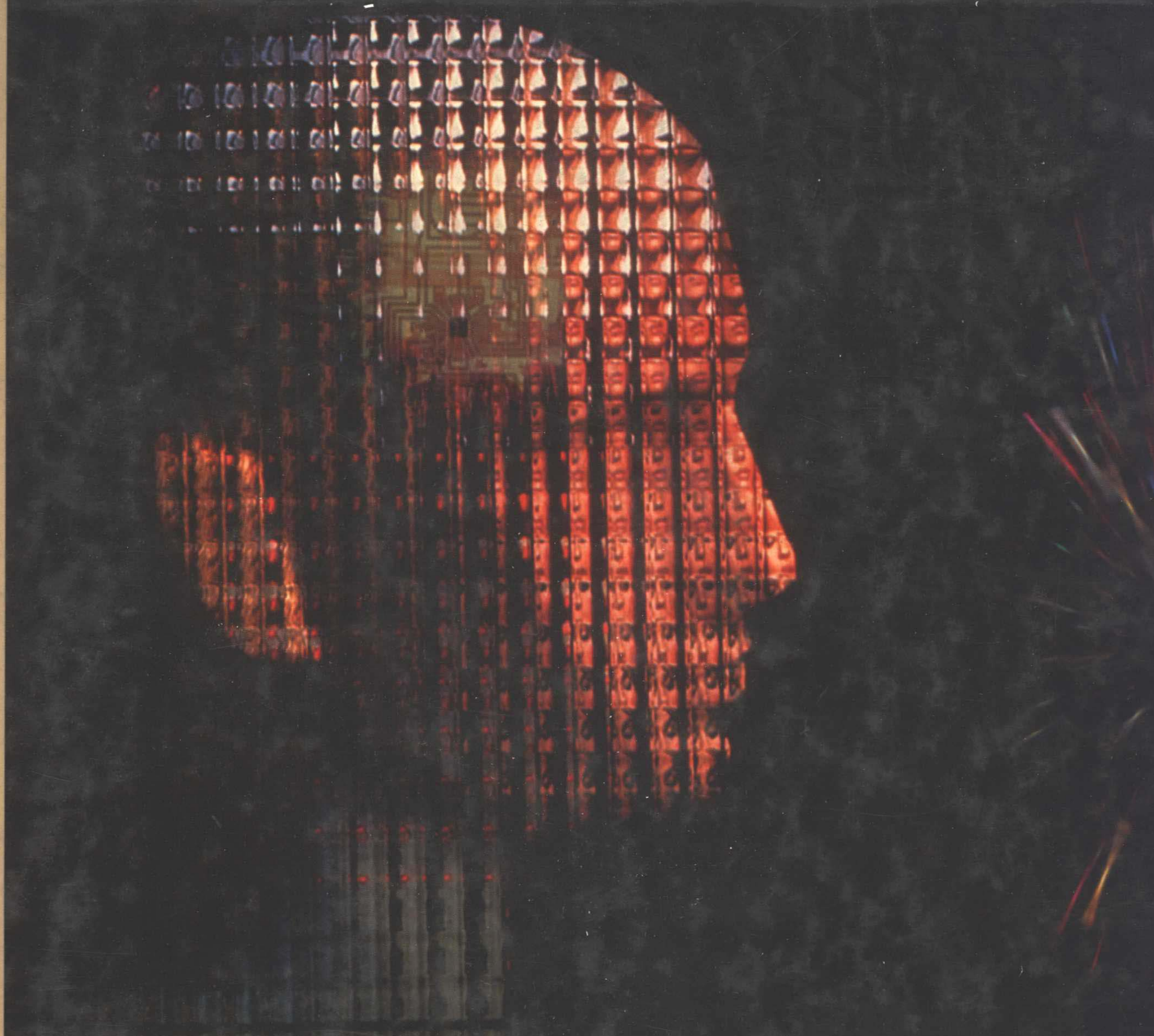

THE BIOLOGY OF BEHAVIOR AND MIND

Bruce Bridgeman

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PREFACE

Physiological psychology is not an easy subject, but it is an enormously exciting one. Magnetic resonance imaging of the living brain, functional grafts to replace missing nerve cells, new chemical therapies for behavioral disorders, and other innovations are coming from the laboratories at a rapid pace. To understand and evaluate these developments, and to know a bit more about ourselves, it is necessary to learn something about the machinery of mind and brain.

The study of the brain covers many subdisciplines, at levels from single molecules to group behavior. To unify the diverse levels and approaches, this book is organized around an evolutionary perspective and an information-processing approach. Signs of one or the other theme appear on almost every page. I have tried to tell a story, rather than just reviewing the relevant experiments in each area. The evolutionary perspective shows not only what happens but why it happens. It relates human to animal studies, and it brings together disparate aspects of the narrative. I hope it also offers a historical basis and a unification with other areas of biology. Information processing is used not in the narrow sense of the information-processing models in cognitive psychology but in the broader sense of information flowing through an organism and being stored and transformed along the way. The basic concepts of both evolution and information processing are introduced in the first chapter.

TO THE STUDENT

To study how the brain works, you need some knowledge of biology, psychology, physics, and chemistry. The text provides background in these areas, but an introductory course in psychology or biology would be helpful too, as would a year of high-school chemistry or one chemistry course at the college level. You should understand the following terms before starting: atom, molecule, atomic number, atomic weight, molecular weight, bond, and charge. If you don't have this background, read the first few chapters of an introductory college-level chemistry textbook or ask a roommate or friend for information when the terms come up.

When you are reading the book, keep a bookmark at the beginning of the glossary and look up unfamiliar words. All important terms are printed in **boldface** in the text and are defined in the glossary. They are also defined in the text at their first appearance. Some other key terms are also defined in the glossary. When you come across a reference to a figure, read to the end of the sentence before examining the figure. Each figure caption begins with a brief description of the figure. Some captions also contain more advanced or specialized material as a supplement to the main text.

Each chapter begins with a chapter outline to give you an idea of where the text is going. Some of the longer or more difficult passages end with mini-summaries whose opening words are *In summary* or *In conclusion*. These mini-summaries (which do not have separate headings) wrap up a section without reviewing all its details. In addition, each chapter ends with a chapter summary. If you understand the terms and ideas in the chapter summary, you have grasped the important messages of the chapter.

Physiological psychology depends on *reductionism,* the idea that one can gain insight into the whole by studying its parts. Everyone is curious about the workings of the mind, the basis of experience, and why we perceive things the way we do. But much of our knowledge about these issues is obtained from studies of small aspects of the problem, often in animals. As you read, try to fit these studies into the bigger picture, and remember that one cannot understand the insights in the field without knowing their factual basis.

Most of all, read with an open mind. The field contains many areas of controversy, and some of its long-held ideas have been found to be false. I have tried to point these out along the way. I envy you a bit, beginning this intellectual adventure at a time when so much is known about the biology of behavior and mind—and when there is so much yet to discover.

TO THE INSTRUCTOR

One of the features of this text that differentiates it from other physiological psychology texts is more emphasis on graded potentials (Chapter 2). Graded cable properties of nerve cell membranes are introduced before the active action potential mode to let students see how information from various sources combines and interacts before it is sent elsewhere. This is the real site of information processing, as opposed to information transmission. In Chapter 3, brain organization is introduced in a phylogenetic and embryological context, beginning with the oldest structures and the most basic subdivisions. The emphasis is on topology and function rather than on topography. Sensory modalities are introduced in the order of their complexity in Chapter 4. Peripheral processes, because they are so different in each modality, are treated separately from central processes, which are similar in all modalities. The senses are also introduced in a functional way, as perceptual systems (Chapter 6) as well as anatomical entities. Many aspects of sensory systems are easier for students to grasp in the context of interactions between perception and behavior. Methods are introduced as they are needed rather than in a separate (and often dry) methods chapter. For example, a passage on anatomical methods introduces Chapter 3.

Rather than trying to decide whether to incorporate material on applications in the body of the text or to concentrate it in specialized chapters, I have done both. Applications that can be explained in a few paragraphs, such as the experimental uses of drugs to combat Alzheimer's disease (Chapter 11), are incorporated in the text; topics requiring more background, such as the biochemistry of schizophrenia (Chapter 15), are covered in separate chapters.

The first 11 chapters, the core of the book, are essential for courses in physiological psychology and neuroscience. The chapters are organized in a fairly standard sequence, with transitions between them to help students bridge the gaps. It is probably best to stick to the order in which they appear in the text, though you can skip or reverse a few chapters if students are adequately prepared for the jumps. The final 5 chapters—applications and implications—follow a less structured approach. The material in each chapter does not depend on background in the previous chapters. These chapters can be used to tailor the course to your preferred sequence and emphasis.

Two of the final 5 chapters have unique contents. The chapter on brain models and artificial intelligence (Chapter 13) speaks to an area of interest to many students, an area in which contact with the neurosciences is growing rapidly. It introduces the history and uses of brain modeling and examines intelligence and emergent processes as applied to brains. The chapter on consciousness and long-term planning (Chapter 14) provides a context for material on the prefrontal areas, as well as reviewing physiological approaches to issues of mind and body that were previously considered mostly by philosophers.

The text contains several unique pedagogical devices. Distributed coding in memory, for example, is introduced in Chapter 11 with an optical analogy, beginning with an examination of the distribution of information at the lens plane of a slide projector. This situation is, of course, familiar to students. The section goes on to introduce distributed coding and retrieval in a concrete manner. Another pedagogical device is the use of a puzzle defined in terms of formal systems (Chapter 13) to explain the difference between information processing in formal systems and intelligent information handling in humans. When students discover that the puzzle cannot be solved, they realize the extra mode of processing they possess. I have found that stories, metaphors, and examples are more useful than the most exhaustive explanation; these devices are used throughout the book.

The text has already benefited greatly from the input of many instructors of physiological psychology and similar courses. If you have suggestions or (is it possible?) corrections, please send them to me at Clark Kerr Hall, University of California, Santa Cruz, CA 95064.

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ORIGINS OF PHYSIOLOGICAL PSYCHOLOGY

Physiological psychology examines the physical basis of human behavior and experience. It is fundamental to our understanding of experience and therefore of all human endeavor. But if the content of physiological psychology is so fundamental, why is the discipline so new? Curiosity about the subject is as old as humanity, yet only in the last 60 years has physiological psychology emerged as a separate area of inquiry. Most of the contents of this book are the result of an explosion of knowledge during the last 30 years. The reasons for the youth of the discipline are both philosophical and technical. The philosophical issues had to be addressed before the technical ones even arose, and philosophy continues to shape the discipline. To examine the philosophical issues, we must look at the history of ideas about the relationship of mind and body.

INTELLECTUAL HISTORY

ANCIENT ORIGINS

As with many areas of human thought, the examination of the mechanisms of mind began with the ancient Greeks. For the earliest Greeks experience was centered in the mystical soul, or "psyche," which was capable of detaching itself from the body. The soul was separate from the life force, "spirtu," and the reasoning power, "pneuma." Objective examination of these concepts was out of the question until Socrates and his pupil Plato invented philosophy in the modern sense and separated it from mysticism. For Socrates sensory experiences were not to be relied on as the basis of a philosophy; they were ephemeral and unreliable and could be tricked and deceived. Where was the certainty on which a philosophy—a system of organized knowledge—could rest? The answer was that out of sensations, but separate from them, grew an **idea**—an abstraction taken from life but more permanent and unchanging than experience. No one has ever seen a perfect triangle, but the idea can exist separate from its external representations. In modern language the abstract idea is an internal state, the stuff of psychology. In a second brilliant insight Socrates asserted that an ordering of the tumble of sensations was possible only if some innate ideas existed. Thus two of the philosophical roots of psychological psychology, **idealism** (the existence of ideas apart from external objects) and **nativism** (the reality of innate ideas), were born (Boring, 1950).

Although most of the ancient Greeks believed that the psyche was not a physical entity, a few philosophers (such as Democritus) held that the soul itself was material. This was not a new idea, even for Democritus; those whom the Greeks themselves considered to be "the ancients" all represented thought as dependent on bodily disposition (Theophrastus [ca. 300 B.C.], translated by Stratton, 1917). Equally important, the Greeks had a belief upon which science depends: that there are unchanging rules underlying the natural world.

The ancient Greeks were excellent philosophers, but they were not experimenters. They had no real idea of brain function; indeed, some thought that the brain was an organ for cooling the blood. (In this thought they were not as far off as it might seem; at rest the body loses 30 percent of its heat through the head.) It wasn't until 500 years later that others, especially the physician Galen (second century A.D.), began developing a knowledge of the correlation of brain structure with function. By examining brain-damaged neurological patients, Galen began to understand the anatomical specialization of brain functions. The idea of the immaterial soul persisted, however, and the later dominance of Christianity prevented the investigation of the divinely endowed human being until the 17th century (though some progress, notably in anatomy, was made by the Arabs in the interim).

DESCARTES AND THE MIND-BODY PROBLEM

The next major advances were made by René Descartes, a 17th-century philosopher and perhaps the world's first physiological psychologist in the modern sense. Though some of his theories today seem almost comically flawed, he contributed to both philosophy and science. The principle of **reciprocal innervation**—that muscles come in pairs with opposite actions—was among his many achievements. He also introduced the concept of **reflex** to describe quick, automatic responses.

Descartes's philosophy of mind is **dualism,** the idea that body and mind are separate entities. Descartes's dualism is very different from the implicit dualism of the Greeks; for Descartes only a person's will operates in the service of the nonphysical soul. The rest of the organism, including the control mechanisms of all the behaviors performed by animals, is purely physical and a legitimate object of scientific study. Dualism of any sort is firmly rejected by modern physiological psychologists, but in Descartes's day it represented an enormous step forward. In a single stroke Descartes snatched from under the eyes of the Grand Inquisitor three-quarters of what is now neurobiology, simply by asserting that the control of behaviors did not concern the soul. (Even so, Descartes [1665, 1972] let this part of his work be published only after his death, just to be on the safe side.) The study of the mechanisms of most behaviors, considered heresy for a thousand years, was now open to the fast-developing tools of the scientist. Serious work on brain and behavior could begin.

Cartesian (from Descartes) dualism was the predominant philosophy up to the 19th century, even though it contains a fundamental logical flaw. The doctrine asserts that biological materials obey all physical laws, being influenced only by physical forces acting on them, but the nonphysical mind can somehow influence behavior. If one can talk about one's mind, for instance, the mind must influence the brain to affect the speech machinery. For Descartes the site of this interaction was the pineal gland, chosen because of its location at the center of the head and because it is a single structure, not doubled on the left and right, as are most other structures.

Let us examine the junction of body and mind more closely. Part of the definition of a physical system is that it obeys physical laws. Therefore the mind's influence at this **interface** (point of interaction) must be a physical one, and the interface between body and mind must itself be physical. We need another interface to transfer from the nonphysical mind to the physical interface just described. But this second interface raises the same objections as the first one, and so on ad infinitum. Either matter doesn't always behave according to the laws of the physicists or the mind itself is a physical entity, an organization of matter and energy somewhere inside the brain.

Modern physiological psychology has adopted the latter alternative—that all functions of the brain, including the mind, can be described in physical terms as organizations of matter and energy. Historically, this view, known as **mechanism,** eventually triumphed over **vitalism,** the idea that there was something qualitatively different about living material. (If dualism survives, it is as a distinction between organization on one side and matter and energy on the other.) But the change did not take place until the middle of the 19th century, a period that saw the settling of most of the philosophical issues that were required to enable brain research to progress (Cranefield, 1957). Some are still discussed by philosophers, but physiological psychologists and other scientists agree, for instance, that there is a real world, that our senses bring us information about it, and that we can act on the world.

Philosophers are sometimes surprised that science is as productive as it is given that scientists are so naive philosophically. But scientists stand at the apex of a long tradition of philosophy, which gives them powerful conceptual tools to use in deciphering nature. An outgrowth of this tradition is the set of approaches and attitudes grouped together as the "scientific method." It has become a powerful way of formally bridging the gap Socrates pointed out between the unreliable senses and the permanent ideas. Because the design of our own sensory systems parallels the techniques of the scientific method in many ways, these techniques will be introduced in the chapters on sensory systems.

ORIGINS IN PSYCHOLOGY

Modern scientific disciplines have branched off from philosophy one by one for the past four centuries, beginning with astronomy and physics and continuing with the biological sciences in the 18th and 19th centuries. By the late 19th century philosophy consisted largely of doctrines about the nature of reality, experience, and behavior—areas that then branched off from philosophy to form the new science of psychology.

Progress in psychological research within philosophy led to Wilhelm Wundt's founding of the first psychological laboratory, in 1879. Wundt combined philosophical reasoning and careful **introspection**—the breaking down of one's own experience into elements analogous to the basic elements in chemistry. Wundt's students and prolific writings spread his ideas widely but also led to the development of schools of introspectionist psychology headed by rival professors. One of the great disputes of the new psychology concerned the issue of imageless thought. Wundt's school (at Leipzig) maintained that pure imageless thought was possible; E. B. Titchener's school (at Cornell University) maintained just as forcefully that thought was always accompanied by mental images and consisted of manipulations of these images (Boring, 1950). Each group produced voluminous records of introspections proving its point and contradicting the other's. Finally it became clear that neither side could win because the data—the observations—were private, subjective experiences not open to public scrutiny. That is, they were not objective, repeatable experimental results. Controversies of this sort were unresolvable. By the turn of the 20th century the whole area of introspective psychology had fallen into disrepute.

At this point, beginning about 1913, John Watson revolutionized American psychology with **behaviorism.** Watson asserted that the proper content of psychology was not experience but behavior, for only behavior could be measured objectively. It could be analyzed by finding relationships between stimuli and responses. This **stimulus-response psychology** considered the steps intervening between stimulus and response to be unmeasurable. (The standpoint is best summarized in Watson, 1920.) The promise of objectivity caused behaviorism to dominate psychology, especially in the United States, until the 1950s. But objectivity was achieved at the expense of disregarding the very problem that had gotten psychology started: the understanding of experience. Another revolution in psychology has recently brought experience back under scrutiny with powerful new objective methods, under the name of *cognitive psychology* (Neisser, 1967). Cognitive psychologists now talk of internal processes, such as memory strategies, in ways unthinkable to behaviorists. Without looking inside the brain, however, they do not have direct access to much of what is studied by physiological psychologists, who examine mental processes by looking at the structure and activity of the brain itself.

The situation of psychologists is like that of imaginary Martian behavioral scientists. Landing on earth, they discover that the dominant form of life (at least in North America and Europe) is the automobile. They study its behavior, finding relationships between pressure on the gas pedal and acceleration, between the steering wheel and the direction of travel, and so on. They can describe the behavior of the automobile in some detail; but they wil never understand how it works, and they will have no idea how to fix it when something goes wrong. For that they must open up the hood and learn about the mechanisms of the beast in terms of cyliners and pistons. Similarly, those who study humans can benefit from looking inside the brain to begin finding out how the machinery of the mind works.

ORIGINS IN PHYSIOLOGY

During the second half of the 19th century, a separate neurophysiology was developing from physiology and medicine. Neurologists codified the knowledge they had acquired from studying patients with brain damage, and they began experiments with the brains of living beings. The neurophysiological tradition culminated in the work of Sir Charles Sherrington (1906), who discovered or summarized much of what we know about reflexes today (see Chapter 7). Another important figure, the Russian physiologist I. P. Pavlov, had little respect for introspective psychologists of his day. With his famous experiments on conditioning in dogs (described in Chapter 11), he began a separate, physiologically based study of the brain mechanisms of behavior (Pavlov, 1927). Pavlov's theory was a stimulus-response scheme much like that of the behaviorists, but Pavlov was the last stimulus-response theorist in physiological psychology.

Shortly after Pavlov's major work became available in English, another psychologist, Karl Lashley (1929), indicated that the brain is not organized in a stimulus-response manner but instead shows a much more distributed processing of information (Chapter 11). The business of the brain is not a passive connecting of stimuli to responses, like a telephone switchboard. Rather it is a rich and subtle combining of sensory information with remembered experience and genetically given instructions. From these raw materials the brain generates new memories and behaviors. This process takes place in a highly integrated and densely interconnected network. In this sense physiological psychology has always been cognitive, not suffering from the limitations of the stimulus-response analysis. The task of the physiological psychologist has always been to understand the internal processes that come between stimulus and response. The stimulus-response analysis meanwhile has moved to a more microscopic level. In invertebrates it is being usefully applied to the brain-behavior relationships of sea slugs and other simple animals (Davis & Mpitsos, 1971).

THE CURRENT SYNTHESIS

In the years since World War II a new discipline has grown up from these roots. It combines the new cognitive psychology of experience with physiological psychology and neurophysiology to create a new physiological study of experience and behavior. The discipline is so new that even its name has not yet been settled; it is recognized as physiological psychology, neuroscience, biopsychology, psychobiology, and several other combinations, each with a different emphasis. It has absorbed elements of some newer disciplines, such as neurochemistry and information sciences. Thus some older disciplines that had split from philos-