

JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN
1968

"THREE VIEWS OF THE
NERVOUS SYSTEM

KENNETH D. ROEDER

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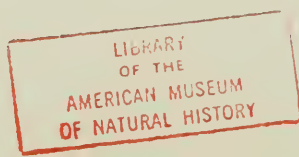
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- Frederick Tilney, *The Brain in Relation to Behavior*; March 15, 1932
- C. Judson Herrick, *Brains as Instruments of Biological Values*; April 6, 1933
- D. M. S. Watson, *The Story of Fossil Brains from Fish to Man*; April 24, 1934
- C. U. Ariens Kappers, *Structural Principles in the Nervous System; The Development of the Forebrain in Animals and Prehistoric Human Races*; April 25, 1935
- Samuel T. Orton, *The Language Area of the Human Brain and Some of its Disorders*; May 15, 1936
- R. W. Gerard, *Dynamic Neural Patterns*; April 15, 1937
- Franz Weidenreich, *The Phylogenetic Development of the Hominid Brain and its Connection with the Transformation of the Skull*; May 5, 1938
- G. Kingsley Noble, *The Neural Basis of Social Behavior of Vertebrates*; May 11, 1939
- John F. Fulton, *A Functional Approach to the Evolution of the Primate Brain*; May 2, 1940
- Frank A. Beach, *Central Nervous Mechanisms Involved in the Reproductive Behavior of Vertebrates*; May 8, 1941
- George Pinkley, *A History of the Human Brain*; May 14, 1942
- James W. Papez, *Ancient Landmarks of the Human Brain and Their Origin*; May 27, 1943
- James Howard McGregor, *The Brain of Primates*; May 11, 1944
- K. S. Lashley, *Neural Correlates of Intellect*; April 30, 1945
- Warren S. McCulloch, *Finality and Form in Nervous Activity*; May 2, 1946
- S. R. Detwiler, *Structure-Function Correlations in the Developing Nervous System as Studied by Experimental Methods*; May 8, 1947
- Tilly Edinger, *The Evolution of the Brain*; May 20, 1948
- Donald O. Hebb, *Evolution of Thought and Emotion*; April 20, 1949
- Ward Campbell Halstead, *Brain and Intelligence*; April 26, 1950
- Harry F. Harlow, *The Brain and Learned Behavior*; May 10, 1951
- Clinton N. Woolsey, *Sensory and Motor Systems of the Cerebral Cortex*; May 7, 1952
- Alfred S. Romer, *Brain Evolution in the Light of Vertebrate History*; May 21, 1953

- Horace W. Magoun, *Regulatory Functions of the Brain Stem*; May 5, 1954
- Fred A. Mettler, *Culture and the Structural Evolution of the Neural System*; April 21, 1955
- Pinckney J. Harman, *Paleoneurologic, Neoneurologic, and Ontogenetic Aspects of Brain Phylogeny*; April 26, 1956
- Davenport Hooker, *Evidence of Prenatal Function of the Central Nervous System in Man*; April 25, 1957
- David P. C. Lloyd, *The Discrete and the Diffuse in Nervous Action*; May 8, 1958
- Charles R. Noback, *The Heritage of the Human Brain*; May 6, 1959
- Ernst Scharrer, *Brain Function and the Evolution of Cerebral Vascularization*; May 26, 1960
- Paul I. Yakovlev, *Brain, Body and Behavior. Stereodynamic Organization of the Brain and of the Motility-Experience in Man Envisaged as a Biological Action System*; May 16, 1961
- H. K. Hartline, *Principles of Neural Interaction in the Retina*; May 29, 1962
- Harry Grundfest, *Specialization and Evolution of Bioelectric Activity*; May 28, 1963
- Roger W. Sperry, *Problems Outstanding in the Evolution of Brain Function*; June 3, 1964
- José M. R. Delgado, *Evolution of Physical Control of the Brain*; May 6, 1965
- Seymour S. Kety, *Adaptive Functions and the Biochemistry of the Brain*; May 19, 1966
- Dominick P. Purpura, *Ontogenesis of Neuronal Organizations in the Mammalian Brain*; May 25, 1967
- Kenneth D. Roeder, *Three Views of the Nervous System*; April 2, 1968

THREE VIEWS OF THE NERVOUS SYSTEM

INTRODUCTION

The theme of the James Arthur Lecture series is the evolution of the human brain. Taken in its broadest functional sense, this topic is the most baffling that faces biology today, for man is trying to understand the instrument of his own intelligence. Part of the problem is that there is at present no hint of a "break-through"—nothing equivalent to the elucidation of the DNA structure that led to such an upsurge of work on the mechanisms of inheritance. The only recourse is attacks on the problem from many directions, some seemingly oblique and indirect. One of these directions seeks to understand how simpler nervous systems determine adaptive behavior.

This may be taken as a formal justification for my presence here, although the truth is that I work with insect nervous systems because I enjoy it. But one cannot remain absorbed in any specialty for thirty years without wondering about its wider implications. Therefore, I welcome this chance to discuss the working of the nervous systems of insects in relation to the way insects behave, and to search for a view of my interest set in a wider framework.

INSECTS AND VERTEBRATES

Insects and vertebrates compete ecologically to a degree found in no other two classes of land animals. Man, as the dominant vertebrate, bears the brunt of this competition. There are mutterings in some quarters about the advantage to man in the extermination of this or that insect species

or even of whole insect groups. To my mind it makes better biological sense to compare the workings of our competitors with our own with the object of outmaneuvering them rather than exterminating them.

Insects and vertebrates represent widely divergent branches of the phylogenetic tree. Consequently, they show striking contrasts as well as similarities. Because these contrasts and similarities are important to my general theme, I shall begin by commenting briefly on examples of each.

Some of the contrasts are self-evident. Approximately one million insect species have been described, and it is estimated that millions more await description. Approximately thirty thousand vertebrate species have been catalogued. Individuals of the great majority of insect species weigh less than one-tenth of an ounce; some vertebrates weigh many tons. This is not the place to discuss the architectural plan of the insect skeleton and how it has imposed a mechanical upper limit on its body size. An important corollary of this size limitation, however, is that insect nervous systems are correspondingly small, even though some of their neurons are as large as or larger than our own. It follows that insect nervous systems must contain fewer neurons, and that there must be parsimony in the way neurons are involved in the multifarious patterns of insect behavior. I shall try to illustrate this at a later point.

Insect and vertebrate similarities are, at first glance, less apparent. It is generally true, however, that if one dissects different animals and inspects their body mechanisms, the similarities become more apparent as the grain of the inspection becomes finer. For instance, at the molecular level nearly all living things find a common ground. At a coarser level, say, that of the light microscope, it is still much easier to determine by inspection what the tissues are for, that is, contraction, conduction, or secretion, than it is to

say whether they belong to an insect or to a vertebrate. This is also true when such tissues are functionally examined. For instance, insect neurons and vertebrate neurons seem to operate on the same general principles.

THREE VIEWPOINTS

Comparing the workings of insect and human brains is like trying to understand a strange and primitive culture from the viewpoint of our own civilization. The outward cultural expressions—mores, economics, religion, and “foreign policy”—seem to us quite difficult to understand, and we can make only blanket generalizations from an external study. On learning more about individual members of that culture, we find that they are very like ourselves and that they have the same joys, anxieties, and motivations. The last and most difficult stage of understanding is to learn how individual members of the citizenry relate to their fellows to form the cultural mesh that determines the image of the strange land.

I shall try to present what I know about insect brains and behavior from three similar viewpoints. First I shall discuss in a general fashion the functions of the insect brain in relation to certain behavioral patterns. Next, I shall summarize the main attributes of that common denominator of all higher nervous systems, the neuron. Finally, I shall attempt the most difficult task of all—to examine how neurons transpose signals from the outer world and interact with other neurons forming the neural mesh to generate an adaptive behavioral pattern.

THE INSECT BRAIN

For an overview of any nervous system, it is best to begin by glancing at its origins. Insect ancestors were probably wormlike forms having a series of similar body

segments (fig. 1A). The activities of each body segment were largely autonomous and were controlled by a ganglion or, rather, a bilateral ganglion pair. The ganglia were serially connected by a pair of longitudinal bundles of nerve fibers. These connectives played little part in determining the local affairs of the individual segments and

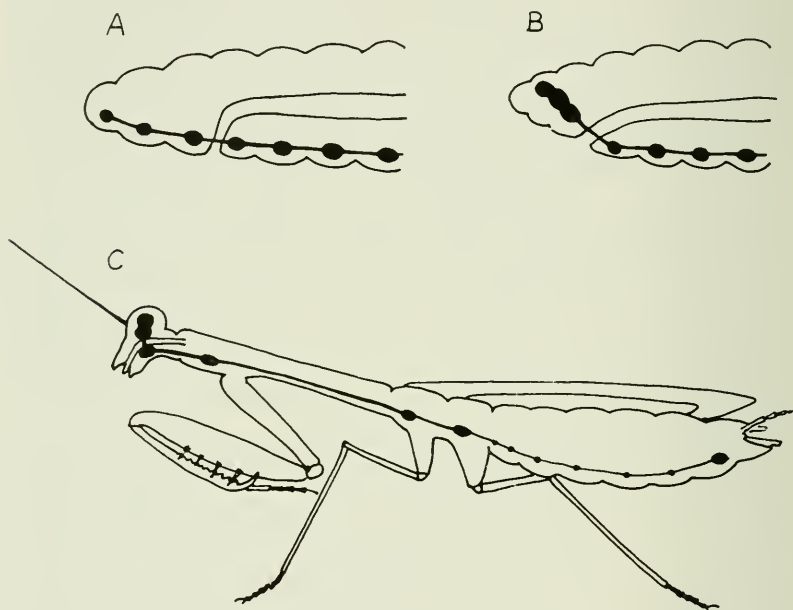


FIG. 1. A. Nervous system of hypothetical ancestor of segmented worms. B. Later stage in the evolution of the arthropod brain. The three anterior ganglia have moved to a dorsal position and have become practically fused. C. Nervous system of the praying mantis. A relatively unspecialized insect nervous system with most of the ventral ganglia distinctly separated. The front pair of legs are specialized for grasping prey.

served mainly to coordinate rapid movements such as those needed in evading a predator. The system of the worm can be likened to a group of self-sufficient rural communities that resort to cooperation only when faced by a general threat.

At least three, and possibly more, of these ganglia lay in front of the ventrally placed mouth of the worm. The remainder were arrayed behind it and along the ventral surface of the segment chain. The mouth moved to the front end of this primitive creature (the logical spot for gathering food), and the anterior ganglia came to assume a dorsal position while fusing to form a brain (fig. 1B). As the worm became more mobile its "distance" receptors, vision and chemo-reception, clustered at its front end and became more complex and discriminating. Neurons subserving them multiplied, forming the bulk of the adjacent brain.

Broadly speaking, the nervous systems of insects still follow this plan (fig. 1C). The organs of vision and olfaction have increased enormously in complexity and diversity, and corresponding regions of the brain have enlarged accordingly. Similarly, many of the body segments and their appendages have diversified for walking, grasping, hopping, swimming, flying, egg laying, and copulating. Others have atrophied or become fused with their neighbors. The segmental ganglia, however, still retain much of their primitive autonomy in coordinating and regulating the local muscle sequences needed for these special action patterns. The brain plays no part in determining which, or in what order, the muscles of a given segment will contract in performing a given action. This is determined by the relevant segmental ganglion or by the ganglia of a few adjacent segments acting in concert, as in the coordination of the three pairs of legs during walking.

CONTROL BY INHIBITION

At first glance, this arrangement seems to leave the brain with no higher function beyond that needed to process the information coming from the eyes and antennae. There is much evidence, however, that the brain exerts what might

be called an over-all direction, or command function, in determining the particular action pattern or behavior mode shown by the whole insect under a particular set of conditions. This control seems to be exerted primarily through selective suppression of certain of the locally organized action patterns, the behavioral mode shown at any given moment being released from this suppression. This conclusion is based on experiments such as the following.

The praying mantis waits in ambush for its food, and thus remains motionless most of the time; after removal of its brain a mantis walks continuously (Roeder, 1937). Most insects exhibit sexual behavior only in the presence of appropriate releasing stimuli provided by the opposite sex; decapitated male mantids make continuous copulatory movements irrespective of the presence of a female (Roeder, 1935). Ovipository behavior seems to be similarly controlled. The motor patterns responsible for song production in crickets are coordinated by the thoracic ganglia, yet song patterns specifically connected with different courtship phases can be released in inappropriate circumstances by electrical stimulation of certain regions of the brain (Huber, 1960, 1967). Flapping of the wings in flight normally ceases as soon as the feet of an insect touch the ground. If the insect is, however, decapitated while in flight this natural "either/or" method of replacing the flight mode by the walking mode is often ineffective, the insect continuing in its attempt to fly even after tarsal contact has been made.

These examples suggest that a considerable proportion of the direction from the head ganglia is accomplished by proscription, that is, by selective suppression of specific activities generated and organized in the ganglia of the several body segments. There is further evidence that inhibition may occur at several levels within the brain. Centers

in the right and left halves having inhibitory control over activities organized at a lower level may also inhibit one another (Roeder, 1937). Although the brain seems to have this "either/or" control over what the whole insect does, the same principle extends to the local segmental activities presided over by the segmental ganglia. This is evident in the control of alternate stepping movements of the right and left legs of a segment and in the control of grooming behavior in locusts (Rowell, 1965).

THE "ONENESS" OF BEHAVIOR

One of the most commonplace, but to me most remarkable, aspects of the behavior of animals is the "oneness" or singularity of their acts. An animal seems able to select just one mode of behavior even under such circumstances as being exposed to stimuli capable at other times of releasing a wide variety of behavior patterns. It is easy to justify the adaptive value of this unity of response, but, regarded mechanistically, it seems surprising that a system with so many input channels should so rarely compromise between conflicting signals. In essence, this problem is one of "attention," which is no less marked in insects than in higher animals. It is also present at lower levels of the nervous system, for the reflex contraction of one muscle group automatically inhibits the contraction of its antagonist muscles.

Do the command functions of the insect brain play a part in this "oneness" of behavior? In releasing one behavioral pattern does the brain increase the suppression of others? If such is the case one would expect to observe conflicting behavior patterns in a brainless insect.

There is some evidence for this. A praying mantis normally remains motionless for hours at a time, waiting in ambush at the top of a vertical surface. From this vantage

point it strikes at passing insects which are grasped in its specially modified forelegs. If placed on the ground a mantis will usually walk until it encounters a vertical object, such as a plant stem. It then climbs to the top of this object and remains motionless in the in-ambush posture. After the removal of its brain, however, a mantis walks continually, persisting in its attempts to travel forward even after reaching the top of a vertical object. If, during these travels, a twig or other small object happens to touch the inner, spined surface of its foreleg, the object is grasped firmly and persistently. The insect appears to be unable to release its grip even though this action may impede further forward progress. The action of grasping does not, however, suppress continuous attempts to walk forward, with the result that the insect frequently becomes hopelessly entangled in twigs and grass stems (Roeder, 1937). It might be thought that this abnormal behavior is due to sensory deprivation, but it is not produced by removal of the eyes, optic ganglia, or antennae. In the intact insect the two action patterns (grasping and walking) rarely, if ever, occur simultaneously, and their simultaneous appearance in the brainless mantis places the insect in a behavioral cul-de-sac. This suggests that, when the brain is present, either one, or neither, but never both, of these behavioral modes is released.

ENDOGENOUS ACTIVITY

There is little detailed physiological information as to how these segmentally determined activities are organized. Nor do we understand the nature of the inhibition that patterns them locally and controls them selectively from the brain. In some cases inhibition appears to operate by raising the threshold of a locally organized reflex response, that is, by rendering it less likely to occur. This is seen in

the grasping reflex of the mantis described above and in the grooming reflexes of locusts (Rowell, 1965). In other cases the segmental neural systems seem to be intrinsically unstable, that is, capable of endogenous generation of behavior patterns. Organized sequences of nerve impulses are transmitted to appropriate muscles even after the ganglion has been deprived of all sensory input. This has been shown to be the case with copulatory movements generated by the last abdominal ganglion of the male praying mantis (Roeder, Tozian, and Weiant, 1960) and with wing flapping in locusts (Wilson, 1961, 1967).

It has long been known (Adrian, 1931) that insect ganglia discharge patterns of impulses for considerable periods after they have been isolated from all sensory input. Some of this endogenous activity may be abnormal (Rowell, 1965), that is, caused by the surgical insult and unrelated to normal behavior. In the two cases cited above, however, endogenous neural activity seems to be the basis for movements that have significance in the lives of the animals concerned. There is, indeed, no satisfactory way to distinguish between a reflex response, the threshold of which has been reduced to extremely low levels, and a system that is endogenous or self-excitatory (Roeder, 1955).

THE BEHAVIOR OF NEURONS

So far, I have considered only the external or behavioral signs of nervous system function. I have glanced, as it were, at the "foreign policy" of the cell community that makes up an animal. In the preceding paragraph it was necessary to mention neurons and nerve impulses. Neurons are the unit components of the nervous system or, if you prefer the sociological analogy, members of the community that formulate the foreign policy. Somehow, the details of the mass transactions between brain and ventral ganglia must

originate in transactions between neurons. Such transactions are accomplished mainly through nerve impulses.

It is perhaps as misleading to generalize about a "neuron" as it is to generalize about a "person." The transactions of neurons in the central nervous system have been most closely scrutinized in studies of vertebrates, particularly through the monumental work of Eccles (1953, 1964) on the spinal cord of the cat. There is no evidence that insect neurons operate on basically different principles, so I shall draw largely on this work in making my brief generalizations.

The central nervous system can be regarded as an organized mesh of nerve fibers. Extending into this mesh are fibers from a multitude of sensory neurons (sense cells) that are acted upon by the outer world. Out of the mesh extend fibers belonging to motor neurons. These connect with effectors—the muscle fibers and gland cells that act upon the outer world. The patterning of muscle contractions that manifests itself as behavior is determined in part by the organization and functional state of neurons forming the central mesh and in part by the pattern of input signals reaching the central mesh from sensory neurons.

Those neurons lying entirely within the central mesh are called interneurons. They are of many sizes and configurations and have many ways of interacting. I must neglect entirely the interactions based on neurosecretion and hormones, and will limit this discussion to rapid, short-term, neuron transactions carried out by means of nerve impulses.

A generalized diagram of an insect interneuron is shown in figure 2. It receives excitation from impulses arriving at close contacts (synapses) after traveling in nerve fibers (axons) belonging to other neurons. Nerve impulses can be detected as small, transient, electrical

“spikes” propagating along a nerve fiber. Information is contained in the frequency, timing, and pattern with which nerve impulses recur.

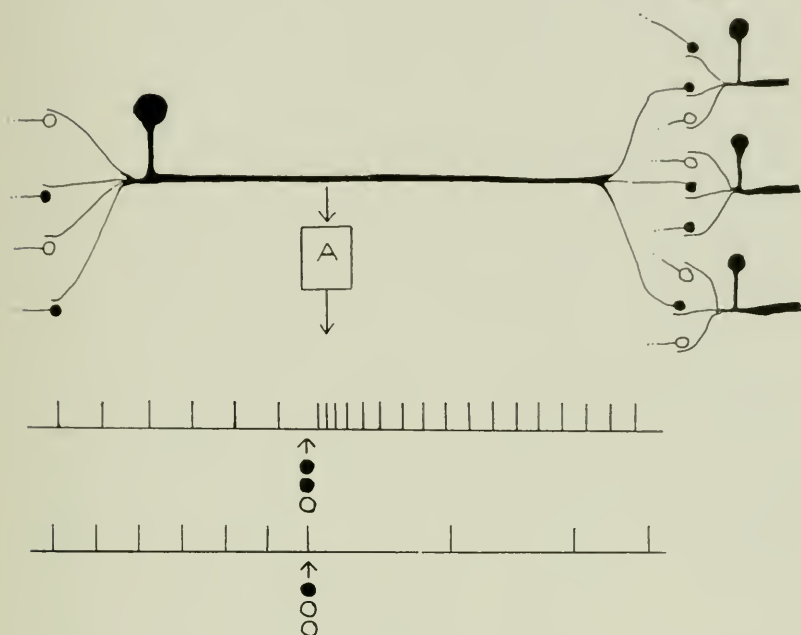


FIG. 2. A generalized diagram of an insect interneuron. At left, four pre-synaptic fibers make two inhibitory (open circles) and two excitatory (solid circles) contacts with its dendrites. The axon of the interneuron forms excitatory synapses with other interneurons (at left). An electrode (arrow) leading to an amplifier (A) registers the pattern of spikes discharged by the interneuron. When presynaptic impulses arrive at two excitatory and one inhibitory synapse (upper trace), the integrated result is an increase above the free-running spike frequency. Activity of two inhibitory and one excitatory synapse (lower trace) causes a decrease in spike frequency.

Synaptic contacts are of several kinds and are often highly complex, but in the present context their most important property is that most of them represent a hiatus or hindrance to the process of impulse propagation through the mesh. This means that the arrival of an impulse at an

excitatory synapse does not generate in one-to-one fashion another impulse in the downstream neuron. It merely increases for a few milliseconds the *tendency* of the recipient neuron to fire off an impulse of its own. The excitatory state wanes exponentially. This means that impulses arriving roughly coincidentally at neighboring synapses formed on the same interneuron will summate in promoting the firing tendency of the neuron, which may cause it either to discharge impulses or, if it is already active, to increase its firing rate (fig. 2). In the same way, impulses arriving with greater frequency at a given synapse summate in their effects on the recipient neuron to a greater degree than if they impinge on it at more extended intervals.

A proportion of the synapses formed on many interneurons are inhibitory. The arrival of an impulse at an inhibitory synapse decreases for a few milliseconds the tendency of the recipient neuron to fire off an impulse of its own. The collective effects of impulses arriving at several inhibitory synapses summate in time and space as do those arriving at excitatory synapses, and the effects of both types are continuously integrated by the recipient interneuron. Thus, one must picture an interneuron as being exposed to a running barrage of excitatory and inhibitory effects, each with a "half-life" of a few milliseconds. Its own discharge pattern reflect the running integration of this barrage. Elsewhere (Roeder, 1967b) I have compared the activity of an interneuron to the actions taken by an administrator. He bases his actions on decisions reached by integrating the positive and negative opinions of others, the most recent opinions being the most influential. Some interneurons, like lower-level administrators, merely relay forward the impulse pattern reaching their synapses. But in the central nervous system these are probably in the minority, and in any case their behavior is relatively unin-

teresting in our efforts to understand the transactions of the brain.

References must be made to other sources (Eccles, 1953, 1964) for the details of synaptic action, chemical effects, types of synapse, and the complex feedback arrangements found in neuron populations. The point is that synaptic interaction of neurons is the only known way in which fast-acting integrations and transformations of the central nervous system are carried out. Admittedly, it is hard to believe that higher nervous functions, such as learning, memory, and abstract thought, are based only on such a system. New modes of neuron interaction and special properties that emerge from the mesh may be discovered, but it must be realized that it would be hard to predict the properties of a computer if one were given only the properties of a single transistor.

Next, I shall attempt to describe some of the neuron signals and transactions concerned in a relatively simple piece of insect behavior.

MOTHS AND BATS

It is observed that a certain pattern of stimuli impinging on an animal bears a causal relation to action having adaptive value. The problem facing the neurophysiologist is to untangle the mechanisms transforming stimulus into action. Commonly, the problem is formidable at the outset; the stimulus pattern may be complex and hence difficult to define in physical or chemical terms, and it usually impinges on the animal via thousands of receptor neurons, each having a separate fiber leading to the central nervous system. Therefore, many pathways must be monitored simultaneously in order to assess fully the incoming sensory information. The initial difficulty is often insurmountable, but it must be overcome before one can know, in terms

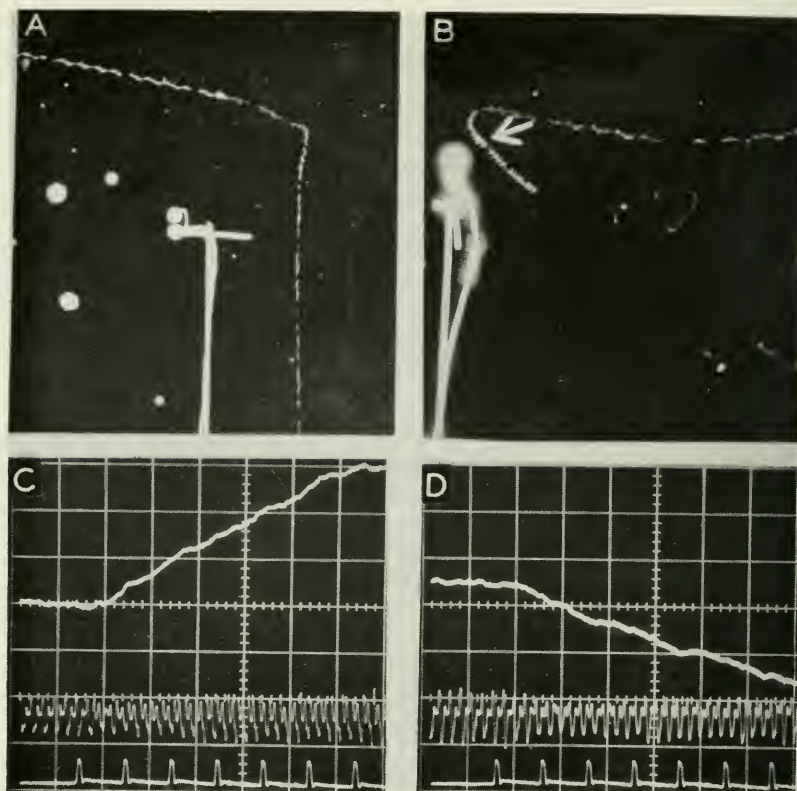


FIG. 3. A, B. Photographic tracks registered by moths flying free in the field at night. The loudspeaker on the mast began emitting a series of ultrasonic pulses in simulation of a bat at the instant indicated by the bright spot in A and by the arrow in B. The tracks have breaks every 0.25 second. The oscillations on the tracks are due to the flapping wings of the moths. A. Diving in response to a loud sound. B. Turning-away in response to a faint sound (Roeder, 1962). C, D. Electronic registration of the attempts of a captive moth to turn away from a loudspeaker emitting a train of faint ultrasonic pulses. Upward deflection (top trace) indicates an attempt to make a right turn; downward deflection, an attempt to turn left. Middle trace shows wing movements of moth. Lower trace indicates onset of pulse train (10 per second). Vertical grid marks 100-millisecond intervals. C. Loudspeaker was in horizontal plane and at 90 degrees to body axis of moth on left side. D. Same, loudspeaker on right side. Attempts to turn away began about 50 milliseconds after first sound pulse. The moth was a female of *Leucania commoides* (Roeder, 1967).

of nerve impulse patterns, how the outer world is being reported to the central nervous system under the given

circumstances. The example I wish to present overcomes this initial difficulty.

Several species of insectivorous bats of North America fly and feed in darkness. They use a kind of sonar to avoid obstacles in their path and to find, track, and capture flying insects. The operation of this sonar has been clarified by the elegant work of Griffin and his students (1958). A cruising bat emits a series of ultrasonic cries and appears to be able to estimate the distance and direction of objects in its flight path from changes in the echoes returning to

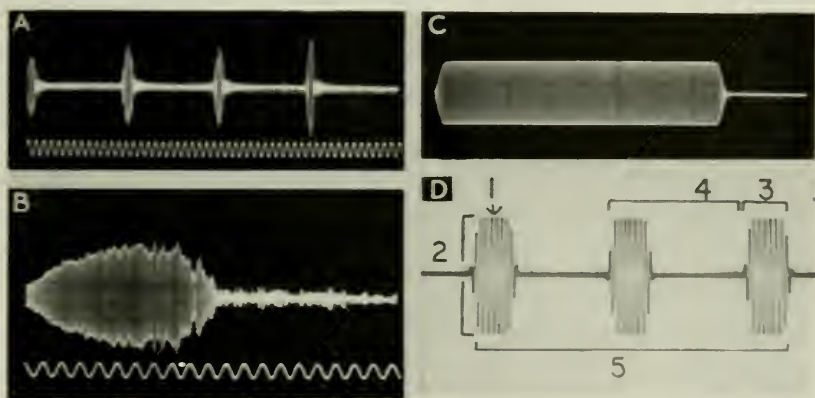


FIG. 4. A. Ultrasonic cries recorded from a cruising bat flying in the field. Time, 100 cycles per second. B. A Single cry on expanded time base. Time, 1000 cycles per second. C. Artificial ultrasonic pulse similar to those used in the experiments described in the text. Vertical grid, 2-milliseconds per division. D. Diagram showing the individually variable parameters of the stimulus: 1, frequency; 2, amplitude; 3, pulse duration; 4, pulse repetition rate; 5, pulse train length.

its ears. The range of this sonar system for an object the size of a flying moth appears to be less than 10 feet.

Moths of several families, notably the Noctuidae, have auditory organs maximally sensitive to the pitch of bat cries. They serve the moth as counter-sonar detectors, and they are able to register bat cries at distances of up to 130

feet (Roeder, 1966a). Moths show two types of reaction when they are exposed to real or simulated bat cries (fig. 3A, B). If the sounds reach the moths at high intensity, as from a nearby bat, the insects show various kinds of unpredictable behavior, such as twisting, turning, and diving toward the ground. If the sounds are received at low intensity, for example, by a moth flying 50 to 100 feet distant from a hunting bat, the moth turns and steers a course directly away from the source of the ultrasonic pulses (Roeder, 1962).

The survival value of turning-away behavior is fairly clear. It carries the slower-flying moth out of the feeding area of the bat before its presence has been detected by the sonar of the predator. Turning-away behavior has been examined more closely (Roeder, 1967a; also fig. 3C, D). When a moth is mounted in stationary flight (attached to a support) and exposed to faint ultrasonic pulses from a loudspeaker placed either to its right or its left, the moth begins its attempt to turn away 45 milliseconds after the beginning of stimulation. The experiments (fig. 3C, D) show that it is able to choose the correct direction (right or left) after receiving only the first pulse of the series, and that it makes the change in flight direction by partially folding its wings on the side of the body away from the sound source.

THE ACOUSTIC SIGNAL AND THE EAR OF THE MOTH

These facts narrow the search for what takes place between the arrival of a stimulus and the change in flight direction. Two other circumstances give additional encouragement to the search.

First, the cries made by a bat (fig. 4A, B) can be duplicated electronically (fig. 4C) with sufficient accuracy to produce turning-away behavior. The artificial signal may

be said to have five different parameters or dimensions, each of which can be varied independently. It is possible, therefore, to determine what aspects of the cries of a bat will release and steer the evasive behavior of a moth. The five parameters of the stimulus (fig. 4D) are: (1) the frequency (pitch) of each sound pulse; (2) the amplitude (intensity) of each pulse; (3) the duration of each pulse; (4) the interval between pulses (repetition rate); and (5) the duration of the whole pulse train.

The present question is: How are these parameters translated or encoded by nerve-impulse patterns coming from the ear of the moth and integrated by interneurons in its central nervous system? The question may be put slightly differently: Which of these parameters is significant in determining what the moth finally does?

The second encouraging circumstance is the extreme anatomical simplicity of the ear of a moth, which was pointed out more than forty years ago (Eggers, 1925). A noctuid moth has only two receptor cells in each ear, compared with about fifty thousand in each ear of a human being. Such a difference is a striking example of the parsimonious distribution of neurons in insect nervous systems mentioned above. Practically, it simplifies the task of reading out and assessing the total information reaching the central nervous system of the moth via the channel that connects it with the outside world. Electrodes can be placed on the acoustic nerve, and the spike patterns delivered by these two sense cells are readily interpreted under different conditions of stimulation.

The details of the ear of a moth are shown in figure 5. The bipolar sense cells (A_1 and A_2) are connected to the eardrum by fine and complex organelles that transduce the acoustic energy into a train of nerve impulses. The central ends of A_1 and A_2 extend as two nerve fibers in the tym-

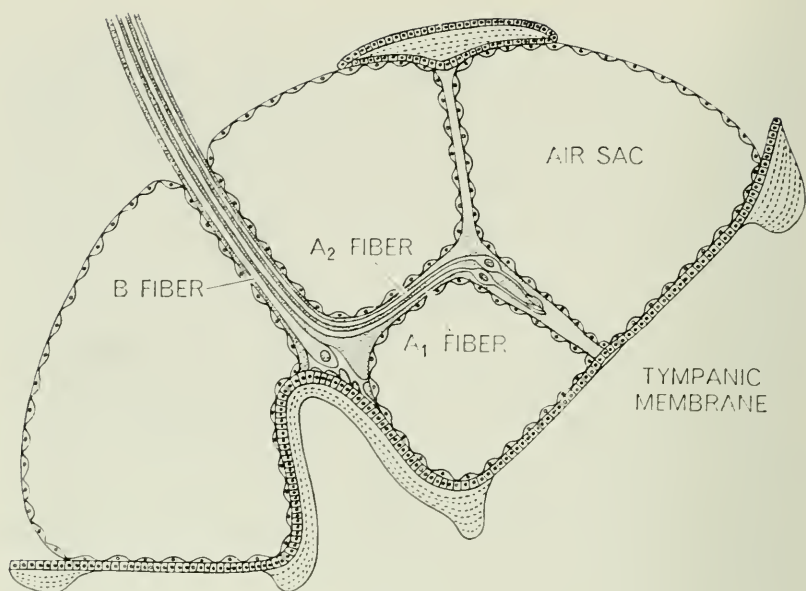


FIG. 5. Diagram of dorsal view of the right tympanic organ of a noctuid moth. The tympanic membrane faces obliquely rearward and outward into the constriction between thorax and abdomen. The scoloparium is a thin strand of tissue attached to the inner surface of the tympanic membrane and suspended in the air-filled sac by a ligament (top). The acoustic sense cells, A_1 and A_2 , lie in the scoloparium. Their distal processes, extending toward the tympanic membrane, transform sound energy into a series of nerve impulses, transmitted to the central nervous system by the A_1 and A_2 nerve fibers. The B fiber arises from a non-acoustic sense cell, serving probably to register mechanical distortions of the tympanic organ. Courtesy of *Scientific American*.

panic nerve connecting with the pterothoracic ganglion. This nerve mass, which consists of the second and third thoracic ganglia, is the site for the major neuronal transactions concerned in bat avoidance.

NEURAL TRANSFORMATIONS AND TRANSACTIONS

The traffic of nerve impulses flowing from the tympanic organ to the central nervous system is detected by an electrode placed on the tympanic nerve. The sequence of frames (fig. 6) shows how the spike patterns generated by the more sensitive sense cell (A_1) changes as the intensity

of a brief, ultrasonic pulse is increased by measured steps. As the sound becomes louder, the spike pattern changes in several respects: (a) more spikes are generated, that is, a longer train is produced, although the duration of the stimulus remains constant; (b) the spikes are more closely spaced; (c) the latency or interval between the stimulus

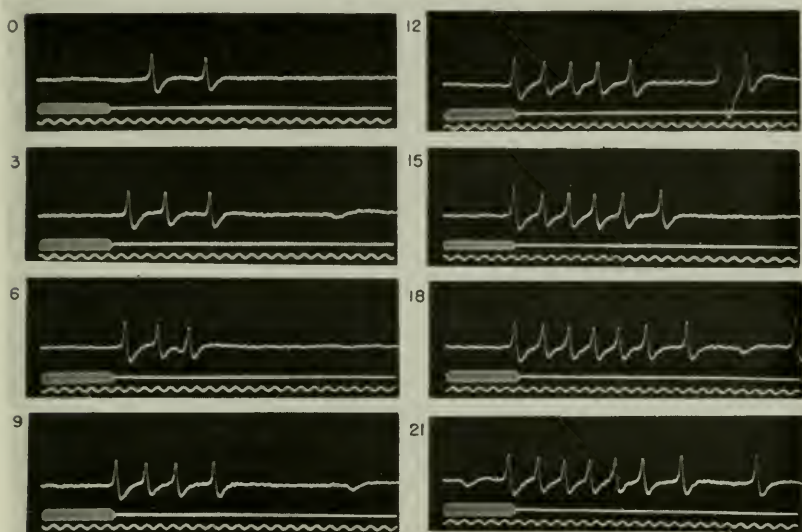


FIG. 6. Spike responses (upper traces) recorded from an electrode on the tympanic nerve of the moth, *Xylena curvimaecula*, when pulses of 25 kilohertz and 5 milliseconds in duration (middle traces) were directed at the ear. Sound intensities are given in decibels above an arbitrary value (0) producing a minimal acoustic response. Time marker (lower traces), 1000 cycles per second.

and the first spike of the series becomes less; and (d) at lower intensities only the sense cell A_1 is stimulated, whereas, at sound intensities ten times greater, it is joined by responses of the A_2 sense cell (not shown in fig. 6).

Stated in another way, a hypothetical homunculus, stationed at the central termination of one tympanic nerve in the thoracic ganglion, could determine intensity differ-

ences in the stimulus by four different criteria, not all of them equally good. Criterion "a" might be ambiguous in pulse duration, a longer pulse being confused with a louder pulse. Criterion "b" would give a fairly accurate measure of differences in pulse loudness. Criterion "c" would be useful to the homunculus only if he could compare signals coming from the right and left ears in response to the same sound pulse. Criterion "d" would be a rough measure and useful only in comparing very large differences in sound intensity. Because we are concerned solely with the neuronal mechanism of turning-away, which occurs at intensities capable of exciting only the A_1 sense cells, criterion "d" can be neglected.

The same experiment, carried out with sound pulses of different frequency (parameter 1), gives the same results over a wide frequency range, roughly 15 to 100 kilohertz. Thus, the moth appears to be tone deaf. The homunculus could not measure parameter 1 from the spike signals reaching him, although inspection of figure 6 shows that the other four parameters of the stimulus are measured in the spike pattern generated by the sense cells.

The next step is to find interneurons influenced by the A_1 signal and to determine in what ways they further transform the spike pattern. A metallic microelectrode is lowered into the ganglion and used as an electrical probe. It is moved about in search of the A_1 signal and of events showing some causal relation to it.

From here on the trail becomes confused by a babel of spike patterns, mostly of unknown origin and significance. The A_1 pattern is easily recognized (fig. 7A). It reaches the ganglion 3 to 5 milliseconds after sound reaches the tympanic organ. Downstream from this point in the neuronal mesh a number of interneurons have been encountered whose signals show various types of relation to the

A_1 response (Roeder, 1966b). I shall mention only three of these, as they hint at ways in which the central nervous system may convert stimulation into behavior.

The pulse-marker neuron is excited by a train of three

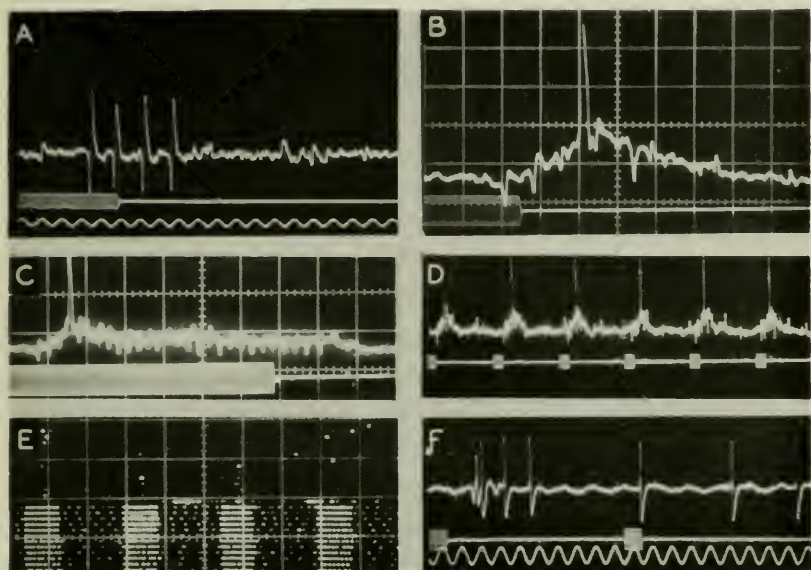


FIG. 7. Responses to stimulation of the tympanic organ recorded with micro-electrode from sensory and interneurons in the pterothoracic ganglion of noctuid moths (*Caenurgina erechtea* and *Heliothis zea*). A. A_1 spikes recorded from neuropile in response to a 5-millisecond ultrasonic pulse (middle trace); time (lower trace), 1000 cycles per second. B. A_1 spikes (small downward deflections) and single pulse-marker spike (large upward deflection) in response to 5-millisecond sound pulse (lower trace). Time, 2 milliseconds per division. C. The same, response to a longer (38-millisecond) sound pulse. Time, 5 milliseconds per division. D. Single pulse-marker spike recurring in response to each of a series of short ultrasonic pulses (lower trace) repeated 40 times a second. E. Train-marker response. Spikes are indicated as dots on a raster that should be read like consecutive lines on a printed page. Groups of larger dots are A_1 spikes, and indicate parameters 2-5 of the stimulus. Smaller dots are train-marker spikes, recurring at a frequency independent of the pulse repetition rate throughout the stimulation period. F. Change in the pattern of spikes in the motor nerve supplying a muscle controlling extension of the forewing in response to stimulation of the tympanic organ (middle trace). Motor response begins about 20 milliseconds after first sound pulse reaches the ear. Second sound pulse appears to have no effect. Time, 100 cycles per second.

or four A_1 impulses coming from the ear on the same side of the body (fig. 7B). The synaptic effects of the A_1 impulses produce sufficient summation to trigger the pulse-marker only if they are separated by intervals of 2 milliseconds or less. Typically, the response of the pulse-marker is a single large spike, irrespective of the duration of the stimulating sound pulse (parameter 3) and of the resulting train of A spikes that impinges upon it. This curious behavior of the pulse-marker (one spike per ultrasonic pulse irrespective of its duration) seems to depend on a neuronal mechanism that requires 4 or 5 milliseconds without synaptic bombardment by A_1 impulses in order that the interneuron be "reset" to respond. This pause does not occur when a long and moderately intense pulse reaches the ear (fig. 7C). The pulse-marker will, however, generate spikes up to 40 times per second if the long pulse is broken into short pulses (fig. 7D). This behavior is interesting in three respects.

First, the pulse-marker spike transmitted downstream can be said to have discarded parameters 2 and 3 as defined by the original ultrasonic stimulus. A homunculus observing only the signal generated by one pulse-marker could not judge differences either in the intensity or in the duration of the original stimulus. He could still determine pulse intervals (parameter 4) and the duration of the pulse train (parameter 5).

Second, pulse-markers connected to the right and left ears and sending their spikes into a mechanism that compared relative times of arrival would be capable of steering a moth in flight away from a distant sound source, because the latency of the pulse-marker spike is long and variable, depending as it does on the arrival of three or four A spikes at sufficiently short intervals. Therefore the latency is inversely related to intensity, and relative intensity (right versus left ear) could be determined by marking whether

the right or the left pulse-marker fired first in response to a given pulse. A neuronal mechanism making such a comparison has not yet been found.

Third, the behavior of the pulse-marker shows a striking correlation with the behavior of flying moths exposed to different ultrasonic pulse patterns (Roeder, 1964, 1967a). Long, continuous tones produce only transitory turning-away or none at all, whereas pulsed ultrasound causes a sustained attempt to turn.

Among the neurons the signals of which have been intercepted, two others seem relevant to the present account. The first has been termed the train-marker neuron.

The train-marker neuron is inactive during silence, but begins to discharge a train of spikes at an independent frequency throughout the period in which a train of ultrasonic pulses reaches the ear (fig. 7E). The spike repetition rate of the train-marker bears no relation to the pulse repetition rate of the stimulus. Thus, the homunculus provided only with the train-marker signal would be able to measure only the duration of a pulse train (parameter 5). The other parameters of the stimulus would be lost to him.

Another interneuron, rarely encountered, appears to add the A_1 signals coming from the right and left ears. It fires twice as many spikes when both ears are stimulated as when either ear alone is exposed to ultrasonic pulses.

TURNING-AWAY

These and other bits of information (Roeder, 1966b, 1967b) are insufficient for a definition of the neuronal mechanism that is responsible for turning-away behavior. The reason may be likened to the uncertainty principle in physics—the deeper one searches for answers the greater is the disturbance created by one's searching methods in the beautifully poised living system. But one is heartened by

the hope that the biological obstacles are mainly technical rather than theoretical as in the uncertainty principle facing the physicists.

Many attempts have been made to approach the turning-away response from the motor end, but the percentage of success has been very small. In a few cases changes in the pattern of motor impulses traveling to the wing-folding muscles have been registered when the ear had been stimulated with ultrasonic pulses (fig. 7E).

Incomplete though they are, the data presented give

TABLE 1
PARAMETERS OF THE ULTRASONIC STIMULUS PRESENT
IN VARIOUS SIGNAL PATTERNS

Signal Pattern of	1 Frequency	2 Amplitude	3 Duration	4 Pulse Interval	5 Train Length
Stimulus	x	x	x	x	x
Tympanic nerve	—	x	x	x	x
Pulse-marker	—	—	—	x	x
Train-marker	—	—	—	—	x
Turning-away behavior	—	—	—	^a	x

^a Not present at the pulse repetition rates in bat cries.

hints as to the *kind* of processing occurring in the central nervous system. The original stimulus had five variable parameters. The first of these, frequency (parameter 1), is omitted from the tympanic nerve signal. Similar stages in which other parameters are discarded are represented by the pulse-marker (parameters 2 and 3) and the train-marker (parameter 4) interneurons (table 1). It is as if each parameter present in the original stimulus is a separate key that permits admittance to a specific door but becomes useless once the door in question has been passed.

At this point it seems worthwhile to compare the informational content regarding the original stimulus that

is contained in the signal patterns registered at various points in the nervous system of the moth with that contained in its ultimate reaction—the turning-away behavior. Such a comparison is summarized in table 1. A train of sound pulses reaching one ear at higher intensity causes a steady, sustained attempt to turn away from the stimulus. A continuous tone or a single pulse causes only a transitory turning attempt. As the table shows, an observer of this behavior could infer from it only the direction and the pulse-train length of the stimulus; none of the other parameters of the original stimulus would be reflected in the response. The neurophysiological experiments summarized in table 1 suggest some of the steps in this elimination of stimulus parameters as nerve signals propagate through the nervous system and eventually shape the reaction of a moth to a passing bat.

CONCLUSION

The mechanisms whereby nervous systems generate adaptive behavior have been regarded from three different viewpoints. The first, which might be called the “center” viewpoint, observes changes in behavior following relatively massive surgical interference with the sense organs or with parts of the central nervous system. It provides only a broad picture of the functional topology of the nervous system, and leads to concepts of “regions,” or “centers,” interacting with each other. The center viewpoint has been of particular heuristic value in analyzing insect nervous systems because insect ganglia show a high degree of anatomic separation, which is to some extent correlated with function. For instance, it suggests that the insect brain determines the “oneness,” or “singularity,” that is so universal in animal behavior. Such determination is accomplished under given conditions by the inhibition of all but

one of the action patterns organized by the segmental ganglia.

At the present time, the center viewpoint seems unrelated to the much closer and more fine-grained viewpoint of modern neurophysiology. Indeed, its conclusions do not even require the postulation of neurons, nerve impulses, or synapses. When regarded from the viewpoint of neurophysiology, the widely separated phylogenies of insect and vertebrate nervous systems find a common base in the behavior of single neurons. But when observed only from the tip of a microelectrode differences between these two groups of animals become mainly quantitative. There, the second, or neuron, viewpoint also has its limitations.

The third viewpoint takes the findings of neurophysiology for its basic assumptions. Given the intramural properties of neurons, it is concerned with neuron interaction, with information transfer in neuron populations, and with the way these and other functions could transpose a stimulus pattern significant in the life of an animal into a response promoting its survival.

At present, the neuron communities that can be comprehended from this viewpoint are small and simple, several orders of magnitude simpler than those that are the concern of the center viewpoint. Attempts to describe behavior in terms of neuron populations are in their infancy. An infant can handle, however, only simple toys, and hence I believe that the simpler neuron communities—the nervous systems of insects—have much to offer.

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