Auditory System of Noctuid Moths

Complex nerve mechanisms enable moths to detect the ultrasonic cries of insect-eating bats.

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Significant questions in biology and psychology concern the nature of the organization of nerve cells that converts a specific stimulus configuration into an adaptively significant pattern of animal behavior. What kind of organization is responsible for escape behavior when an animal is presented with a certain stimulus pattern, and what kind of organization is responsible for courtship activity or indifference when the pattern is changed in certain particulars? How is the nervous system specifically organized so that these stimulus patterns may evoke different reactions in another, closely related, species of animal? How is the incoming nerve signal transformed by the nervous system into an action that differs entirely from it in quality?

The problem implicit in these questions divides into a number of subproblems, each of considerable complexity. Most animals scan their environment with numerous sense organs, each with a different mode of sensitivity. A sense may present an array of many thousands of sense cells, each reporting to the central nervous system by a separate nerve fiber. The temporal pattern of nerve impulses in which an individual sense cell reports changes within its response mode is well known and almost universal. But it is technically not possible to follow this activity in more than a few sense cells at a time. This makes it difficult to define the total informational content of the sensory input causing a given behavior pattern. Even should such definition be possible, there would remain the further step of trying to understand how the information assembled in the sensory channels is integrated and transformed by the central mesh of neurons into an equally complex pattern of motor nerve impulses that finally expresses itself through muscles, glands, and other effectors as an adaptively significant behavioral response.

In many cases it is difficult to reach even the biological stages of such an inquiry because of inability to define and manipulate separately the variable parameters of the stimulus pattern that evokes a meaningful behavioral response. The situation described below is of interest to me because the major stimulus parameters can be varied independently, because the relevant sensory mechanism of the recipient animal consists of only two sense cells in each ear, and because the evoked behavior has evident value for survival.

Bats find their way in darkness by emitting a series of ultrasonic cries and detecting their echoes from nearby objects (*1*). Insectivorous bats use this sonar to locate and track flying insects even smaller than mosquitoes (*2*). Moth species in several families have ears sensitive to the range of frequencies in bat cries (*3*) and make evasive maneuvers when they are being tracked by bats (*4*). In noctuid moths the ultrasonic detector consists of two auditory sense cells in each ear.

Many moth species, when flying freely (Fig. 1, left) under natural conditions, react in either of two ways when presented with an artificial approximation of bat cries, generated by a loudspeaker on a mast (*5*). If the sounds are received at high intensity —that is, when the moth is flying close to the loudspeaker—a miscellaneous assortment of power-diving, looping, and dropping with closed wings is observed (Fig. 1, middle). These reactions show no directional component relative to the source, and all carry the moth toward the ground. If the ultrasonic signals are received at low intensity (when the moth is at some distance from the loudspeaker), the insect frequently turns and, after some "hunting," flies directly away from the source (Fig. 1, right). This behavior has how been confirmed in the laboratory (*6*).

The survival value of these two reactions becomes clearer on considering other conditions of this "war game" between moths and bats. A moth's central nervous system first receives a consistent signal from its more sensitive auditory receptor cell when a chirping bat is cruising at a distance of about 35 to 40 meters (*7*). Rough estimates suggest that a bat does not receive a consistent echo from the average-sized moth until the moth is less than a tenth of this distance away. Thus, turning and flying away from the sound source would seem to be a reasonable tactic for the slower-flying prey when it is still well beyond the range of the predator's sonar system. On the other hand, random diving and looping seem to be the only recourse when the moth is within range of the bat's sonar (*6*), since a bat can probably outfly most moths on a straight course.

The Acoustic Receptor

Several facts make it worth while to investigate the nervous mechanisms of the turning-away reaction in moths. There are two sense cells in each ear, and one of them is 10 times as sensitive to ultrasound as the other. It seems probable that only the more sensitive sense cell is excited by the ultrasonic intensities that cause turning-away. Although a bat's cry is indeed a fairly complex sound, field observations (*6*) suggest that moths can be "fooled" by an electronically generated and consequently more definable substitute. Turning-away appears to be, like many other animal reactions, a taxis that is continuously steered by the differential in the signals received from right and left receptors.

One can intercept nerve signals from the ears of a moth by placing microelectrodes on the auditory nerve or at various points within the central nervous system of a specimen mounted on the stage of a dissecting microscope (*8*). The nerve signals take the form of transient electrical potentials or spikes. The timing and pattern of

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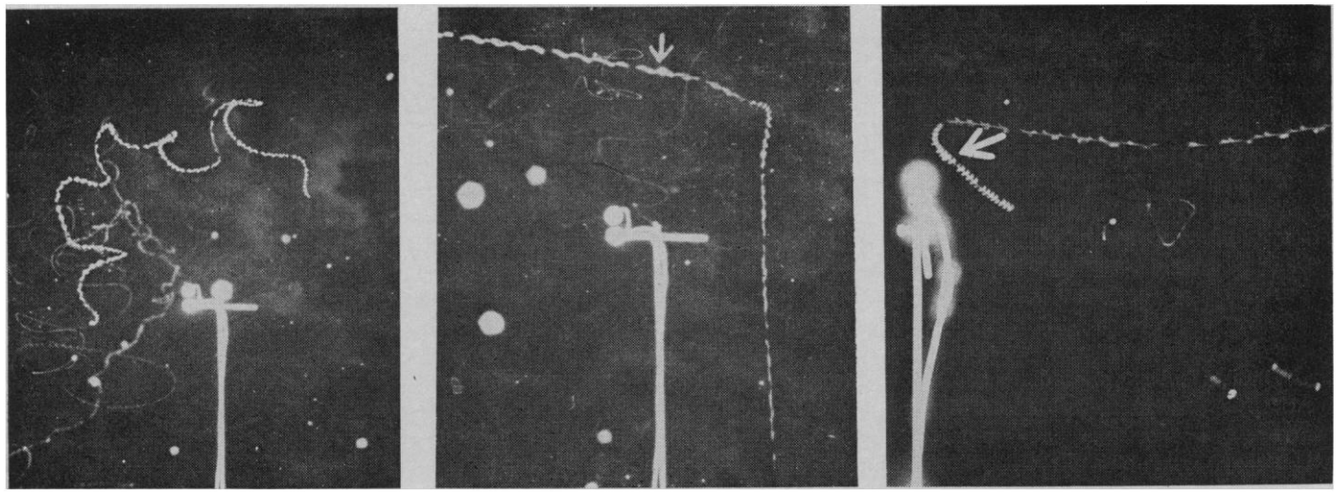

Fig. 1. Streak photographs of the tracks made by moths flying in the field. The track is interrupted by a rotating shutter every 0.25 second. The single white dots are made by small insects close to the camera lens. The arrows point to extra illumination of the track by a brief electronic flash when the ultrasonic signal from the loudspeaker on the mast is switched on. (Left) Meandering track made by an unstimulated moth; (middle) power dive made by a moth encountering an intense ultrasonic pulse train; (right) turning-away reaction of a moth encountering a train of faint pulses.

these trains of spikes is recorded while one or both ears are being exposed to various patterns of ultrasonic stimulation from appropriately placed miniature loudspeakers.

Records of a series of chirps emitted by a cruising bat are shown in Fig. 2A. Details of the pulse structure are shown in Fig. 2, B–D. A single artificial pulse of the sort that evokes diving and turning-away in a field population of moths is shown in Fig. 2E. Similar stimuli were used in the laboratory studies described below. The overtones and frequency modulation in the bat cry have been omitted from the artificial pulse, in order to simplify the problem, and because there is no evidence that these parameters influence the nerve signal generated in the moth's ear.

Trains of these artificial pulses were used to stimulate one or both ears of an experimentally restrained moth. Such trains have a number of independently variable parameters (Fig. 2F). They are (i) the ultrasonic frequency (pitch) of each pulse; (ii) its intensity or amplitude; (iii) the duration of each pulse; (iv) the interval between consecutive pulses; and (v) the duration of the train of pulses. A sixth parameter, rise and fall time at the beginning and end of each pulse, was introduced in order to avoid the transient click. However, since the rise and fall time seems not to modify the nerve response when this time is less than 0.5 millisecond in duration, it is disregarded in the present discussion. Rough values for the five parameters in the cruising cries emitted by an insectivorous bat such as *Myotis lucifugus* are, respectively, as follows: (i) frequency, 60 to 25 kilocycles per second at close range; (ii) intensity, dependent on distance, but probably more than 6 dynes per square centimeter at 1 meter (*7*); (iii) pulse duration, 1 to 15 milliseconds; (iv) interval between pulses, 100 to 150 milliseconds; (v) pulse-train duration, indefinite.

Variations in these five parameters of the stimulus must produce comparable variations in the displacements occurring in the moth's ear drum. The first question is, How much information about these variations is transmitted to the moth's central nervous system from the more sensitive of the two auditory receptor cells attached to the ear drum? Nerve spikes from this receptor cell have been intercepted as they enter the ganglia concerned with flight control (Fig. 3).

In the responses shown, the only parameter varied is intensity. Analysis of similar records in which the other parameters are varied leads to the following conclusions.

There is no measure of ultrasonic frequency in the nerve signal. That is to say, an observer scanning the spike pattern and knowing the frequency range [roughly 15 to 80 kilocycles per second (*7*)] detectable by the moth's ear could determine that the stimulus frequency lay within this range, but within this range he would be unable to discriminate the frequency of one signal from that of another. The moth, then, is tone deaf.

Variations in the second and third parameters—pulse intensity and pulse duration—can be read from the nerve signal, although the records are slightly ambiguous. The more intense sound pulse (Fig. 3C) produces a longer train of nerve spikes, but this effect could be approximately mimicked by a longer pulse of lower intensity. A difference in pulse intensity, however, can be read from two other criteria in the nerve signal. First, higher intensities cause shorter time intervals between individual spikes. Second, higher intensities shorten the latency of the response (the interval between the onset of the stimulus pulse and the appearance of the first spike). This is evident in a comparison of records A and C of Fig. 3.

The latency difference is revealed on the oscilloscope when the onset of the nerve signal is compared with the stimulus marker. Such a marker would, of course, be unavailable to a moth. However, the two ears of a moth are directionally sensitive (*9*). This means that if they were asymmetrically placed with respect to a distant sound source they would receive the same signal at different intensities. The difference in arrival time of right and left nerve signals in the moth's central nervous system might then provide information on the bearing of the source.

The two other parameters—the interval between successive pulses and the duration of the whole train of pulses —are accurately represented in the auditory nerve signal. This is shown in

Fig. 3, B and D, where individual nerve spikes are registered as dots and consecutive responses (horizontal rows of dots) are shown in the vertical succession of rows. Adaptation of the auditory receptor cell distorts these parameters of the signal only at pulse-repetition rates and pulse lengths well outside the range of the natural signals (bat cries).

In summary, the sensory signal transmitted to the moth's central nervous system by the more sensitive of the acoustic receptor cells contains no information on ultrasonic frequency differences, fairly accurate information on differences in pulse intensity and duration, and precise information on interpulse intervals and on the duration of the pulse train.

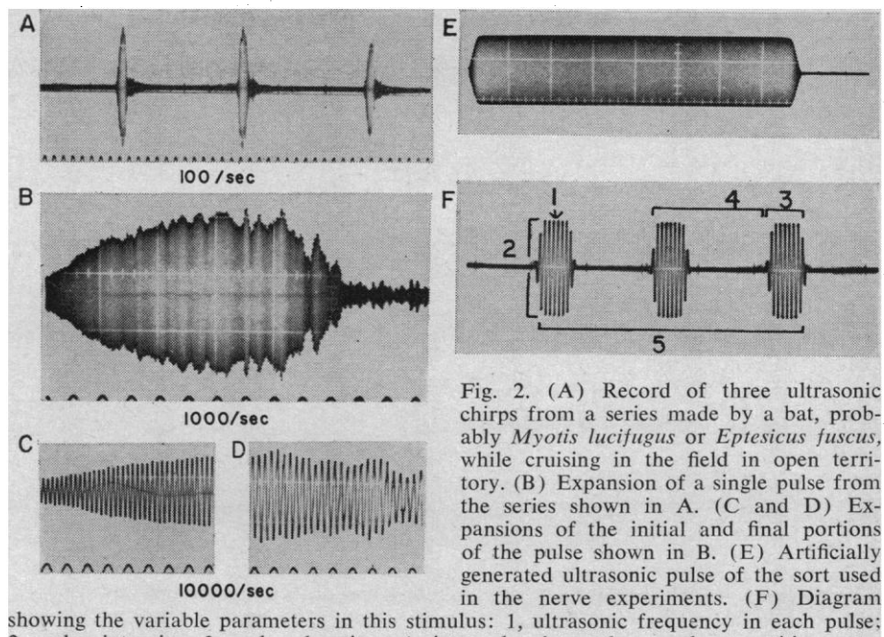

Fig. 2. (A) Record of three ultrasonic chirps from a series made by a bat, probably *Myotis lucifugus* or *Eptesicus fuscus*, while cruising in the field in open territory. (B) Expansion of a single pulse from the series shown in A. (C and D) Expansions of the initial and final portions of the pulse shown in B. (E) Artificially generated ultrasonic pulse of the sort used in the nerve experiments. (F) Diagram showing the variable parameters in this stimulus: 1, ultrasonic frequency in each pulse; 2, pulse intensity; 3, pulse duration; 4, interpulse interval or pulse repetition rate; 5, pulse-train duration.

Central Transformations

Additional steps in the processing of information delivered by the more sensitive of the acoustic sense cells are revealed only through probing the "circuitry" of a moth's central nervous system with microelectrodes and noting the timing and pattern of nerve spikes while one or both of its ears are being stimulated.

This is necessarily a very haphazard procedure. Nerve fibers are not visible in the central nervous system of a living moth. The neuropil, that central portion of the ganglion where most neural transactions are accomplished, is closely packed with fine nerve fibers. A microelectrode can record mainly only extracellular events in this fine fiber mesh, the larger spikes deriving from the nerve fibers closest to the microtip. Since it is not possible to place the electrode at will in contact with a given nerve fiber, reduction, by the observer, of the received signals to some degree of order and causal relation to the stimulus depends on correlation of the results of a large number of separate experiments. The spatial organization is gradually worked out from the position of the electrode in relation to surface landmarks on the ganglia, and temporal order is determined through relating the latency and patterning of spikes to the latency and patterning of the input signal—the train of spikes generated in the more sensitive auditory fiber by each ultrasonic pulse (Fig. 3). The problem is like trying to complete a picture puzzle when given only one or two randomly selected pieces each day. Progress becomes more rapid as more pieces become available, but we cannot yet speculate on the subject of the finished picture and can offer only a few generalizations on some of the principles of its layout.

Probing the central nervous system in this manner has revealed several types of neuron whose activity is causally related to trains of nerve impulses from the auditory receptor. The responses of these neurons are described in detail elsewhere (*10*), and my present purpose is to select one or two in order to illustrate how the stimulus appears to be processed by the moth's central nervous system.

The nerve signal reaching the central nervous system from one of the acoustic receptor cells is relayed to more distant regions of the thoracic ganglia and brain by various repeater neurons. These repeater neurons produce little change in the sensory signal driving them.

A more radical transformation in the signal relayed by the acoustic receptor is carried out by an internuncial neuron found most often in the mesothoracic ganglion—the nerve center that contains the main motor supply to the flight muscles. Typically, this neuron, or "pulse-marker," responds to the arrival of three or four sensory

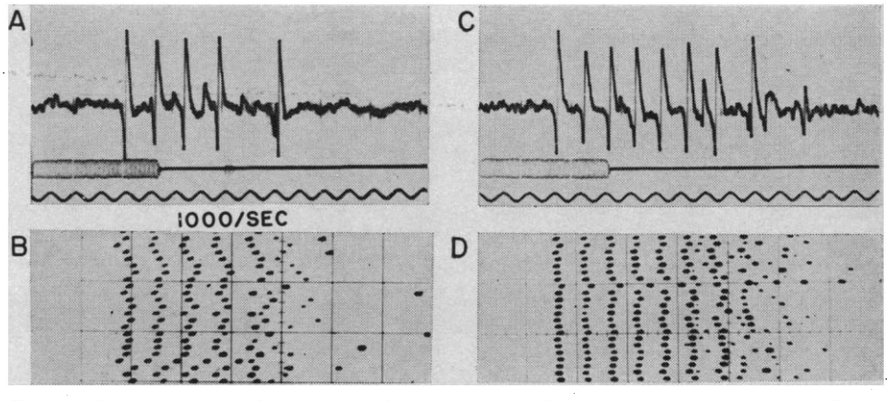

Fig. 3. Nerve responses from the auditory organ of *Caenurgina erechtea*. A and C are single responses from the corresponding series shown in B and D. The intensity of the stimulus was 10 decibels higher in C and D than in A and B. The 5-millisecond stimulus (second trace, A and C) begins at left. In B and D the vertical lines mark 2-millisecond intervals; each spike is registered as a dot, and a horizontal row of dots represents a response to each of a series of stimuli. Consecutive responses are aligned vertically. The more intense stimulus (C and D) caused a shorter and more constant latency, shorter interspike intervals, and a larger number of spikes in each response.

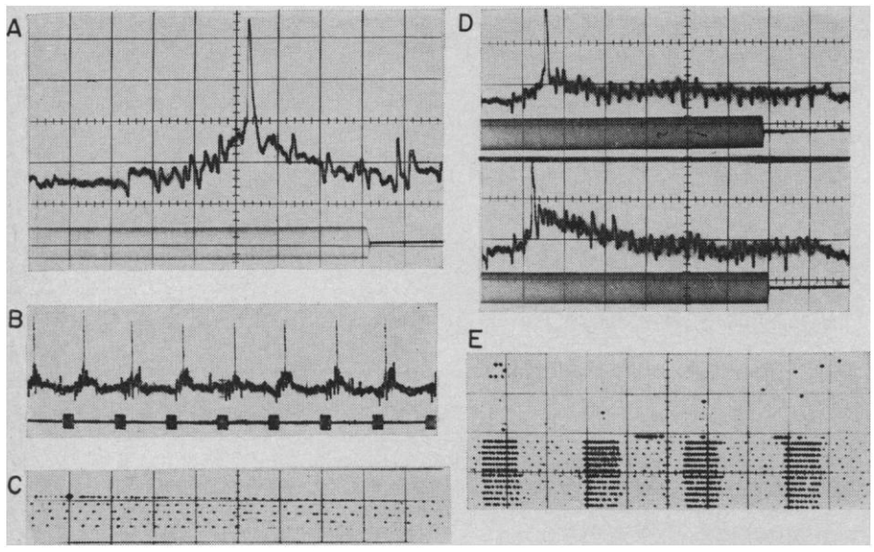

Fig. 4. (A–D) Responses of a pulse-marker neuron in *Heliothis zea*. (A) Responses of auditory neuron (small deflections) and pulse-marker neuron (large upward deflection) to single ultrasonic pulse (lower trace) beginning at the first vertical line (lines mark 2-millisecond intervals). (B) Response of pulse-marker neuron (upward spike) to 5-millisecond stimuli (lower trace) recurring at a rate of 40 per second. (C) Continuous record of auditory fiber responses (small dots) and single pulse-marker spike (large dot on second vertical line) to a tone of 450-millisecond duration; verticals mark 10-millisecond intervals. (D) Responses of pulse-marker neuron to pulses of 25-millisecond duration. In the lower record of D the intensity of the stimulus was increased by 10 decibels. Note the shorter latency of the pulse-marker spike. Verticals mark 5-millisecond intervals. (E) Continuous record of a train-marker neuron response to stimulation by pulses of 5-millisecond duration repeated at a rate of 20 per second. Verticals mark 20-millisecond intervals. Stimulation was begun half-way through the record; the arrival of responses in the moth's nervous system is marked by groups of repeater spikes (large dots). Unphased activity of the train-marker neuron is marked by the series of small dots occurring only during the period of stimulation.

impulses separated by sufficiently short intervals (2 milliseconds or less) by generating a single spike (Fig. 4A). However, conditions needed for activation of the pulse-marker are more complex than mere temporal summation. Although it can be made to respond at quite low sound intensities, it delivers but a single spike on reception, by the ipsilateral ear, of sound intensities 50 to 100 times as high. Even more interesting is the fact that the pulse-marker delivers only a single spike per sound pulse irrespective of the duration of the sound pulse [and consequent length of the train of sensory spikes generated in the sensory fiber (Fig. 4C)]. In other words, ultrasonic pulses covering a wide range of intensities and having durations ranging from 0.5 millisecond to more than 500 milliseconds are "seen" by the pulse-marker as being identical, even though measures of these parameters of the stimulus are contained in the train of sensory spikes that elicits the pulse-marker's response.

This behavior is not due to an intrinsically slow mode of operation. If the moth's ear is presented with short pulses (of 2- to 10-millisecond duration) at repetition rates of up to 40 per second, the pulse-marker responds to each sound pulse with a single spike (Fig. 4B). These and other experiments show that the pulse-marker requires a "silent" period during which no sensory impulses impinge on it in order to be reset for the next response.

Thus, the output of the pulse-marker neuron contains no measures of the first three parameters of the ultrasonic stimulus—ultrasonic frequency, pulse intensity, and pulse duration. The first of these was eliminated by the auditory receptor, and the second and third were eliminated by the synaptic interaction of the auditory fiber with the pulse-marker. The fourth and fifth parameters—pulse repetition rate and pulse train duration—are accurately measured by the pulse-marker signal. However, this is true only for the signal from a single pulse-marker, and there appear to be two, each driven by the ipsilateral ear.

In Fig. 4D it is evident that the latency of the pulse-marker spike is shorter at high stimulus intensities. A nerve-cell system that accepted right-side and left-side pulse-marker spikes and compared them for temporal precedence could derive a measure of the intensity difference at which a given ultrasonic pulse was received by the two ears. No such system has as yet been found.

Another internuncial neuron found only very rarely in the experiments discussed illustrates an even more radical transformation in the incoming signal. This neuron appears to be inactive in the absence of acoustic stimulation but discharges a regular train of spikes at some intrinsic frequency when a series of ultrasonic pulses reaches the ear (Fig. 4E). In the experiment of Fig. 4E the electrode also registered the responses of a repeater neuron (regular rows of large dots), which mark the arrival of discrete ultrasonic pulses. The finer dots begin soon after the onset of stimulation and continue until the pulse train terminates. The timing of the dots bears no relation to the timing of the stimulus pulses. This neuron, called a train-marker, registers only the duration of the ultrasonic pulse train, the other four parameters present in the original ultrasonic stimulus reaching the ear being unmeasured in its response.

Whether these and other internuncial neurons are arranged in series or in parallel is still unclear. The acoustic receptor obviously precedes them, and the train-marker cannot precede the pulse-marker because information in the pulse-marker signal is not present in the train-marker signal. It might be thought that measurement of the parameters originally present in the stimulus is superfluous, since most of these have been eliminated at the stage of the train-marker response. Perhaps each stimulus parameter can be thought of as a key fitting one of a group of doors, some arranged in parallel and some in series. A given key gives admittance to a given door but becomes superfluous when the door has been passed. For instance, ultrasonic pulses within a certain broad frequency range are necessary to gain admittance to the auditory receptor, but there is no measure of frequency in the receptor's response. A range of pulse intensities and durations is measured in the auditory receptor signal and appears to be required in order to gain admittance to the pulse-marker neuron, yet there is no measure of these parameters in the pulse-marker's signal. The train-marker neuron indicates an additional step of this sort.

Horizontal Localization

The foregoing passage suggests how the reception of a train of ultrasonic pulses received at low intensity might be transformed by a moth's central nervous system into a change in its mode of behavior. One may then ask how this behavior is continuously steered by reception of a series of bat cries so that the moth is able to maintain a course away from a distant source. Field observations (*6*) suggest that this steering is accomplished in the vertical as well as in the horizontal plane. Here again, evidence of actual mechanisms is still fragmentary and mostly indirect.

The ears of a noctuid moth are situated on either side in the midsection of its body and just below and behind the attachment of the second pair of wings (Fig. 5G). They appear to be fairly directional with respect to most untrasonic frequencies, being most sensitive to sounds originating on the ipsilateral side and at right angles to the body axis (*9*). Figure 6, A–D, shows simultaneous recordings of spike potentials generated by the right and left acoustic receptors of a restrained moth while bats flew overhead. It is not difficult to tell from various criteria in the nerve signals (number of spikes, interspike interval, relative latency) which ear of the moth received the louder signal as the bat maneuvered around the restrained moth.

One can postulate several mechanisms which would compare these two sensory signals and might serve to steer the flight of the moth in the horizontal plane. A system which measures the differences in latency of the spike for right and left pulse-marker neurons has already been mentioned. A mechanism that extracted the difference between the right and left receptor or repeater signals is also a possibility.

Only traces of such a system have yet been found. In the midline of the mesothoracic ganglion an interneuron has often been found which is excited by signals from either or both ears (Fig. 6E). Low-intensity stimulation of both ears causes this interneuron to discharge about twice as many spikes per stimulus pulse as it discharges when either ear is stimulated alone. Thus, this unit adds the signals from the two ears, but the model would call for a unit that subtracted them—in other words, one that operated through inhibition. A neuron unilaterally inhibited by a train of impulses from the auditory receptor has been found only once (Fig. 6F). In the absence of acoustic stimulation this neuron fired steadily at about 90 spikes per second. It ceased this activity during, and for some time after, the reception of each ultrasonic pulse. I suspect that both these interneurons play some part in steering the flight of a moth, but the organization of this system is still far from clear.

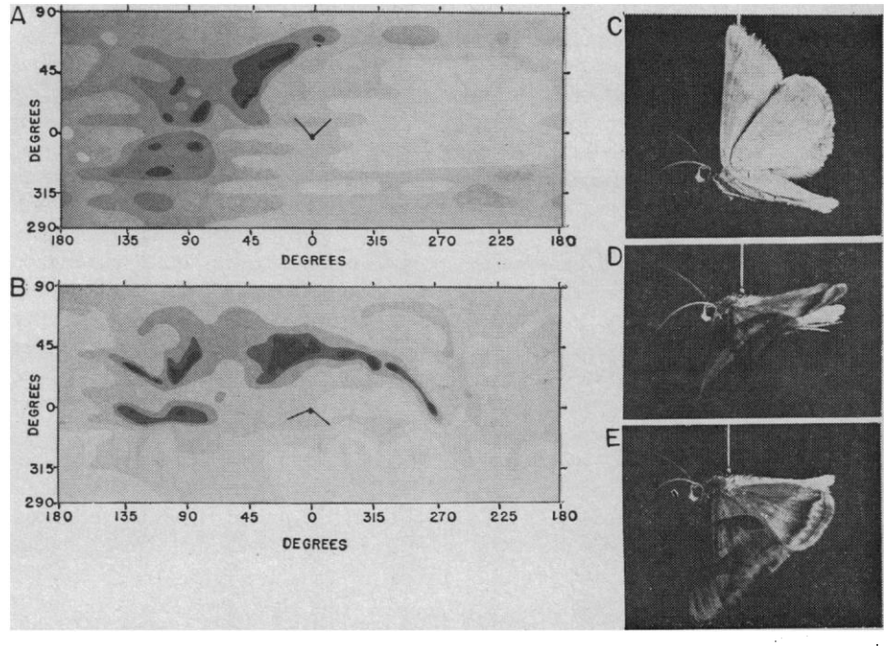

Fig. 5. (A and B) Mercator projections showing the directional sensitivity of the left ear of *Catocala neogama*. Areas of equal tone (light tone = high sensitivity) outline angular zones of equal (to within ± 5 decibels) sensitivity. Profile of the moth, headed toward viewer, is shown by the linear diagram at center of A and B, with wing angle roughly as indicated. The right-left acoustic asymmetry evident when the wings are up is replaced by dorsoventral acoustic asymmetry when the wings are at the bottom of their stroke. (C–E) Strobe-flash photographs of *Caenurgina erechtea* in stationary flight. Three phases of the downstroke are shown. The opening to the ear is visible in C as a small vertical slit below and behind the attachment of the hind wing. The camera was aimed at an angle of about 270 degrees in terms of the Mercator projections.

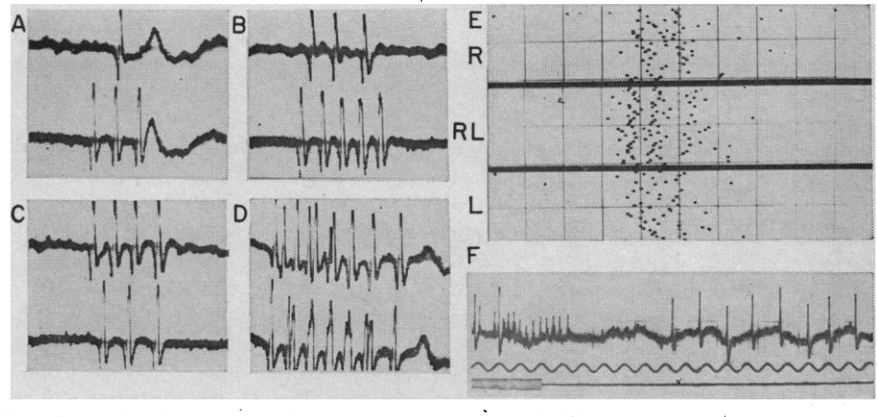

Fig. 6. (A–D) Binaural auditory neuron responses of *Feltia* sp. to the cries made by a bat flying in the field. The differential in the response from the two ears is evident in the latency, interspike interval, and number of spikes as the bat moved from one side of the specimen (A, B) to the other (C), and then (D) approached close enough for the sound to reach the saturation point for both ears. (E) Response of interneuron that responded to stimulation of either the right (R) or the left (L) ear and generated a larger number of spikes on stimulation of both ears (RL). Verticals mark 2-millisecond intervals. (F) Response of interneuron that was inhibited by auditory stimulation with a 35-millisecond pulse (lower trace). Time marker, 100 cycles per second. The stimulus produced a train of repeater spikes (small, closely spaced spikes) and suppressed the activity of the interneuron producing the large spike. It did not resume steady activity until 50 milliseconds after the train of repeater spikes had ended.

Vertical Localization

Many moths appear to be able to steer a course away from a source of faint ultrasonic pulses when the source is above or below their initial flight path, as well as when it is to the right or left (*6*). It is hard to see how the mechanism outlined above could provide the information needed for steering a course that required climbing or diving to carry the moth away from the source. Some signal in addition to the differential in the response from right and left auditory receptors is required.

The progress of a moth flapping its way through the darkness is anything but smooth (Fig. 1, left). In addition to the up-and-down movement caused by the wing oscillation (20 to 40 strokes per second) there is an inestimable amount of yawing, pitching, and sideslipping. Moreover, the wings are hinged just above the openings to the ears and might be expected to serve as oscillating baffles changing the directional characteristics of the acoustic field many times a second as they move up and down (Fig. 5, C–E).

It has not been possible to record auditory nerve impulses from the ear of a moth while it is still able to flap its wings; still less is this possible when it is in free flight. However, we have been able to map the directional sensitivity of the ear when the wings are held in different attitudes approximating those assumed during normal flight (*11*). This was done by directing a loudspeaker, generating ultrasonic pulses, at the ear from all angles 10 degrees apart with reference to the body axis of a stationary moth while measuring the sound intensity needed to produce an auditory-fiber response of an arbitrary criterion value (about that needed to excite the pulse-marker neuron) at each wing position. Several "spheres" of such data were obtained from each specimen with the wings fixed in different attitudes.

Data on relative acoustic sensitivity from each "sphere" of readings were entered on a Mercator projection with the moth at its center. Two of these, made with the same moth, are shown in Fig. 5, A and B. The attitude of the wings is shown by the linear symbol at the center of each projection.

The main point demonstrated by these projections is that, when the wings are at the top of their stroke, the sound fields of the ears are unimpeded on their respective sides. Then each ear is most sensitive to sounds coming from a direction at roughly 90 degrees to the body axis on the ipsilateral side, and least sensitive to sounds coming from a corresponding point on the contralateral side of the body. As the wings approach the bottom of their stroke they shield the ears, so that the region of minimum sensitivity for both sides lies directly above the moth. This can be seen from a comparison of the Mercator projections with the natural attitudes of the wings in flight (Fig. 5, C–E).

This finding suggests that the ears of a flying moth would experience maximum "flicker," at the moth's wingbeat frequency, in the intensity of a train of ultrasonic pulses when these originated from a source above its line of flight. Flicker would be less, and perhaps inverted in phase relative to wing position, when the source lay below the line of flight. Minimum modulation of the pulsed signal by the wingbeat over a broad angle would occur only when the source lay behind the moth. The flight path of most moths is quite erratic, and it is possible that this modulation of the signal by the wingbeat causes the moth to make a series of random turns. If these were to cease when there was no further wingbeat modulation of the signal, the moth would probably be flying a course directly away from the ultrasonic source.

If this is the case, an extra piece of information—the moth's wing attitude—must be continuously integrated with the signals from its two ears. This information is available, in the thoracic ganglia, from the rhythm of motor nerve impulses activating the flight muscles. Other possible sources are proprioceptors on the moving wings and thoracic exoskeleton.

Summary

Insect-eating bats find their aerial food by sonar, through emitting ultrasonic chirps and locating sources of echoes. Certain moths have ears sensitive to these chirps and can detect bats well beyond the range of the bats' sonar. On hearing a distant bat, many moths turn and fly directly away from the source of ultrasound. Only one sense cell in each ear of a moth provides the primary nervous information for this response. This article describes my initial attempts to find out how a moth's central nervous system processes the train of chirps reaching its two ears.

The ear of a restrained moth is exposed to a sequence of artifically generated ultrasonic pulses that approximates the cries made by a bat. This stimulus can be varied with respect to ultrasonic frequency (pitch), pulse intensity, pulse duration, the interval between pulses, and pulse-train duration.

The more sensitive acoustic sense cell responds to all frequencies between about 15,000 and 80,000 cycles per second, but the signal that it transmits to the moth's central nervous system contains no measure of frequency within this range. However, this nerve signal reports variations in the other parameters of the stimulus. The acoustic fiber connects, in the central nervous system, with various nerve cells that transform the signal farther. The signal from a pulse-marker neuron contains no measures of pulse intensity or pulse duration, reporting only changes in interpulse interval and pulse-train duration. A train-marker neuron reports only the duration of the pulse train. The stimulus parameters may be likened to keys, each of which is necessary to gain admittance through a given door but becomes superfluous once this door has been passed. This analogy suggests one of the ways in which a signal is transformed in its passage through the nervous system, and how its specificity is assured in eliciting a given response.

In addition to undergoing this kind of transformation, neural signals generated in the two directionally sensitive ears must be combined if a flying moth is to steer a course away from a distant bat. Neurons have been discovered in the central ganglia which summate signals from the right and left ears. Other neurons are inhibited in their activity by stimulation of one ear. The moth may combine signals from these neurons with motor-nerve information on the attitude of its own wings, which act as oscillating baffles modifying its directional acoustic sensitivity 20 to 40 times a second as it flaps an erratic path through the darkness.

References and Notes

1. D. R. Griffin, *Listening in the Dark* (Yale Univ. Press, New Haven, Conn., 1958).
2. ———, F. A. Webster, C. R. Michel, *Animal Behaviour* **8**, 141 (1960).
3. F. Schaller and C. Timm, *Z. Vergleich. Physiol.* **32**, 468 (1950); A. E. Treat, *Ann.*

Entomol. Soc. Amer. **48**, 272 (1956); P. T. Haskell and P. Belton, *Nature* **117**, 139 (1956); K. D. Roeder and A. E. Treat, *J. Exp. Zool.* **134**, 127 (1957).
4. K. D. Roeder and A. E. Treat, *Proc. Intern. Congr. Entomol., 11th* (1960), vol. 3, p. 1; ———, *Amer. Scientist* **49**, 135 (1961).
5. K. D. Roeder, *Animal Behaviour* **10**, 300 (1962).
6. ———, *Science* **153**, 1634 (1966).
7. ———, *J. Insect Physiol.* **12**, 843 (1966).
8. ———, *ibid.* **10**, 529 (1964).
9. ——— and A. E. Treat, *Sensory Communication*, W. Rosenblith, Ed. (M.I.T. Press, Cambridge, Mass., 1961), p. 545.
10. K. D. Roeder, *J. Insect Physiol.* **12**, 1227 (1966).
11. R. S. Payne, K. D. Roeder, J. Wallman, *J. Exp. Biol.* **44**, 17 (1966).
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Basic Research in the University and Industrial Laboratory

University and industrial research directors have contrasting roles in the basic-research enterprise.

R. E. Marshak

Warren Weaver, in an essay (*1*) entitled "A great age for science," tells us that pure science is "not technology, it is not gadgetry, it is not some mysterious cult, it is not a great mechanical monster. Science is an adventure of the human spirit; it is an essentially artistic enterprise, stimulated largely by curiosity, served largely by disciplined imagination, and based largely on faith in the reasonableness, order, and beauty of the universe of which man is a part." This characterization is a bit flowery, but it correctly emphasizes the point that a pure scientist derives his chief satisfaction from fashioning a new piece of knowledge, just as an artist derives his greatest pleasure from composing a symphony or carving a piece of sculpture. The emphasis here is on new knowledge, not merely the accumulation of isolated pieces of factual information, but knowledge of the kind which leads to a deeper understanding of natural phenomena and, indeed, is a contribution to natural law. The basic research enterprise starts with wonder and an intense curiosity about the nature of the world, is fed by devoted and almost passionate activity in search of new knowledge by truly creative individuals, and yields ordering principles where none existed before and powers of prediction which could only be dimly envisioned when the work was started. The objectives of the basic research enterprise are furthered by allowing the individual scientist complete freedom both to choose the subject matter of his investigations and to draw the conclusions to which they lead, consistent with the laws of logic and nature.

The situation is different in applied science. The applied scientist has a practical (that is, human) goal in mind and attempts to enlarge existing scientific knowledge in rather well-defined ways to achieve this specified human purpose; usually the purpose encompasses the creation of new materials, devices, systems, methods, or processes. In other words, applied science comprises the technological applications of newly discovered scientific knowledge. It is a truism that applied scientists may create new knowledge—interpreted in the broadest sense—and that pure scientists, motivated solely by curiosity, may make revolutionary discoveries of the greatest possible practical application. But the point is that applying science to satisfy certain specific needs of man automatically involves the social group which has spelled out this particular set of needs, and we must expect this social group or agency or organization (whether governmental or private) to call the tune. That is to say, a practical goal necessarily imposes constraints and controls on the applied scientist which would hamper productive and original work in pure science.

Basic Research at a University

After these preliminary and somewhat general remarks, let me try to come to grips with some of the questions which have been put to me. The first major question has to do with how we carry on basic research at a university and what role, if any, the research director plays in planning research programs, selecting scientific personnel, and achieving optimum research performance. Before commenting on the various facets of the research director's job in the university setup, I should like to point out that the preponderant position of the university in the basic research output of the U.S. is not a universal phenomenon. In this country, pure science is pursued largely in university laboratories where the senior scientists pass on the torch to the young students and where the students, through their enthusiasm and inventiveness, help to break down traditional patterns of thought. By combining graduate teaching and research at a single institution, as we do in an American university, we expose our young people to exciting new ideas and the most modern research techniques. Indeed, many research programs at the university are planned so that graduate students will receive the maximum benefit from the availability of up-to-date equipment and contribute significantly to the research. In contrast, in the Soviet Union, for example, the bulk of the scientific research is concentrated in the specialized institutes of the Soviet Academy of Sciences, not in the universities, which play primarily a pedagogical role. In the academy institutes of the U.S.S.R. there is a reluctance to accept young students because, supposedly, they will interfere with the research activity of the senior scientist. The result of the dichotomy between the instruction-oriented university and the research-oriented academy institute

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