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## THE DETECTION AND EVASION OF BATS BY MOTHS

By KENNETH D. ROEDER and ASHER E. TREAT<sup>1</sup>

A CENTRAL objective of a large segment of biological and psychological research is to provide a physiological basis for behavior. The first step toward this objective is analytic, and consists of determining the structure and function of neural components after they have been isolated from their connections with the rest of the nervous system. There has been much progress in this direction, and it is now possible to describe in terms of input and output performance the operation of many isolated sense cells, neurons, and muscle fibers, even though the principles of their internal operation are mostly not understood.

The next step, the synthetic process of assembling this information on isolated neural components and relating it to the behavior of the intact animal, is hampered by two kinds of difficulty. The first appears to be methodological, but is somewhat hard to define. When one regards the evergrowing literature on the unit performance of sense cells, nerve cells, and muscle fibers, it is to experience that sense of dismay first encountered at a tender age when the springs, gears, and screws of one's first watch were strewn upon the table. The *modus operandi* of analysis or taking apart seems to come naturally, and the problems encountered are essentially technical in nature. Synthesis or the derivation of a system from its components seems to lack the *a priori* logic of analysis.

The second general difficulty is technical, and stems from the fact that even the simplest behavior of the higher animals and man is accompanied by the simultaneous activity of millions of sense cells, nerve cells, muscle fibers, and glands. Even if it were possible to register the traffic of nervous and chemical information generated and received by each and all of these neural elements during the behavior, it is doubtful whether the record would provide a meaningful description of the action. Even though these problems cannot be solved directly at the present

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FIG. 1. External opening of the right ear in *Agrotis ypsilon*. The external surface of the tympanic membrane faces obliquely backwards and outwards into the cavity below arrow. The body of the moth is about  $\frac{3}{4}$  inch in length.

time, they become less formidable if the behavior selected for study is simple and stereotyped, and only a small number of nerve cells are concerned in its execution. These conditions are partly fulfilled by the sensory mechanisms whereby certain nocturnal moths detect the approach of insectivorous bats.

#### *Echolocation and Countermeasure*

Bats detect obstacles in complete darkness by emitting a sequence of high-pitched cries or chirps and locating the source of the echoes. As Griffin (1958) and others have shown, this form of Sonar is unbelievably precise. By means of it, insectivorous bats locate and track flying moths, mosquitoes, and small flies (Griffin, *et al.*, 1960). North American bats,

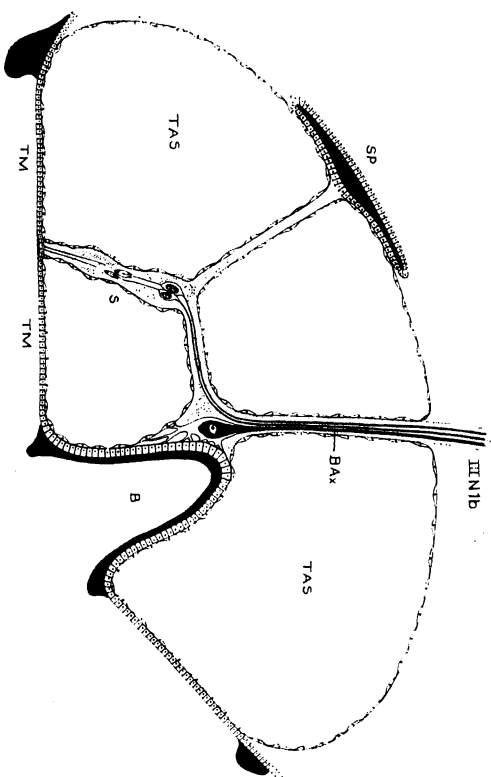


FIG. 2. Diagram of the tympanic organ of a noctuid moth. The sensillum (S) contains the pair of acoustic receptors or A cells. The A nerve fibers are joined by that of the B cell (BAX) to form the tympanic nerve (IINIB). TAS, tympanic air sac; B and SP, skeletal supports; TM, tympanic membrane. (After Treat and Roeder, 1959.)

such as *Myotis lucifugus* and *Eptesicus fuscus*, emit chirps about 10 times a second when they are cruising in the open. Each chirp lasts from 10 to 15 milliseconds (msec) with an initial frequency of 80 kilocycles (kc) dropping about one octave in pitch toward its end (see Figure 5).

The frequencies in these chirps are ultrasonic, that is, inaudible to human ears, which cannot detect tones much above 15-18 kc. The higher frequencies used by bats make possible more discrete echoes from smaller objects. The chirps can be rendered audible by detecting them with a special microphone and rectifying the ultrasonic component. They then can be heard through headphones as a series of clicks. These clicks fuse into what Griffin has called a "buzz" when the bat is chasing an

insect or avoiding an obstacle.

Several families of moths (in particular the owl moths or *Noctuidae*) have evolved countermeasures enabling them to detect the chirps of bats. A pair of ultrasonic ears is found near the "waist" of the moth between thorax and abdomen (Figure 1). An extremely thin eardrum or tympanic membrane is directed obliquely backward and outward into the recess (dark area) found at this point.

Internal to the eardrum is an air-filled cavity that is spanned by a thin strand of tissue running from the center of the eardrum to a skeletal support (Figure 2). This tissue contains the sound-detecting apparatus, consisting of two acoustic sense cells (A cells). A single nerve fiber arises from each A cell and passes close to the skeletal support, where the pair is joined by a third nerve fiber arising from a large cell (B cell) in the membranes covering the support. The three fibers continue their course to the central nervous system of the moth as the tympanic nerve.

The traffic of nerve impulses passing over the three fibers from A cells and B cell to the nervous system of the moth can be followed if a fine metal electrode is placed under the tympanic nerve. Another electrode is placed in inactive tissue nearby. As each impulse passes the site of the active electrode it can be detected as a small action potential lasting about 1 msec. Since the tympanic nerve contains only three nerve fibers, it is not difficult to distinguish and to read out the respective reports to the nervous system from the pair of A cells and the B cell. A similar experiment in a mammal is practically meaningless since the auditory nerve contains about 50,000 nerve fibers.

This method of detection shows that the A cells transmit organized patterns of impulses over their fibers only when the ear is exposed to sound (Roeder and Treat, 1957). The B cell transmits a regular and continuous succession of impulses that can usually be distinguished from the A impulses by their greater height. The B impulses are completely unaffected by acoustic stimulation, and change in frequency only when the skeletal framework and membranes lining the ear are subjected to steady mechanical distortion (Treat and Roeder, 1959). The B cell behaves in a manner similar to receptors found in other parts of the body that convey information about mechanical stress on joints, muscles, and skeleton. The role of such a receptor in the ear of a moth is unknown.

In the absence of sound, the A cells discharge irregularly spaced and relatively infrequent impulses (Figure 3A). A continuous pure tone of low intensity elicits a more regular succession of more frequent impulses in one of the A fibers (Figure 3B). The other fiber is not yet affected. Any slight increase in the intensity of the tone causes a corresponding increase in the impulse frequency of the active fiber. When the intensity

of the tone is increased to about 10-fold that producing a detectable response in the more sensitive A fiber, the second A fiber begins to respond in like manner. Its action potentials are superimposed on those of the first (Figures 3C and D) by the method of recording, but actually reach the central nervous system over their own pathway. This experiment reveals two of the ways in which the moth ear codes sound intensity. It is like an instrument having a graded fine adjustment (the

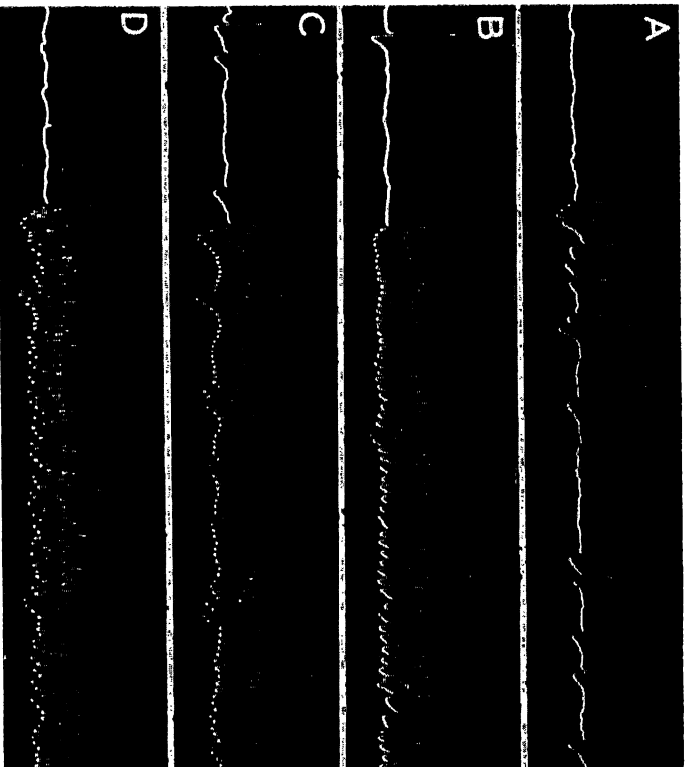


FIG. 3. Tympanic nerve response in *Prodenia eridania* to a pure tone of 40 kc. The occasional large spikes originate in the B cell. (A) Response to a sound intensity close to the threshold of the sensitive A cell. (B) Intensity 7 db above that in (A). (C) Intensity 15 db above that in (A). (D) Intensity 23 db above that in (A). The less sensitive A cell discharges occasionally in (C), and frequently in (D), as indicated by the double peaks. Time line 100 msec. (From Roeder, 1959.)

intensity-frequency relation) and a coarse adjustment of two steps (the pair of A cells). Other ways of coding intensity will appear later.

The moth ear responds in this manner to tones from 3 kc to well over 100 kc but there is no evidence that it is capable of discriminating between tones of different frequency. It is most sensitive near the middle of its range, that is, to frequencies such as those contained in bat chirps.

In Figure 3 it will be noticed that, in each of the recordings, the intervals between the successive impulses increase as the pure tone stimulus continues. In terms of the nerve code outlined above, the A

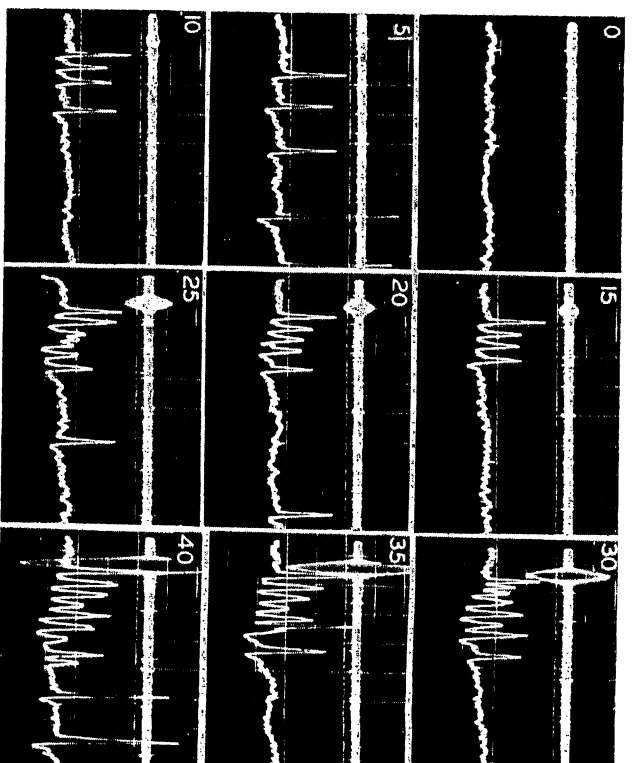


FIG. 4. Tympanic nerve responses (lower traces) of *Noctua* (= *Anathes*) *c-nigrum* to a 70 kc. sound pulse recorded simultaneously by a Granth microphone (upper traces). The numbers indicate the intensity of the sound pulse in decibels above a reference level (0). The threshold of the sensitive A cell lies between 0 and 5 db. The large spikes appearing in some of the records are from the B cell. The less sensitive A cell responds in the 25 db recording. Vertical lines, 4 msec. apart.

cells report that the sound is declining in intensity with time, although in fact it was kept constant. This adaptation to a constant stimulus occurs in most receptors registering changes in the outside world. In terms of our own experience, the impact of our surroundings would be shocking and unbearable if it were not distorted in this manner by sense organs. The brilliance of a lighted room entered after dark would continue to be blinding and the noise of a jet engine would remain unbearable. However, the A cells of the moth's ear adapt very rapidly to a continuous tone, and their full effectiveness as pulse detectors is revealed only when they are exposed to short tone pulses similar to bat chirps.

In the experiment illustrated in Figure 4 a tone pulse of 3 msec duration was generated at regular intervals. It is similar to a bat chirp except for its regularity and the absence of frequency modulation. A microphone (upper trace) and moth ear (lower trace) were placed within range, and the intensity of the stimulus pulse was adjusted so that it just produced a detectable response in the most sensitive A fiber (0 db). The intensity was then increased by 5 decibel (db) steps as each

<sup>1</sup> The decibel (db) notation expresses relative sound pressures. An intensity of 20 db is 10-fold that of the reference level (0 db), a 40 db sound is 100-fold the reference level.

recording was made. It will be seen that the microphone begins to detect the sound pulse when it is about 10 db above the threshold of the most sensitive A cell in the moth's ear. As before, the increase in frequency of A impulses is evident if the 5 and 10 db records are compared, and a response of the less sensitive A cell appears first in the 25 db record where the extra peaks of its action potentials overlap those of the more sensitive A unit. In addition to these two ways of coding intensity, two more can now be recognized. If the interval between detection of the sound by the microphone and by the moth ear is compared at different sound intensities, it will be noticed that the tympanic nerve response occurs earlier and earlier on the horizontal time axis. In other words, the latency of the response decreases with increasing loudness. Also, the sense cells are seen to discharge impulses for some

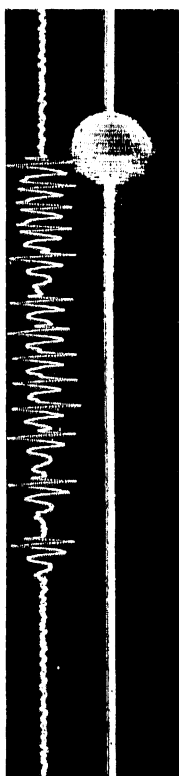


Fig. 5. The cry of a flying bat (*Myotis*) recorded by a Granth microphone (upper trace) and the A cells (lower trace) of a noctuid moth (*Agrotina dubitans*). The A spikes shown in the lower trace have been distorted in form by the recording technique. Time line, 10 msec. Made in collaboration with Dr. Fred Webster in his laboratory.

#### The Detection of Bats

These experiments with artificial sounds suggest how the moth ear might be expected to respond to a bat cry. A few laboratory observations were made with captured bats. In one of these, in collaboration with Dr. Fred Webster, the cries of a flying bat were picked up simultaneously by a moth ear and a microphone, and recorded on high-speed magnetic tape (Figure 5). Interesting though they were, these experiments served mainly to show that the full potentialities of the moth ear as a bat detector could not be realized within the confines of a laboratory, and efforts were made to transport the necessary equipment to a spot where bats were flying and feeding under natural conditions.

Finally, about 300 pounds of equipment was uprooted from the laboratory and reassembled at dusk of a July evening on a quiet hillside in the Berkshires of western Massachusetts. Moths attracted to a light provided experimental material. The insect subject was pinned on cork so that one of its ears had an unrestricted sound field, and with the help of a microscope its tympanic nerve was exposed and placed on electrodes. After amplification, the action potentials were displayed on

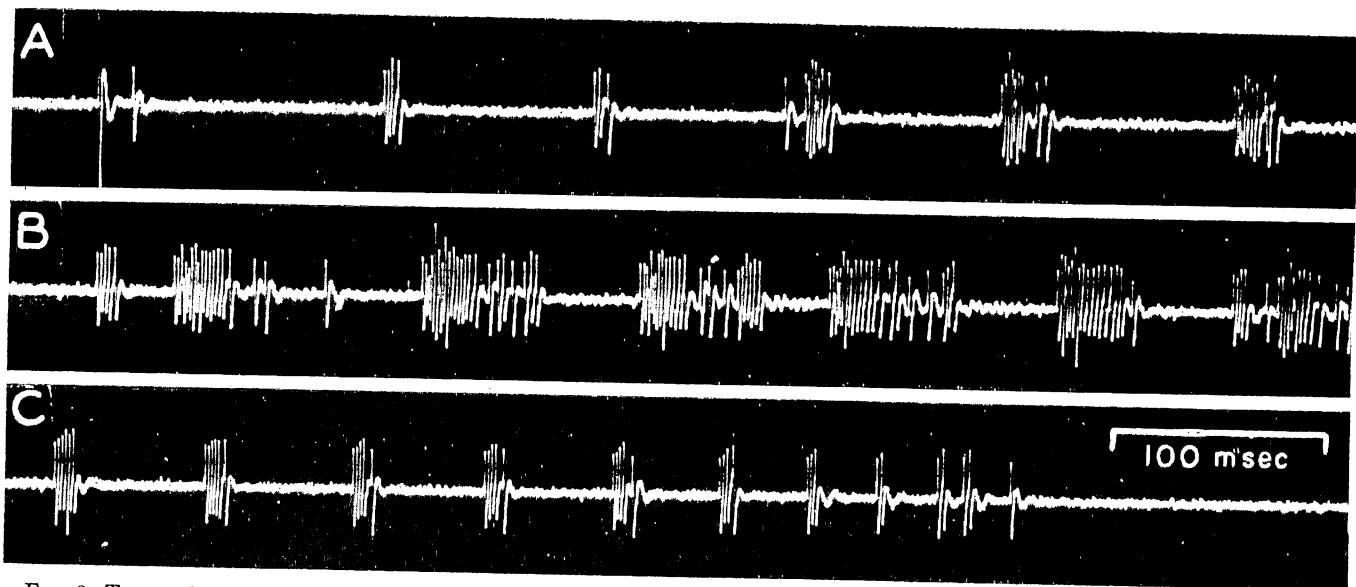


Fig. 6. Tympanic responses of *Noctua* (= *Amathes*) *c-nigrum* to the cries of bats flying in the field. (A) The approach of a cruising bat emitting pulses at about 10 per second. (B) Tympanic response to the original cry and its echo made by a bat cruising nearby. (C) A "buzz." Time line, 100 msec. (From Roeder and Treat, 1961.)

an oscilloscope. They were also made audible as a series of clicks by means of headphones connected to the amplifier, and were stored on magnetic tape for later study.

It was dark before all was ready, but bats immediately revealed their presence to the moth ear by short trains of nerve impulses that recurred about 10 times a second (Figure 6A). The approach of a cruising bat from maximum range was coded as a progressive increase in the number and frequency of impulses in each train, first from one and then from both A fibers. It was not long before we learned to read something of the movements of the bats from these neural signals. Long trains, sometimes with two frequency peaks, suggested the chirps of nearby bats that echoed from the wall of a neighboring house (Figure 6B). An increase in the repetition rate of the trains coupled with a decrease in the number of impulses in each train signified a "buzz" as the bat attacked some flying insect in the darkness (Figure 6C).

All of this was inaudible and invisible to our unaided senses. With a powerful floodlight near the nerve preparation we were able to see bats flying within a radius of 20 feet, and some attacks on flying insects could then be both seen and also "heard" through the "buzz" as coded by the moth's typanic nerve. However, most of the sounds detected by the moth ear were made by bats maneuvering well out of range of the light. A rough measure of the sensitivity of the moth ear to bat chirps was obtained at dusk on another occasion when the bats could still be seen. The A cells first detected an approaching bat flying at an altitude of more than 20 feet and at a horizontal distance of over 100 feet from the moth—a performance that betters that of the most sensitive microphones.

#### Direction

Since differences in sound intensity are coded by the tympanic nerve in at least four different ways, the horizontal bearing of a bat might be derived from a comparison of the nerve responses to the same chirp in the right and left ears. A difference in right and left responses might be expected only if each ear had directional properties, that is, a lower threshold to sounds coming from a particular direction relative to the moth's axis.

Directional sensitivity was measured in an open area where echoes were minimal. A source of clicks of constant intensity was placed on radii to the moth at 45 degree intervals. The source was moved in and out on each radius until a standard tympanic nerve response was obtained, and the distance from the moth noted. Horizontal distances along 8 radii were combined to make a polar plot of sensitivity (Roeder and Treat, 1961). The plot showed that, although there was little

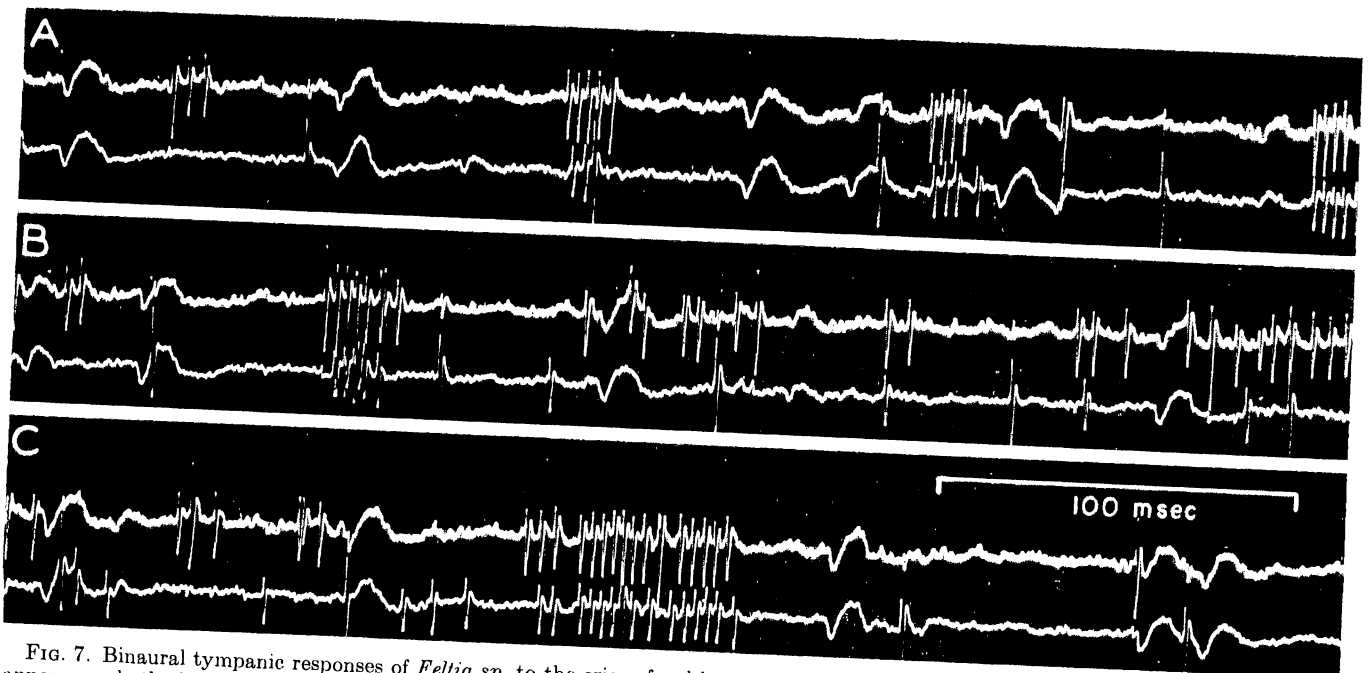


FIG. 7. Binaural tympanic responses of *Felicia* sp. to the cries of red bats flying in the field. The electrocardiogram of the moth also appears on both channels as slow waves. B impulses (large spikes) appear regularly in the records from both tympanic nerves. (A) An approaching bat. Differential response is marked at first (response latency, number of spikes) but has practically disappeared in the final train. (B) A "buzz" registered mainly by one ear. (C) A "buzz" registered by both ears. Time line, 100 msec.

difference in sensitivity fore and aft, a click on the side nearest the ear at about 90 degrees relative to the moth's longitudinal axis was audible at about twice the distance of a similarly placed click on the far side.

This led to further field experiments in the presence of flying bats. The tympanic nerve responses from both ears of a moth were recorded simultaneously on separate tracks of a stereophonic magnetic tape. The tape was subsequently re-played into a two-channel oscilloscope and the traces photographed (Figure 7). In the upper record (A) the increase in number of impulses in each succeeding train suggests the approach of a bat. When the signals from right and left ears are compared, it is evident that the greatest difference exists when the signal is faintest, the first response of the series occurring in one ear only. When both ears respond, the differential nature of the binaural response can be seen first as a difference in the number of spikes generated in right and left ears, second in the differential spike frequency, and third in the latency of the response, which is greater on that side generating fewer spikes. It is also evident that, as the sound intensity increases (presumably due to the approach of the bat), the differential becomes less until the responses of right and left ears become almost identical. In another experiment, it was found that the tympanic nerve response saturates, i.e., becomes maximal, when the sound intensity is about 40 db (100-fold) above threshold. From this it can be concluded that the moth's nervous system receives information that would enable it to determine whether a distant bat was to the right or left, but if the bat was at close quarters this information would not be available. In Figure 7C the "buzz" was picked up by one ear only, presumably because during this part of its performance the chirps of a bat are much less intense.

It is tempting to estimate just how close the bat must be before the moth fails to get information on its location. If it is assumed that a bat is first detected at 100 feet and approaches on a straight path at right angles to the moth's course while making chirps of constant loudness, the differential tympanic nerve response would diminish throughout the approach and disappear completely when the bat was 15 to 20 feet away. However, we have not yet determined how much of the information that we are able to read out of its auditory mechanism is actually utilized by the moth in its normal behavior.

#### *The Evasive Behavior of Moths*

Although the evasive behavior of moths in the presence of bats must have been witnessed hundreds of times, it is hard to find an adequate account of the maneuvers of either party. The contest normally takes place in darkness, and, even when it is illuminated by a floodlight, the action is too fast and complex to be appreciated by the eye. The flight path of the bat and its ability to intercept and capture its prey have

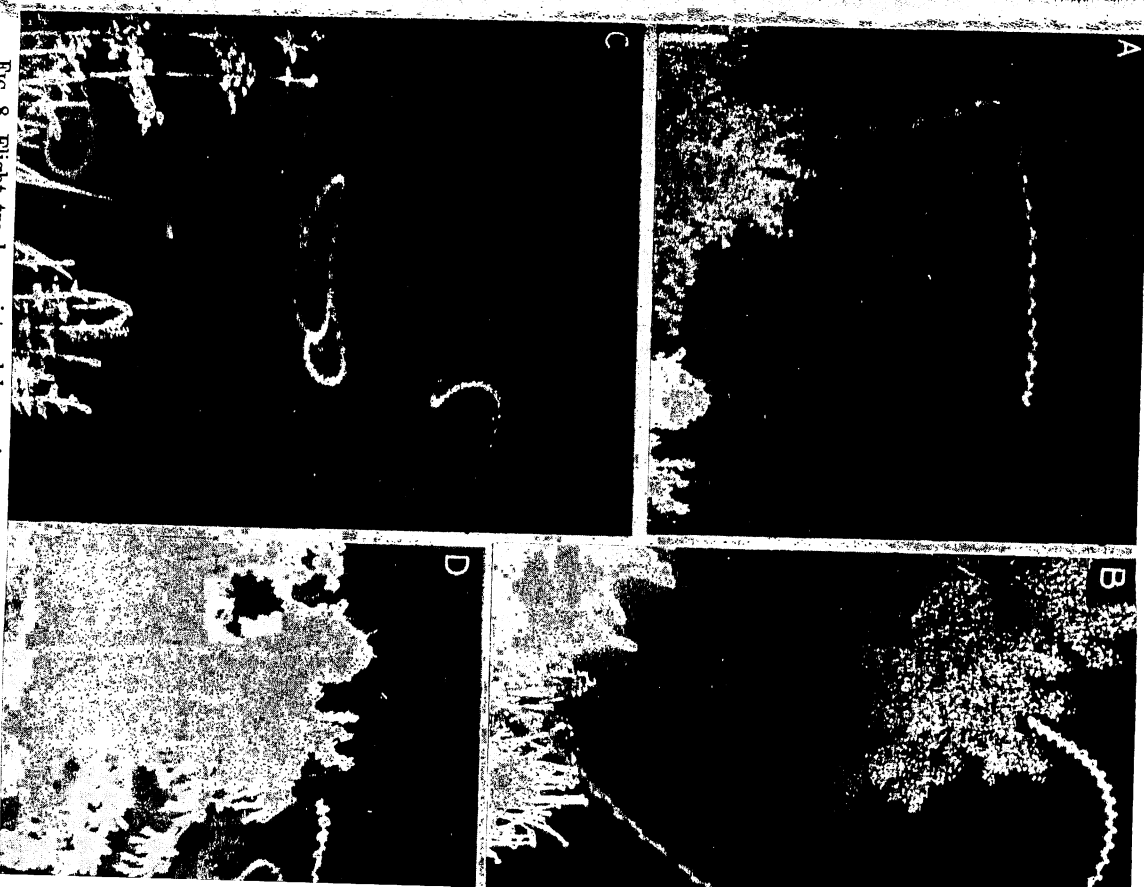


FIG. 8. Flight tracks registered by various moths just before, and immediately following, exposure to a series of simulated bat cries. The dotted appearance of the tracks is due to the individual wingbeats of the moth. The beginning of each track appears in each photograph, and the moth finally flies out of the field.

been studied by Griffin (1958) and his students. More recently, Webster (in press) has shown by means of high-speed sound motion pictures that bats become adept at using echoes to plot an interception course with an object moving in a simple ballistic trajectory. Many people have noted the seemingly erratic dives and turns made by moths when bats

are near, and similar behavior has been described when moths are exposed to artificial sources of ultrasound (Schaller and Timm, 1950; Treat, 1955).

In an effort to learn more about the behavior of moths under field conditions their flight was tracked photographically as they reacted to a series of ultrasonic pulses simulating bat cries. The sounds were generated by the equipment used in the experiment shown in Figure 4. The pulses were similar in form to those shown, although longer in duration (6 msec). Each pulse ranged from 50 to 70 kc with a rise and fall time of about 1 msec. Pulse sequences up to 50 per second could be released on closure of a switch. The sounds were emitted by a plane-surfaced condenser loud-speaker mounted so as to project a fairly directional beam over an open area of lawn and shrubs illuminated by a 250-watt floodlight.

The observer sat behind the sound generator and floodlight, holding in one hand the cable release of a 35 mm camera set on "bulb," and in the other the switch controlling the onset of the sound-pulse sequence. Many moths and other insects flew out of the darkness into this floodlight arena. A number were attracted directly to the light and were disregarded. Many others moved across the arena at various angles but without marked deviation toward the light. When one of these appeared to be in line with the loudspeaker the camera shutter was opened and the sound pulses turned on.

Some of the tracks registered by the camera as the illuminated moths moved against the night sky are shown in Figure 8. Many insects, including some moths, showed no change in flight pattern when they encountered the sound. In others, the changes in flight path were dramatic in their abruptness and bewildering in their variety. The simplest, and also one of the commonest reactions was a sharp power dive into the grass (Figure 8A, B). Sometimes the dive was not completed and the insect flew off at high speed close to the ground. Almost as frequently the dive was prefaced or combined with a series of tight turns, climbs, and loops (Figure 8C, D).

It is not known whether these maneuvers are selected in some random manner from the repertoire of individual moths, or whether they are characteristics of different species. However, Webster (in press) has shown that bats soon learn to plot an interception course with food propelled through the air in a simple ballistic trajectory. The random behavior elicited by simulated bat cries in the natural moth population seems to be a natural answer to this predictive ability in bats, while the sharpness of the turns must certainly tax the maneuverability of the heavier predator.

The reacting moths shown in Figure 8 were mostly within 25 feet of the camera and sound source, and were exposed to an unknown

but probably high sound intensity. Under these circumstances, the evasive behavior appeared to be completely unorientated relative to the sound source, as might be predicted from the binaural tympanic nerve recordings. In some instances, moths flying at a greater distance or only on the edge of the sound beam appeared to turn away from the area and fly off at high speed. This must be checked in future experiments.

#### *The Survival Value of Evasion*

In spite of the evidence that the moth ear is an excellent bat detector, and that acoustic stimulation releases erratic flight patterns, one may well ask whether this behavior really protects moths from attack by bats.

This question has been answered (Roeder and Treat, in press) by observing with a floodlight 402 field encounters between moths and feeding bats. In each encounter we recorded the presence or absence of evasive maneuvers by the moth, and the outcome, that is, whether it was captured by the bat or managed to escape. From the pooled data we determined the ratio of the percentage of nonreactors surviving attack to the ratio of reactors surviving attack. Thus computed, the selective advantage of evasive action was 40 per cent, meaning that for every 100 reacting moths that survived, there were only 60 surviving nonreactors.

This figure is very high when compared with similar estimates of survival value for other biological characteristics. It seems more than adequate to account for the evolution of the moth's ear through natural selection even if the detection of bats turns out to be its only function.

#### *Conclusion*

As with most investigations, this work raises more questions than it has answered. The role of the B cell remains completely obscure. There is no evidence to connect it with the auditory function even though it is located in the ear, and its regular impulse discharge is a characteristic feature of the tympanic nerve activity of many species of moth (Treat and Roeder, 1959. See also Figure 7). The manner in which the A cells transduce sound waves recurring 100,000 times a second into the much slower succession of nerve impulses remains a mystery, and the synaptic mechanisms whereby information from the A fibers is translated into action by the nervous system of the moth, await investigation.

During the field experiments it was noticed that many other natural sounds initiated impulses in the A fibers. These included the rustling of leaves, the chirp of tree and field crickets, and, in one instance, ultrasonic components in the wingbeat sounds made by another moth. Occasionally, the A fibers discharged regularly as if detecting a rhythmic

sound, though none was audible to the observers and its source (if any) remains a mystery. There is no evidence that these identified and unidentified sounds are important in the life of a moth, yet it must be said that a moth can detect them, and a careful study of moth behavior in their presence would be of value.

Several families of moths lack ears and show no response to ultrasonic stimuli. Some of these, such as the sphinx or hawk moths and the larger saturniid moths, are probably too much of a mouthful for the average bat, and might find no survival advantage in a warning device. Others are of the same size and general habits as the noctuids and might be expected to suffer attacks by bats. Included in this group are some common pests such as the tent caterpillar. It will be interesting to learn whether these forms owe their success in survival to some structural or behavioral countermeasure that compensates for the lack of a tympanic organ.

In spite of these unanswered questions, we believe that some progress has been made in putting together the sensory information received by an animal, and relating this to what the animal does. That this has been possible in moths is only because of the small number of channels through which acoustic information reaches the nervous system in these insects. Further examples of this favorable situation have been described in other insects, and still others are waiting to be explored.

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## THE COMPUTER-RELATED SCIENCES (SYNNOETICS) AT A UNIVERSITY IN THE YEAR 1975\*

BY LOUIS FEIN

FOREWORD

One indicator of a changing culture is the set of new names and words for new ideas, things, modes of behavior, activities, vocations, avocations, intellectual disciplines, and so on. Consider the following set of names and words that have appeared in this generation: Information Theory, Communication Sciences, Automation, Cybernetics, Autonomics, Intellectronics, Computer Sciences, Bionics, Human Engineering, Operations Research, Theory of Games, Data Processing, Management Science, Artificial Intelligence, Adaptive, Cognitive and Self-Organizing systems. With these terms, we can describe roughly the ways in which we handle some of society's chores and how we solve some of society's problems. Much of the theory and practice in these fields are common and applicable in the treatment of a system (comprising people, computers, and other such "mental" aids) whose distinctive attribute is that its (the system's) "mental" power is usually greater than the "mental" power of its components. The name Synnoetics has been coined as the science treating of the properties of such systems. Subjects such as Cybernetics, Computer Science, Bionics, are thus branches of Synnoetics.

I believe that developments in Synnoetics will be among the more important determinants of our cultural, social, and economic progress and of our security. I urge, therefore, that universities now deliberately plan and set up Departments or Schools of Synnoetics despite some in the universities now resisting such action or indifferent to it. Enough money, facilities, faculty and students could be obtained. All that is needed in addition is a recognition of the need and the drive to do it.

#### Alumni and Friends:

Last year, we changed the name of our Computer-Related Science Department to the Department of Synnoetics. Since then, we've received many inquiries concerning this department from people who think it is newly formed rather than newly named. Today, I would like to talk to you about Synnoetics at our university.

This talk will consist of two parts. In the first part, I shall define Synnoetics and I will describe its present role and impact at our university: In passing, I shall mention the university climate and policies under which Synnoetics has been able to flourish. In the second part, I shall discuss its history. Afterward, I shall be glad to answer your questions.

#### *What Synnoetics Is About*

In coping with his environment, man uses his physical and mental powers more or less efficiently. His mental powers are used predominantly when he invents machines and processes, conceives ideas, plans, paints,

\* The reader is asked to imagine that this is a reprint of an address to an alumni audience in the year 1975 by the president (a famous historian) of one of the major universities in the U.S. Following the text of the address is a verbatim transcript of the question-and-answer period that ensued. The title of the address is "Synnoetics at Our University."