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KENNETH DAVID ROEDER

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A Biographical Memoir by

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KENNETH DAVID ROEDER was born in Richmond, a suburb of London, England, on March 9, 1908. His father, Carl David Roeder, grew up in Germany and was of Scots and German parentage; his mother, Grace (Phillips) Roeder, spent her childhood in Australia, her parents having migrated there from England.

His first school was Bruce Payne School in Bishops Stortford, Essex, where his education was strict and formal. From there he advanced to Bembridge School, Isle of Wight. The headmaster, Mr. Howard Whitehouse, who was a Ruskin enthusiast, active in the Liberal Party, and interested in American education, made this school a happy compromise between British and American systems and awakened Roeder's interest in ideas and pleasure in working with his hands. He leaned toward physics and chemistry through the enthusiasm of a science teacher, Mr. E. J. Baggaley. In 1926 he entered St. John's College, Cambridge University, and received the degrees of B.A. (1929) and M.A. (1933). He was awarded an honorary doctor of science from Tufts University in 1952.

As a child he had become "imprinted" on insects, and at the age of ten, learning from his father the joys of collecting insects and surgaring for moths, he amassed a large collection of British butterflies and moths. This zoological bent followed him to Cambridge, where he was trained in classical zoology. His special interest was insect metamorphosis. At this time there was little interaction between the departments of zoology and physiology; nevertheless, he became interested in what was then called experimental zoology. He took Part II of the Natural Science Tripos under the tutelage of James Gray and C. M. A. Pantin. He also received superb instruction in entomology and invertebrate zoology from L. E. S. Eastham, L. A. Borradaile, F. A. Potts, and Stanley Gardener.

In 1930 he was appointed teaching assistant at the University of Toronto. In 1931, in the nadir of the Great Depression, he returned to Europe and married Sonja von Cancrin of the Weiberhof, a farm in Bavaria, Germany. He then moved to Tufts College as instructor in biology. He became successively professor of physiology (1951), chairman of the Department of Biology (1959–64), research professor on a National Institutes of Health Career Award (1964–75), and professor emeritus (1976).

In the summer of 1932, while he was enrolled in the physiology course at the Woods Hole Marine Biological Laboratory, his interest in invertebrate nervous systems was stimulated by C. Ladd Prosser, the instructor in the course. The most significant outcome of a laboratory demonstration involving ablation on the brains of dogfish, worms, and lobsters was, from Roeder's point of view, the augmentation of certain kinds of behavior that followed reduction in the mass of central tissue. He decided to investigate this phenomenon with praying mantids as experimental animals. While at Toronto he had mailed fifty cents in response to an advertisement for eggs and had become intrigued with the behavior of these attractive insects. Now, building upon what he had learned from Prosser, he began to investigate the consequences of various brain lesions on behavior. He found that continuous copulatory activity in males and locomotion in both sexes could be released by removing specific parts of the brain. Control of behavior seemed to be exercised mainly through inhibition of inappropriate patterns. Roeder was invited to describe this work at the Cambridge Entomological Club at Harvard at this time when entomology in America concerned itself almost exclusively with taxonomy and natural history. The potential of insects as "guinea pigs" for solving basic physiological questions was little appreciated.

This was also a period in physiology when the work of Charles Sherrington and Jacques Loeb was generally interpreted dogmatically. Animals were conceived of as reflex input-output machines. On the other hand, E. D. Adrian had already described spontaneous electrical activity in the isolated nerve cords of caterpillars, and Prosser was finding the same phenomenon in isolated crayfish ganglia. The consensus of vertebrate physiologists of the time was that ongoing activity was just physiological "noise." In reflecting on these matters, Roeder sensed some connection between continuous sexual and locomotor activity in his operated mantids and the spontaneous electrical activity observed by Adrian and Prosser.

About this time, George H. Parker at Harvard urged Roeder to become one of his graduate students. Roeder declined. He explained later that a friend who had gone from Toronto to undertake graduate work at Harvard was so busy taking courses which he did not care to take and having someone else tell him what experiments to do that he was not having any fun. Roeder valued his freedom highly and looked upon research as his play. He wanted to approach experiments on his own, free from the biases and preconceived ideas of others.

Tufts College provided a congenial milieu and an opportunity to embark upon electrophysiological experiments. The opportunity came in 1938 when Leonard Carmichael became president of that institution. As Roeder wrote,

> He brought with him from Rochester some very erratic amplifiers and a string oscillograph accompanied by an electronics technician (Bertram Wellman) to nurse them. Carmichael found that his presidential obligations almost precluded research with the result that I practically had the set-up to myself. I went to work on the isolated nerve cords of various arthropods, studying (without much logic, I feel) the action of a wide variety of drugs and cation concentration on long-term changes in the spontaneous level of spike activity. The outcome was several papers in the 1940s which showed that the level of activity in deafferented insect and crayfish cords was much more sensitive to chemical changes in the medium than were the more popular phenomena of neurophysiology such as action potential parameters and simple synaptic transmission.

These experiments were carried out with equipment that was extremely primitive by modern standards. Nearly all the apparatus was home-built and ingeniously tailored to the projected experiment. Roeder was a master in the design and construction of experimental set-ups. He was known to his students as an inveterate "tinkerer." On the wall overlooking one of his self-designed pen recorders for action potentials was a quotation from *The Rubáiyát of Omar Khayyám*:

> The Moving Finger writes; and having writ,
> Moves on; nor all thy Piety nor Wit
> Shall lure it back to cancel half a Line,
> Nor all thy Tears wash out a Word of it.

This sentiment reflected Roeder's honest and uncompromising approach to even the most recalcitrant data.

A longtime colleague wrote, apropos of mechanical and experimental ingenuity, "He encouraged each of us to build black boxes and nerve chambers, realizing the appropriate and ingenious experiment was often the key to solving a research problem." This trait of mechanical ingenuity had also appeared early in his life. His hilarious stories of struggles and pranks with electric generators and automobiles belonging to his father and his headmaster offered ample proof of this. We cannot help but remember with pleasure the loving care expended in making microelectrodes, the artificial eye with compensating pupil, the mealworm cannon for free-flying bats, the homemade or modified cameras, the artificial electrical cockroach, and outdoor electrophysiological studies pursued in woods and fields using the heavy and clumsy equipment of the 1950s and early 1960s.

With this equipment he pioneered on many fronts. He used motion picture films and single-frame analysis to elucidate fast movement sequences performed in prey capture by praying mantids; he modified cameras for photographing at night the maneuvers executed by moths evading hunting bats; he confirmed J. W. S. Pringle's discovery of the myogenic properties of insect flight muscle by combining the recording of fast thoracic oscillations by means of a crystal phonographic pick-up with the recording of electromyograms in rapidly flying Diptera; he was one of the first to use thermistors as differential anemometers for measuring the turning tendency of moths in stationary flight in the presence of ultrasounds.

Although early electrophysiological experiments on the central nerve cord were interesting to Roeder, none seemed to him to have obvious relevance to animal behavior until he read the 1950 essays of Konrad Lorenz and Erik von Holst. As he remarked, these seemed much more heuristic and acceptable to a zoologist than the then current Pavlovian rat psychology. He was stimulated to return to his earlier studies on spontaneous activity and to attempt to prove that spontaneous nerve activity could generate adaptive behavior. In 1960 he published two papers showing conclusively that coordinated patterns of motor spikes destined for the phallic apparatus of mantids and cockroaches are generated endogenously in the last abdominal ganglion and are suppressed most of the time by descending signals from the brain. This demonstration of central inhibition came long before the cellular basis of inhibitory control could be established. His demonstration that rhythmic copulatory and locomotory movements are organized by central pattern generators had already been made before the importance of pattern generators in insects was beginning to be realized.

During this period he was making annual visits to the country of his father's birth, where he relaxed in the hospitality, peace, and freedom of the Weiberhof, Sonja's family home. While in Germany he was able to maintain personal contact with European ethologists, especially Konrad Lorenz, and with Erik von Holst and Nicolaas Tinbergen of The Netherlands. These contacts came at a time when American psychologists were only just becoming aware of European ethology, and confrontations between the two schools of behavior were on occasion extremely acrimonious. At the same time there was minimal interaction between neurophysiologists and behaviorists of either camp. Roeder, in his quiet, forthright, scholarly, and often humorous manner, served as a bridge of understanding. His fluency in German, his European cultural background, and his training in classical zoology at Cambridge played an important role in unifying the thinking in the field of animal behavior. At meetings in Freiburg and Seewiesen he not only enriched his own understanding of animal behavior but also influenced greatly by his quiet wisdom and intellectual honesty the course of neuroethology.

In the 1960s Roeder turned his attention to afference and the central control of acoustic evasive behavior of moths. As with so many of his studies, this interest had its genesis in his field observations of the behavior of moths when hunting bats were in the vicinity. He set up in his backyard in Concord, Massachusetts, an experimental arrangement that was simple and elegant. He reasoned that certain families of moths could hear the ultrasonic cries of bats by means of paired tympanic organs in the thorax. Thereupon he dissected a moth's "ear" and attached recording electrodes connected to a portable oscilloscope. At the same time he rigged a flash camera capable of photographing the field of battle when triggered. At dusk a stream of bats emerged from their roost in a neighbor's barn. The cries of any bat that reached the precincts of the garden were detected by the moth's ear and flashed on the oscilloscope, whereby Roeder was notified that a bat approached in pursuit of a moth. As the work progressed it became clear that the bat changed the character of its cry when echos were received from the moth. When the cry changed, Roeder triggered the camera. In this manner he obtained simultaneously a record of the bat's cry as perceived by the dissected moth ear and a motion picture photograph of the flight path of the moth being pursued. At one point Roeder and Asher Treat hauled about 300 pounds of electronic gear up a grassy hillside in the Berkshires of Massachusetts, where bats were known to feed, and conducted their experiments there.

From these field experiments Roeder moved on to investigate the acoustic properties of the two receptor cells associated with the tympanic organ. He plunged farther and farther into the central nervous system as he sought to understand how sensory signals were perceived at different levels and how this related to evasive flight behavior. In the 1960s he was recording from single cells in the brain. He considered himself fortunate if he found the acoustically sensitive brain cells 50 percent of the time.

The monumental body of work that led Roeder from mantid and cockroach behavior, to spontaneous activity in central nervous systems, to central inhibition, to neurophysiological analyses of prey-predator relationships, and finally to central processing of ultrasonic sounds was conducted uninterruptedly over a period of forty-two years in a cramped, cluttered laboratory in the basement of Tufts College's Barnum Museum, the home of the Biology Department and of Barnum's stuffed elephant Jumbo. In this ecological niche between the years 1933 and 1945 he worked alone with practically no research funds beyond those provided by the department plus a small grant from the American Academy of Arts and Sciences. Toward the end of World War II the Office of Scientific Research and Development, and later the Army Chemical Corps, the National Science Foundation, and the National Institutes of Health, provided support for studies of the mode of action of DDT and other insecticides. During this period, which dealt mainly with insect pharmacology, Roeder viewed the various drugs and toxic compounds mainly as levers for prying out information about the normal machinery of the insect nervous system. In the process, much was learned about the operation of insect synapses, sense organs, and muscles, particularly those concerned with flight. Of the eighty-eight major papers published during his career, two-thirds represented work done by himself alone. In contrast to the modern mode of working with teams of collaborators, Roeder preferred to work alone; nonetheless, the basement laboratory was the home of a small, closely knit group of students, postdoctoral fellows, and visitors from widespread parts of the world. There was a heady atmosphere here, a joie de vivre, an excitement, a unique camaraderie. Ken was always available to discuss, challenge, and offer opinions.

A former student and colleague captured the spirit of the enclave and the personality of Ken when she wrote the following:

> He taught us to ask questions, even in the face of established authority, to tinker and invent, to laugh at ourselves, to believe evidence, to play and to take joy in research, to teach and most of all to love. No teacher can have been so able in guiding and encouraging his students without excessively challenging them or overwhelming them. He cared about each of us personally—Tufts was his world, the kingdom he was looking for. He traveled far, taught many and learned much, but no faculty member was more loyal, devoted, or conscientious in performing his university chores or in serving either his adopted country or his intellectual discipline when the need arose. Honors came and they pleased him, but he cared most for the opinions of his family, his friends and his scientific colleagues.

His interactions with people, his mien, his philosophy were all of a piece whether he was at the college or at home with family and friends. The latchstring was always out at his home in the Concord countryside where, he once remarked in reference to the Battle of Concord and his nationality, "I live on the wrong side of the river."

Over the years, in all seasons, I spent many relaxed hours with Ken and Sonja in that setting, where the conversation ranged through experimental science, personal philosophy of science, music, art, literature, and religion. Always lurking in the background was Ken's acute wit. It expressed itself on one occasion at a seminar in reply to a fulsome introduction wherein the audience was enjoined to be prepared for "the incredible science that Professor Roeder will describe." Ken's opening sentence was "I trust that what I have to tell you will be credible."

Although much of his work was physiology and some concerned basic physiological processes, his approach was essentially that of a zoologist. He described his approach as follows:

> Questions dealing eventually with the whole intact animal in relation to its natural environment hold more interest for me than those of a more atomistic kind that lead to the physico-chemical basis of life. Psychology interested me, although it seemed to me to avoid the central problem of animals' nervous systems in relation to behavior. Consequently, I found more in common with the European ethologists and animal physiologists.

He was not one to lose the animal in the machinery or in the wetlands of ion channels, neurotransmitters, or secondary messengers.

Even though he worked exclusively with insects, he saw them as subjects and models from which one could extract information relative to a mechanistic understanding of behavior. He was frustrated by the lack at that time of some synthetic concepts, ethological or psychological, which would enable him to move up from neuronal levels of analysis to complex behavior.

Among his lasting contributions are his books *Insect Physiology* (1951,2), which he conceived, edited, and contributed to, and *Nerve Cells and Insect Behavior* (1963). The first established him as the founding father of insect physiology in America; the second presented a synthesis of his own physiological work and his broader views about the control of animal behavior.

In 1975 he wrote:

> Today's apprentice scientist is confronted by such a flood of objective literature that he is apt to lose sight of the fact that this public outpouring is the work of very human and fallible creatures like himself. *Logic* determines the framework on which he arranges scientific data, and the scientist must assume that cause and effect operate throughout the material universe. . . . But the doing of science is a very human endeavor, and the direction taken by this expanding edge of this logic framework is often

influenced by human bias, insight, blindness and imagination as well as by chance. When he is reporting research the scientist rightly attempts to discount these imponderables—in fact, he does all that he can to limit their influences on his conclusions. But when he is doing research they play a vastly important part both in his successes and his failures. Not to recognize and admit to, perhaps even to court, one's subjectivity at this time is to delude oneself; it is also to miss the special joy of scientific discovery and to reduce the adventure to a form of computation.

THE MATERIAL WHICH FORMED the basis for this memoir came from my own files, my personal reminiscences, biographical documents from the National Academy, documents supplied by Dr. Nancy Milburn, and a memorial article by Dr. Franz Huber.

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