KENNETH D. ROEDER

# Nerve Cells and Insect Behavior

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# *Preface*

This book is an account of some aspects of nerve activity and insect behavior that have been of particular interest to me. It is not intended as a review of insect nerve physiology. Most of the chapters have been written as self-contained essays, just as I first explored each topic for its intrinsic interest rather than because it fitted into a major plan. But in reviewing these adventures I have also searched for a common connecting theme, and I have included some neurophysiological background in the hope of relating them to the mainstream of research on the neural basis of behavior.

The nature and direction of the book are perhaps best revealed by telling briefly how I came to be involved with insects, nerves, and behavior. An interest in insects began in early childhood, when my father introduced me to the excitement of collecting and rearing British butterflies and moths. Any child who has raised caterpillars and watched the extraordinary transformation of form and function during insect metamorphosis has been exposed to some of the central questions of animal behavior and development. I don't believe that I thought seriously about insects' nervous systems until I was a member of the physiology course given during the summer of 1932 at the Woods Hole Marine Biological Laboratory, when Dr. C. Ladd Prosser, at that time an instructor in the course, showed me the possibilities of experimenting on the arthropod central nervous system. Later, I was carried in an electrophysiological direction through the interest of Dr. Leonard Carmichael, then president of Tufts University, and through his generosity in allowing me to use the electrophysiological laboratory that he rarely had time to enjoy himself. In recent years the study of animal behavior has exerted a renewed pull on me through contact with Dr. Konrad Lorenz and many other ethologists. A number of their concepts, arrived at through long observation of animals under natural conditions, seem to me to have significant analogies in neurophysiological processes. In a sense, this book is a resifting of my own scientific experiences in order to find out whether any of these analogies are signs of deeper causal relations.

Any attempt to spin connecting threads between established and internally coherent fields of knowledge must inevitably distort both fields in the eyes of their orthodox adherents. The threads can be made to connect only at the peripheries of each field, so that the edges tend to become distorted out of proportion to the central core of each. The value of the threads and distortions lies in the transitions and new viewpoints that they uncover. I feel that insects provide an important transition point from ethology to neurophysiology, even though many ethologists probably consider that insects are dull subjects compared with fishes and birds, and most neurophysiologists will rightly claim that insects have not contributed to neurophysiology in the same degree as squid, frogs, and cats. However, if this book provides ethologists with a readable account of some of the notions of neurophysiology that pertain to behavior, and if it encourages some of the neurophysiologists to take time out from the oscilloscope screen for a little patient and passive observation of the normal behavior of their subjects, then it will have been worth while writing.

## ACKNOWLEDGMENTS

It is impossible to name all the students, research associates, visitors, and colleagues who have influenced the thoughts and experiments on insects described in the following pages. A great many people have been and are actively associated with the work on insects in our laboratories at Tufts University, and I shall try to mention a few of these as they are connected with the topics of this book.

The experiments on ultrasonic hearing in moths (Chapters 4 and 5) began in 1955 when Dr. Asher Treat (The City College of New York) visited the laboratory in the hope that it might be possible to record nerve impulses from a moth's ear. His persistence in the face of my initial pessimism established a mutual feedback between us that still continues in the business of bats and moths. The experience of Dr. Donald Griffin (Harvard University) with bats, his encouragement from the sidelines, and his generosity in lending special equipment did much to aid this project.

The experiments of Chapter 6, also some of those in Chapters 8 and 9, are a few of the many that we have carried out at the expense of that alert, elegant, and most misunderstood of insects, *Periplaneta americana* L. The close association of Miss Elizabeth A. Weiant with our work on this insect deserves special mention, not only for her skill in fine surgery, but also for her perseverance in the face of initial antipathy. Others who played an active part in our work with cockroaches are Mrs. John L. Kennedy, Dr. Chester C. Roys, Mrs. Daniel Samson, Dr. Alan Slocombe, and Dr. Betty Twarog. In addition, the outstanding work of Dr. Phillip Ruck on photoreception and Dr. Nancy Milburn on neurosecretion is discussed in Chapters 8 and 9.

All of these are intramural acknowledgements. It is not feasible to go further afield since another book would be needed to discuss all the important work on insect sense

organs, neuropharmacology and neurochemistry, orientation, and behavior that is entirely relevant to the matters to be discussed, but that has been omitted because a line had to be drawn somewhere.

Adequate funds for research are valuable for obvious reasons, but they also play an equally important part as a token of confidence. Twenty years ago a modest grant from the American Academy of Arts and Sciences played the latter role out of all proportion to its monetary value. Since then, the work in our laboratory has owed much to continuous and adequate support from contracts and grants from the Chemical Corps, U. S. Army, the National Science Foundation, and the U. S. Public Health Service.

I am grateful to the following publishers for permission to use some of the figures, in their original or modified form: John Wiley and Sons, Inc., New York (Fig. 23); The Johns Hopkins Press, Baltimore (Figs. 25 and 27); W. B. Saunders Company, Philadelphia (Fig. 28); University of Oregon Publications, Eugene, Oregon (Fig. 46); and Annual Reviews Incorporated, Palo Alto, California (Fig. 47). Previously unpublished figures were kindly supplied by Dr. J. J. G. McCue, Lincoln Laboratory, Massachusetts Institute of Technology (Fig. 6), Mr. Frederic A. Webster, Cambridge, Massachusetts (Figs. 16 and 19), and Dr. Nancy Milburn, Tufts University (Figs. 37 and 39).

The burden of typing the manuscript was born effectively by Mrs. Frances French, and the final drafting and lettering of many of the figures was carried out by Mr. George Johnson.

The book would probably never have been written if the Trustees of Tufts College had not granted me a leave from the information overload of present-day academic life, and if the Weiberhof had not provided hospitality, peace, and freedom from other responsibilities.

K. D. R.

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# 1. *Coding and Complexity*

Philosophers and scientists have invoked many special qualities in attempting to distinguish living from nonliving matter. However, as we learn more about the ultrastructure of proteins and viruses, chemical bonding, and the energetics and kinetics of living and nonliving systems, a sharp dividing line becomes harder and harder to establish. Living and nonliving systems are clearly composed of the same ingredients and subject to the same physical laws.

If life is not made of special stuff, then its uniqueness must lie in the pattern of its structural organization or molecular order. The secret is in the system and not in the materials. Indeed, if this were not the case it would be hard to explain the familiar cycle of growth and assimilation followed by death and decay.

One of the many attributes of living matter is its inevitable tendency to grow, differentiate, and become more complex. In living systems simple chemical compounds are elaborated into proteins, proteins into cells, cells into organisms, each stage requiring the synthesis of molecular configurations that are thermodynamically more improbable and unstable than those of the preceding stage. At first glance, these processes in living matter seem to contradict the second law of thermodynamics. Energy is constantly being transformed from one kind to another; thus, electric energy can be transformed into heat or into energy of motion or in other ways; mechanical or chemical energy can be transformed into electrical energy; heat energy can be transformed into mechanical energy, and so on. But in all of these changes some energy is transformed into heat and some of the heat descends to the temperature of the surroundings and thus becomes unavailable for further transformation into useful work. Thus in a closed universe (one into which energy cannot enter) the prospect is eventual transformation of all energy into heat and the degradation of this energy to a state in which none of it is available for transformation into any other form. This trend would be expected to reduce matter to its simplest possible form.

The apparent contradiction between this consequence of the second law of thermodynamics and the energy transformations that occur in living matter is reconciled when we realize that living matter consists of a multitude of open systems. Energy, in the form of sunlight or entrapped in the chemical bonds of nutrient compounds, streams continuously through each such system. Some of this energy is used to build more complex configurations involving new chemical bonds; some becomes unavailable by transformation into heat but there is a new supply constantly coming into the system from outside. The role of living matter may be likened to that of a hydraulic ram that employs some of the kinetic energy released by water flowing downhill to pump a small portion of the water uphill while the rest of it becomes unavailable for use. Thus the presence of life in one portion of the universe, taken as a closed system, need not alter the over-all process of degradation of energy in the universe, and the physicist is satisfied.

But the biologist is not. Most biological research is directly or indirectly concerned with reaching a fuller understanding of this synthesizing or organizing property of living matter. A penetrating discussion of living matter and the second law of thermodynamics is to be found in Blum's *Time's Arrow and Evolution*,[3] and the huge literature of genetics, systematics, evolution, embryology, morphology, biochemistry, and physiology deals with various facets. Although we are still unable to define with precision the difference between the living and the nonliving, these sciences are informing us about many of the associative properties of life.

The inevitable energy gradient in time predicted by the second law of thermodynamics is, provided we regard it statistically and without regard for the movements of individual atoms, essentially smooth and stepless. Events such as cosmic explosions are minor perturbations in the total energy flux—exceptions rather than the rule. The pathway of life toward order is likewise thought to be unmarked by any major steps or discontinuities. Whether we consider organic evolution from the earliest forms of life to man and his social systems, or the development of an egg into an adult, the picture is one of a continuous and multidirectional unfolding accompanied by many changes of pace and direction but never interrupted by major quantal jumps or saltations. There is as little scientific evidence for the special creation of an Adam and Eve as there is for special annihilation—the instantaneous disintegration and disappearance of a living organism. Even at death, when biological time stops and the second law of thermodynamics operates without the biological countercurrent, the transformation from the living to the nonliving is more gradual than is generally supposed.

The transformation promoted by living matter from simple to higher orders of organization requires a system for the storage and transmission of information from one stage to the next. Biological progress toward complexity would not be possible in the face of the opposing tendency toward randomness unless each stage profited in some way from the experience of those gone before. Perhaps the connection between information transmission and the synthesizing attribute of living matter is not immediately obvious, so let us consider a few examples.

Darwin recognized two important prerequisites when formulating his theory of evolution through natural selection. These are that like tends to beget like and that no two individuals of a species are identical. The biological basis of these conditions did not begin to be understood until the advent of modern genetics and cytology some fifty years after the publication of the *Origin of Species.* We now know that inheritable material in the form of genes is contributed to the offspring by both parents. The identity of each gene is determined in the chromosomes by a relatively simple chemical arrangement which we are now close to understanding. The identity and order of the genes within the chromosomes provide a template from which specific proteins are replicated. The nature and arrangement of proteins in the body determine the anatomic form and physiologic activity characteristic of the individual. Thus, the gene arrangement of an individual could be thought of as a compact code or formula for his body form.

In the formation of germ cells the gene code is replicated, and on fertilization the gene codes of both parents are combined. However, the replication process is not quite perfect, and the combination of parental gene codes does not result in a smooth blending. If this were the case, the outcome could only be uniformity and it would be impossible to account for the novelty and variety so evident in evolution. All organisms would be identical. This is avoided by two contrasting properties of great importance. First, individual genes may retain their identity and potency through many generations even when their capacity to express themselves in body form is suppressed by other genes. Unlike most biological entities, the genes have stability in time. Second, in the process of gene replication some genes may be omitted from the germ-cell nucleus, the gene order may be changed, or certain genes may lose their stability. These mutations or "copying errors" in the replication process probably occur by chance, that is, not in response to need or to the action of specific aspects of the environment, although the frequency of their occurrence may be altered by outside influences such as high-energy radiation. Once they have taken place, these genetic changes become incorporated in the replicated product and are thus transmitted to future generations.

Although this is clearly an example of the transmission of racial information in coded form from one generation to the next, it might be thought that mutations and sexual recombination would tend to garble the message and lead to degeneration and randomness. However, it is just these "errors" and alterations in the coded message that permit evolutionary progress. The ordering factor is the environment to which all the members of a population are exposed. The environment acts like a sieve that favors survival and reproduction of those variants or mutants having characteristics more advantageous than the norm of the population. Similarly, disadvantageous mutants (probably the great percentage) are prevented by death from contributing their special gene arrangements to the racial pool. The same type of variant probably reappears many times in a population, but the alteration in the gene code that produced it will become widely diffused through the population only when the environment alters in such a way that the bodily expression of this gene arrangement confers some advantage in survival and reproduction.

We can conclude from this digression into evolutionary theory that the mechanism for the origin of species requires (1) a fairly stable means for encoding, transmitting, and de-coding bodily characteristics between one generation and the next, (2) the possibility of alterations in the coded message through mutation and sexual recombination, and (3) a means for selecting for transmission those alterations that favor survival.

It is not difficult to recognize an analogous situation in the evolution of human society. The ideas and actions of outstanding individuals are encoded in language, stored and transmitted in various media such as books, and decoded eventually into ideas and actions by other individuals. Alterations in the message take place when the thoughts and actions of the reader are influenced by what he reads, in other words, in the educational process. Society plays the part of the selective mechanism that determines which thoughts and actions are "good" and shall be encoded and transmitted to future generations. As in organic evolution, the selective sieve—society in one case and environment in the other—is an averaging device. Many mutants are not advantageous under present conditions and many ideas are ahead of their time. Both may persist because of the relative stability of the coded message, or they may recur *de novo* a number of times before the state of the sieve is such that they become advantageous.

A third example of the relation between information coding and the development of complex and nonrandom biological systems is to be found in the nervous system of many-celled animals. The following chapters will be concerned with the relation between nerve-impulse coding and insect behavior. As an introduction we will take a cursory glance at the origins and evolution of the nervous system.

Unfortunately we know next to nothing about the internal mechanisms that enable the Protozoa (single-celled animals) to move toward places that are favorable for survival and away from noxious areas. Although these reactions or taxes are frequently simple trial-and-error processes rather than movement along a gradient, they bring their possessors into optimal conditions of light and temperature, and into favorable concentrations of oxygen, carbon dioxide, and other chemicals, and differ little from taxes shown by many-celled animals with nervous systems. Free-swimming protozoa may be observed to collect in a dense cloud at one point. If the optimum condition is moved to another point the cloud migrates in a manner that reminds one of a regiment of soldiers obeying a command.

Higher organisms are thought to have evolved from single-celled ancestors in which the daughter cells budding off at cell division remained adhering to one another instead of swimming off separately. If we assume that the cells composing these ancestral metazoa (many-celled animals) had characteristics like those of present-day protozoa, we can visualize a mat or ball of cells moving through the water to optimal conditions, this time like a squad of soldiers or a chorus line in which the members are physically linked together or follow prearranged rules. Like the squad or chorus, this primordial metazoan presumably had a repertoire of maneuvers each of which could be equally well executed by each one of the members if detached from the group. Orientation of the colony as a unit would be possible only if each motile member had the same set of built-in responses and all members were exposed to the same stimulus, although not necessarily at the same intensity. Good performance by a chorus line requires that all members have the same training and that the whole chorus be exposed to the same conductor or orchestra.

From this it follows that such systems will become unmaneuverable if the number of members becomes so large that different parts of the system are exposed to different stimuli. Similar confusion will result if members of the system differentiate from each other in such a way that they respond in conflicting ways to the same stimulus. The only alternatives