DIRECTIONAL SENSITIVITY OF THE EARS OF NOCTUID MOTHS

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INTRODUCTION

Moths of several families, notably the Noctuidae, Arctiidae and Geometridae, have tympanic organs sensitive to pulsed ultrasound (Eggers, 1919; Haskell & Belton, 1956; Roeder & Treat, 1957). It has long been suspected that moths could hear the cries of approaching bats which prey upon them (White, 1877) and a variety of behavioural responses to natural and artificial acoustic stimuli have been reported (Eggers, 1926; Schaller & Timm, 1950; Treat, 1955). An attempt has been made to track and to describe the reactions of free-flying moths in the field to a fixed source of artificial ultrasonic pulses (Roeder, 1962), and to relate various forms of evasive behaviour to the pattern of afferent nerve impulses elicited by ultrasound in the pair of acoustic sense cells (A cells) of the noctuid tympanic organ (Roeder, 1964).

The behavioural responses of moths are conspicuously different to pulses of high and low intensities. In the presence of high-intensity pulses the moth’s responses take the form of diving and looping, but since these responses generally bring the moth to the ground and show no clear directional relation to the source of ultrasound they will not be considered further. However, it was consistently noted (Roeder, 1962, 1964) that moths flying at greater distances from the sound source, and at various altitudes with respect to it, would turn and fly (with some preliminary ‘hunting’) directly away from the source. This ‘turning-away’ was observed only if the moth encountered a series of low-intensity ultrasonic pulses and it is likely that at such intensities only one nerve cell in each ear is active. Further, it implies that moths with this sensory equipment can extract directional information from sound waves in all planes.

A pair of symmetrically placed ears containing only one responding sense cell per ear can convey information about the direction of a source of sound pulses if two conditions are met. First, the receptor cell must convey, in the pattern of its afferent fibre discharge, differences in the intensity of stimulation. In the present case ‘turning-away’ occurs only at low sound levels. Therefore, the intensity discrimination of the most sensitive tympanic sense cell (A1) must be greatest at sound intensities not much above its threshold. The acoustic sense cells of noctuid moths are indeed

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most sensitive to intensity differences in the first 10 db. of their range. These intensity
differences can be read from four different criteria contained in the A1 cell response
as displayed on an oscilloscope (latency, number of spikes per pulse, inter-spike
interval, number of cells responding) (Roeder & Treat, 1961). These criteria have
been examined for their significance in releasing various forms of avoidance behaviour
(Roeder, 1964). One of them, the number of A cell action potentials in response to
an ultrasonic pulse of fixed duration, is particularly susceptible to electrophysiological
measurement, and has been selected as a measure of intensity reaching the tympanic
organ in the following experiments.

The second condition for conveying directional information about a sound source
is that the external configuration of each ear and surrounding structures must make
it more sensitive to sounds coming from some directions than from others. Pre-
liminary evidence for this in the horizontal plane (Roeder & Treat, 1961) has been
extended in the present paper in greater detail and to all planes relative to the body
axis of the moth.

METHOD

The acoustic arena. The measurements of sound intensity in relation to angle of
presentation required that a tympanic nerve preparation mounted in a free acoustic
field be presented with ultrasonic pulses at a constant distance but from all angles with
respect to the moth’s body axis. It also required that registration of tympanic nerve
responses be continuous and artifact-free with the preparation in all positions.

A plywood box (3 ft. wide, 4 ft. deep, and 6 ft. high) lined with 6 in. of fibreglass
insulation provided an adequately anechoic chamber for the near-threshold ultrasonic
signals employed (the fibreglass reduced echoes by c. 20–25 db.). The preparation
with its implanted electrodes was mounted on a tower 30 in. high constructed of
1.2 mm. metal tubing. This was designed to minimize echoes and distortions of the
sound field near the moth, whose body was the largest object within 30 in. The tower
stood on a turntable mounted on a 1 in. shaft equipped with ball bearings (Text-fig. 1).
This ensured relatively vibrationless rotation in the horizontal plane. A Kuhl capaci-
tative loudspeaker (McCue, 1961) 1.5 in. in diameter was mounted on a boom so
that it could be moved through a vertical arc of 180° at a distance of 30 in. from the
preparation. Both vertical and horizontal movements were calibrated in degrees.

The tympanic nerve preparation. Methods for exposure and recording from the
noctuid tympanic nerve have been described previously (Roeder & Treat, 1957, 1961;
Treat & Roeder, 1959). A decapitated, legless moth was secured dorsal side up, and
the notum, together with the horizontal flight-muscle mass, was dissected away. The
pterothoracic ganglion and main metathoracic nerve trunk (N1, pl. 11, Treat, 1959)
and its tympanic branch (N1b) were located at the bottom of the thoracic cavity.
N1 was severed above and below its tympanic branch, leaving the full length of the
latter available for placement on recording electrodes. The short ‘T’ provided by
the remains of N1 served as a convenient handle for manipulating the fine tympanic
nerve. Once the tympanic nerve had been isolated and prepared in this manner the
moth was transferred to the metal tower. It was secured in a horizontal position by
impalement on a trident of needles. These were electrically connected to the tower
and served as the grounded indifferent electrode.
A piece of 0.015 mm. platinum wire was threaded through 0.2 mm. glass tubing c. \(\frac{1}{2}\) in. long so that the wire protruded about \(\frac{1}{16}\) in. The tube was then thrust downward through the moth, starting from near the pterothoracic ganglion and emerging between the meso- and metathoracic sternites. This short bit of wire, insulated only

by the glass tube, served as the active electrode once it was plugged into a saline-filled cup that was connected to a preamplifier. The cup was a section of gauge 20 hypodermic needle about \(\frac{1}{4}\) in. long, one end of which was closed off by soldering it to the
tip of a fine copper wire. The flexible copper wire allowed placement of the cup in any position appropriate for receiving the platinum–glass electrode. The $\frac{1}{16}$ in. protruding end of wire inside the moth's body cavity was bent into a hook and the previously prepared stump of the tympanic nerve was wrapped around it twice (Text-fig. 2).

When the tympanic nerve was in place on the platinum hook fluid was withdrawn from the thoracic cavity until tympanic nerve spikes of satisfactory amplitude were obtained. Further drying of the tympanic nerve was prevented by sealing the dorsal opening in the thorax with a thin leaflet of wax. Small beads of the same material were used to fix the wings at various angles approximating those assumed in normal flight.

Text-fig. 2. Diagrammatic view of a headless, legless moth impaled on a trident of needles at the apex of the tower. A, Periphery of the excavation made into the thorax in order to expose the acoustic nerve. B, Fine glass tube containing the active electrode wire; the wire may be seen emerging from the tube inside the thoracic cavity. It is there bent into an 'S' and the acoustic nerve draped over it. Later, the nerve is wrapped around the electrode twice, using the small, attached segment excised from N1 as a convenient handle. C, Saline-filled cup made from a length of gauge 20 hypodermic needle soldered to a copper wire that is tied to the tower (but insulated from it). The end of the glass–platinum electrode is inserted into this cup. D, Tip of the tower, showing the trident of needles (the indifferent electrode) penetrating the moth's body. E, Pterothoracic ganglion showing the stump of N1. The continuation of N1 can be seen after a space where the segment attached to the tympanic nerve was removed.

The preparation mounted in this way proved to be adequately stable to biological deterioration, and nerve impulses could be recorded without artifacts during considerable mechanical disturbance. (One could strike the tower a sharp blow sending it into violent vibration with an arc of about an inch, so that the moth fixed to it appeared to the naked eye only as a blur, and yet, even while it vibrated, recordings of acoustic nerve activity were normal.) Occasionally it was necessary to remove body
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Fluid which collected and shorted the active electrode. Except for these interruptions continuous spike discharges from the tympanic nerve could be recorded during rotation of the preparation. In one case data were collected for as long as 14 hr.

Instrumentation. Data collection was greatly speeded by using a feedback amplifier that automatically and continuously adjusted the intensity of the ultrasonic pulses so as to maintain a constant number of action potentials in the tympanic nerve while the preparation made its horizontal transits at a given speaker elevation. Fluctuations of speaker voltage, and hence of sound intensity, in relation to angle of the loudspeaker in relation to the moth's body axis were automatically recorded on a General Radio Graphic Level Recorder.

A block diagram of the instrumentation is shown in Text-fig. 1. The stimulus consisted of 60 kcyc./sec. pulses (on one occasion 30 kcyc./sec.) with a rise–fall time of 1.25 msec., a duration of 6 msec., and a repetition rate of 20/sec. These were generated by an oscillator whose output was chopped with 1.25 msec. rise and fall time by a Grason–Stadler electronic switch. 'On' and 'Off' commands to the electronic switch were the synchronizing and stimulus pulses from a Grass stimulator. The voltage of these 60 kcyc./sec. pulses (approximately 1 V. maximum) was regulated by the feedback system before amplification by an electrostatic transducer driver and emission as ultrasound by the electrostatic loudspeaker (McCue, 1961).

The feedback system operated as follows. The amplified spikes from the tympanic nerve went to a pulse-height analyser (window) (Littauer & Walcott, 1959) which separated (according to spike height) spikes of the cell with which we were concerned, the A1, from those of other cells in the nerve (A2 and B). A1 spikes segregated in this manner went to a pulse generator and were shaped into standard pulses (without changing the number of pulses or their inter-pulse intervals). These pulses were transformed into a fluctuating d.c. potential by means of a frequency meter. This d.c. signal served to control the output of the feedback amplifier. The output of the feedback amplifier went to the power amplifier and loudspeaker, and was also registered continuously as a function of time on the graphic level recorder as the preparation was steadily rotated in the horizontal plane. Horizontal transit time corresponded to degrees in the horizontal plane (angle of the preparation relative to the sound source).

In practice it was necessary to fill in the space between the pulses broadcast at the moth so that the sound level recorder would not oscillate markedly in showing zero intensity between pulses. This was accomplished by inserting 100 cyc./sec. pulses between the 60,000 cyc./sec. pulses. The electronic switch worked by chopping two channels alternately so that when one was on the other was off. We used one channel for producing 60,000 cyc./sec. pulses from one oscillator and the other channel for producing 100 cyc./sec. pulses from a second oscillator. The 100 cyc./sec. pulses were allowed to reach the sound level recorder but were filtered out just ahead of the transducer driver so that they were not broadcast to the moth.

A series of horizontal rotations of the preparation with the loudspeaker at a sequence of angles 10° apart, above and below the horizontal, constituted a 'sphere' of data yielding information about the sensitivity of the moth to sounds from all directions. Ordinarily the criterion response balancing the feedback system was held at two tympanic nerve spikes per ultrasonic pulse with a third spike present about 50%
of the time. The threshold of this preparation to ultrasound cannot be clearly defined owing to minor spontaneous fluctuations in A1 sensitivity, but the level of stimulation we used is within 5-10 db. of the sound intensity eliciting a minimal response (Roeder, 1964). At this response level the tympanic organ is very sensitive to intensity differences when stimulated with frequencies between 20 and 80 kyc./sec., and differences of 1 db. can readily be discriminated by visual inspection of the spike pattern displayed on an oscilloscope. Furthermore, with ultrasonic pulses of this duration and repetition rate there is little or no adaptation over a period of several hours.

With the sound turned on, the turntable supporting the tower was rotated at 1 rev./1.5 min. This slow rate was maintained so that the combined response times of the frequency meter, feedback amplifier and recorder-pen writing speed would not mask sudden changes in intensity over small changes in angle. Thus each full revolution of the turntable produced information regarding the variation of sound intensity from all possible directions at a constant vertical placement of the sound source.

We collected data for each 10° in the vertical plane until 90° above the ‘equator’ and 70° below had been completed. Prior to data collection in a series of horizontal planes a single sweep was made in the vertical plane (at some constant horizontal setting). Using single values from this vertical sweep (for speaker positions common to it and to each horizontal sweep taken later) we were able to make corrections in each horizontal sweep to allow for any sensitivity drift that had occurred during the long process of collecting data in a series of horizontal planes. Such correction was seldom necessary, however, and the remarkable correspondence between repeated runs taken sometimes hours apart (see figure 3) indicates a repeatability of results for any given moth of ±2 db. from run to run. The only exception to this is at the abrupt points of extreme insensitivity, which varied more—undoubtedly owing either to slight changes of the preparation caused by drying out or to inaccurate duplicate placement of the loudspeaker in the vertical plane in the corroborative runs.

Following collection of data for all latitude lines 10° apart any run containing questionable areas or obvious anomalies due to equipment malfunction was repeated until two successive runs gave the same results. After the first few successful experiments we became very familiar with the expected form of records so that any artifacts stood out and were immediately checked. Besides familiarity with the records, we had a further defence against artifacts: at all times a monitoring oscilloscope displayed the fluctuating sound signal on one channel and the response of the acoustic nerve on the other. In addition, the acoustic-nerve spikes were constantly converted by the pulse-height analyser to audible clicks—once for every 10 spikes. Abrupt changes in this click pattern alerted us to look at the oscilloscope screen, where we could usually note discontinuities in the performance of equipment or preparation. As a result we feel that it is unlikely that serious artifacts have crept into the final records.

Following collection of information from a complete ‘sphere’ of bearings of the loudspeaker on the moth, the nerve was bathed in saline and the position of the wings changed by melting the wax at the articulations of fore and hind wings. Then the entire process of data collection was repeated to obtain data for a new sphere of bearings.

Checks on the accuracy with which the moth was centred at the axis of the rotating
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Speaker showed that any variations in sound intensity due to misalignment would account for less than 1 db.—well within experimental error. The possibility that the loudspeaker was producing a discontinuous sound gradient was checked by replacing the preparation with a Weston 640 AA calibrated microphone. We found that the sound field was sufficiently uniform to eliminate any risk that misalignment of the moth would place it in regions of sudden discontinuity of the sound field. In addition to the above precautions we satisfied ourselves that there was a linear relation between signal voltage and acoustic output of the loudspeaker. This was found to be true except at the very highest intensities our equipment could produce, and we invariably worked well below this range. Finally, in order to make sure that no instrumental artifacts were producing the rather unexpected sharp sensitivity changes in our records, on one occasion we removed all of the components for automatic data collection and laboriously substituted for their functions by varying sound intensity and collecting data by hand. Prior to this test we had collected data over a complete sphere using the automatic set-up. Text-fig. 4 shows a comparison of the manual and automated runs. There is no significant difference between these two records except that values between the 5° steps which are present in the automated record...
are missing in the manual record, and consequently the manual record gives a misleading picture of the sensitivity variations.

On rare occasions we had to change from the normal criterion of two to three spikes per pulse to some higher criterion (e.g. five spikes per pulse) as the preparation deteriorated. This brought up the question of whether different criteria would produce qualitatively different patterns of sensitivity. We found that records taken using different criteria of response level were identical in form, within experimental error, except that higher-criterion records required uniformly more intense sounds throughout a run.

The subjects. Many specimens were tested but only twelve preparations survived long enough to yield one or more complete ‘spheres of sensitivity’ for given wing positions. The small size of this effective sample is due to the complexity of the method and to the large amount of data needed before a run could be said to have yielded significant information. However, the detail provided by successful ‘spheres’, the general consistency between ‘spheres’, and the agreement between fragmentary and complete ‘spheres’ seem to justify this small number of subjects.

Numerous noctuid species were tested during preliminary work, but it was found that only large-bodied insects would survive the desiccation inevitable during a run. Accordingly, noctuids of the genera *Catocala* and *Euparthenos* (red underwing moths) proved to be the best subjects and have provided the projections discussed below. Fragmentary data from smaller noctuids indicate similar general patterns of acoustic directionality.

Specimens of *Catocala* and *Euparthenos* were collected, usually singly, in a light trap. They were tested as they became available and subsequently identified. Consequently not all individuals are of the same species. Only a few casual observations have been made of the evasive behaviour of these large and less common noctuids, but there is no reason to believe that it differs from that of smaller and more common noctuids (Roeder, 1962, 1964). *Catocala* species are indeed caught and eaten by bats (Webster, 1962), and are therefore subject to this form of selection pressure.

The positions in which the wings were set for each run are obviously only gross approximations to natural angles of attack assumed by the wings in free flight (Pl. 1).
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There seemed to be no way of avoiding these approximations of wing position and body angle, yet they must be recognized in assessing the results.

Limiting circumstances. Every effort was made to keep each run internally consistent, that is, to maintain the preparation and acoustic conditions constant during the collection of data for a tympanic organ at a given wing position. However, various factors made it impossible to make reliable comparisons of the overall values of sensitivity obtained on different runs. These included gradual deterioration of the tympanic nerve preparation and a temporary increase in acoustic sensitivity by as much as 10 db. that occurred frequently when the preparation was bathed with saline between runs. Therefore, overall differences in sensitivity between right ear and left ear of the same moth, or between runs made at different wing positions, cannot be read from the results. For the same reason, no attempt has been made to express the acoustic sensitivity in absolute units, the decibel values given being an expression of acoustic sensitivity to ultrasound coming from one angle relative to sensitivity at another as measured during a given run. As long as one keeps to relative intensity differences our estimated accuracy is ± 2 db. for data at any given wing position with a given moth.

The echo-locating cries made by insectivorous bats are usually frequency-modulated, dropping by about one octave from beginning to end. Their range is commonly from more than 80 kcyc./sec. to less than 40 kcyc./sec. It did not seem wise to introduce frequency modulation of the signal into an experiment already acoustically as complex as this. Accordingly, most of the measurements were made using a pulse having an unmodulated frequency of 60 kcyc./sec. One set of measurements employed a pulse frequency of 30 kcyc./sec. (Pl. 2). As might be expected, this longer wavelength revealed fewer discontinuities in the moth’s field of directional sensitivity.

RESULTS

Data sufficient to reconstruct one or more ‘spheres of sensitivity’ were obtained from the following species: Catocala ultronia (1 ‘sphere’), C. piatrix (3 ‘spheres’), C. habilis (2 ‘spheres’), C. retecta (2 specimens, 1 and 3 ‘spheres’), C. unijuga (3 ‘spheres’), C. palaeogama (2 specimens, 6 and 12 ‘spheres’), Euparthenos nubilis (1 ‘sphere’), Amphipyra pyramidoides (2 specimens, 1 ‘sphere’ each) and an unidentified noctuid (2 ‘spheres’). When a specimen survived long enough to obtain data for more than one ‘sphere’ these were obtained at different wing positions. Some specimens lasted for as long as 9 hr., and in one case (C. palaeogama) for 14 hr.

Considerable thought was given to the representation in two dimensions of data describing a situation in three dimensions. Much time and effort was expended in constructing three-dimensional wax models in which the length of the radius to any point on the sculptured surface was proportional to the acoustic sensitivity at that point with reference to the axis of the moth’s body (the moth imagined as being at the centre of the ‘sphere’). Whereas these wax models are helpful when viewed directly, they are able to convey little information when seen in the two dimensions of a printed page. Therefore, for the purposes of this account it was decided to display the data as Mercator projections, even though these are inevitably subject to considerable distortion near the poles.

Data on relative sensitivity (in db.), recorded for a ‘sphere’ of speaker placements
at some wing position, were entered on a large grid ruled in latitude and longitude lines 10° apart. Entries were made at each intersection on the grid unless brief sensitivity changes of greater than 1 db. occurred between the intersections, in which case such changes were entered where they occurred (to the nearest 1°). This provided about 500 data points per chart. Contour lines were then drawn so as to enclose all sensitivity values lying within 5 db. of each other, and the area between a given pair of contour lines tinted a shade of grey (from white to black) corresponding to relative sensitivity. Thus, to get the same response from a moth's acoustic nerves, a given sound source would need to be much closer to the moth when directed from black regions than it would when directed from white regions. It must be repeated that all sensitivity values are relative, and have not been calculated in absolute units.

At 0° horizontal and 0° vertical on the Mercator projections the sound comes directly at the moth from in front of the body, parallel with its body axis (the moth is flying directly towards the reader from behind the plane of the paper). In the centre of each projection a diagrammatic silhouette of the moth is shown facing the viewer. In this the moth's wings are indicated in the position at which they were held during the run. Sounds coming from the moth's right side and in the equatorial plane are thus at 90° horizontal; from behind it, 180° horizontal; and, from its left side, 270° horizontal. A sound directly above the moth is at 90° vertical; a sound directly below at 270° vertical (270° vertical was never quite reached because the loudspeaker collided with the tower supporting the moth before this point).

Our decision to draw the projections so that the moth faces the viewer was, in some respects, a poor one. When a moth turns and flies away from a source of ultrasonic pulses it stabilizes its course only when sounds come from directly behind it. Thus in order to make the graphs most interesting from a behavioural viewpoint it would perhaps have been better to show 180° horizontal at the centre of the charts and 0° at the borders.

If one neglects the fine detail and considers only in broad outline the sensitivity gradients revealed by these charts, then two major points emerge.

(1) When the wings are at the top of their beat they interfere minimally with the acoustic directionality of each ear (compare Pl. 2 A, wings up, with Pl. 2 C, minus wings). At this instant during flight each ear is less sensitive (by 30–40 db.) on its contralateral side as compared with its ipsilateral side. This region of hearing loss is slightly above the horizontal and at right angles to the moth's body axis, and is quite sharply defined as compared with the region of maximal sensitivity similarly located on the ipsilateral side. This means that in a binaural moth a given ultrasonic pulse arriving at right angles to the body axis would generate a substantial differential in the tympanic nerve volleys reaching the moth's central nervous system (Roeder, 1964). This will be called the left–right asymmetry.

(2) As the wings move downwards during a stroke (Pls. 2 B, 3 C and 4 C) the contralateral region of low sensitivity appears to move across and above the body axis of the moth, while at the same time the region of high sensitivity appears to move forward to a position in front of and below the body axis. There is a comparable but less pronounced change behind the moth. As the wings beat downwards the region of greatest sensitivity moves to a position below the horizontal. This situation with the wings down will be called the dorsoventral asymmetry.
DISCUSSION

It is now worth considering how these two acoustic asymmetries, alternating with the wing attitude of a flying moth, might play a part in steering the 'turning-away' reactions shown by free-flying moths to a source of faint ultrasonic pulses. For the sake of simplicity let us assume that the moth flies a straight course except when making a turn.

**Horizontal localization.** The simplest situation to consider is that of a moth traveling at the same altitude but at right angles to the path of ultrasonic pulses coming from a distant source. Under these conditions it would experience a maximal difference between right and left tympanic nerve volleys each time its wings moved through the upper half of their stroke. When in this position relative to the source a moth would also have maximum ultrasonic range, and it is also the attitude in which a flying moth could be most readily detected by a still distant bat (Roeder, 1963). A simultaneous comparison of right and left tympanic nerve signals at this moment of maximum left–right asymmetry should enable the moth to change course.

A course change of 90° would bring the moth on to a bearing either directly away from or directly towards the source, for in either case signals from the two tympanic nerves would tend to equalize. It is worth noting that either bearing would provide the moth with acoustic crypsis since both would reduce its 'acoustic profile' to a distant bat (Roeder, 1963). However, moths have always been observed to fly away from a distant source, and never towards it (Roeder, 1962). This change of course is seen to be accompanied by a few rapid twists and turns, although subsequently it is often surprisingly straight. It seems reasonable to suppose that this brief 'hunting' serves to discriminate between the two courses, for a right yaw sensed while the wings were up would increase the tympanic spike differential in favour of the left ear if the moth was approaching the source, and in the right ear if the heading was approximately away from the source.

Assuming the situation as we have analysed it, the programme in the moth's central nervous system that would meet all situations in the horizontal plane would be as follows. If a turn to one side produces a relative increase in the nerve signal reported by the ear on that side, reverse turning direction until both ears are equally stimulated; if a turn to one side produces a relative decrease in the nerve signal reported by that side, continue turning past the region of maximum binaural disparity and stop turning when both sides are equal.

It is readily apparent that the situation is least ambiguous to the moth when the sound source is directly to one side. It is not so obvious that a moth's theoretical accuracy is greatest when the predator approaches from in front or from behind. It has been suggested (Roeder, 1964) that the neural differential that steers these orientations to faint ultrasonic pulses is the spike generation time in the A cells (longer at lower intensities). If this is true it should be a more difficult task for a moth to chart an accurate course at right angles to a bat than towards it or away from it. In the first case (at right angles) some constant delay between first A1 spikes from each ear must be maintained (the moth's central nervous system must be able to judge accurately a set time interval, e.g. 0.9 msec., and therefore some sort of clock is a necessity). In the second case the moth needs no ability to estimate time delays; it can
simply steer until there is ‘no’ delay between first A1 spikes from each ear by correcting its course whenever there is ‘some’ (unspecified) delay. This situation was first described by Mills (1958) for acoustic localization by humans and has been further discussed by Schwartzkopff (1962) in considering the acoustic orientation of owls.

Our data indicate that a one-eared moth could conceivably locate a sound source in the horizontal plane, although it could not find a course directly away from it. If it flew so as to minimize the intensity of sounds reported by the single ear it would tend to circle the source. Treat (1957) has shown that certain noctuid species are subject to the destruction of one ear, but never of both, by certain parasitic mites. This suggests that there is some selective advantage to this compromise between the parasites and their host in not destroying both ears. Thus, though a one-eared moth might be at some disadvantage vis-à-vis a distant bat, it would still be better off than a moth lacking both ears, particularly at close quarters, since in the presence of ultrasound of high intensity the evasive reactions of flying moths contain no directional component related to the position of the sound source (Roeder, 1962).

**Vertical localization.** The right–left asymmetry already discussed must alternate with dorsoventral asymmetry during each cycle of wingbeat. Whereas in assessing right–left asymmetry the moth’s central nervous system may make an almost simultaneous comparison of the impulse pattern delivered by the two ears, in dorsoventral asymmetry there must be a serial comparison of the signals received from both ears at different phases of the wing stroke.

Inspection of the projections shows that, while both ears are affected by wing position, the acoustic ‘flicker’ at wingbeat frequency must be more pronounced in the near-side ear. The wings when ‘down’ probably serve as acoustic baffles, briefly obscuring the right–left asymmetry and replacing it with greatly reduced sensitivity to sounds coming from above. This alternation of acoustic asymmetry must take place at the wingbeat frequency of the flying moth, perhaps 30 or 40 times a second.

Observations of the habits of bats and moths suggest that commonly, though by no means invariably, the predators cruise above their prey. The ultrasonic cries of a bat approaching from above must thus appear to ‘flicker’ at the moth’s wingbeat frequency, being louder by as much as 25–30 db. when the wings are up. This could steer the moth if it triggered a dive that continued until the signals ceased to flicker (source behind), at which point the horizontal mechanisms already discussed could take over. If a bat approached from below, the maximum signal would be detected in both ears when the moth’s wings were down, and, if this phase relation between wing position and loudness triggered a climb followed by orientation in the horizontal plane, the moth would once more be on course upward and directly away from the source.

A certain amount of ‘hunting’, this time taking the form of pitching, might be expected to accompany changes of course in the vertical plane if the moth did not attend to whether the moments of greatest intensity in a flicker occurred with wings up or down. In this case determination of a course away from a bat flying at a different altitude from the moth but in front of or behind it could be made by the following programme. Pitch slightly, and if this brings intensities in both ears nearer to the
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same value at all wing positions, continue in this direction of pitch until the intensities are the same for all wing positions and then maintain course; if the pitch increases the acoustic 'flicker' at wingbeat frequency, pitch in the opposite direction and continue until both ears report the same intensity. Similar commands might be described to control rolls, but since rolls do not change the moth's flight direction unless executed as part of a lateral turn they will not be considered further.

If such programmes as these are actually followed, the system requires at least two types of information. First, there must be discrimination of differences in pulse intensity reported by the A1 receptors from the two ears. Such differences have been demonstrated (Roeder & Treat, 1961), and seem to be contained functionally in the difference in arrival time at the central nervous system of the first impulse of a succession of volleys generated in the A1 sense cells of the right and left ears. The change mentioned above in A1 spike generation time is most pronounced at very low sound intensities. This information is, of course, reiterated a number of times only when the sound is pulsed, as in bat cries. This is confirmed by behavioural observations that 'turning-away' in free-flying moths is reduced or absent if the sound intensity is high or if the artificial pulse sequence is replaced by a continuous tone (Roeder, 1964). Secondly, the moth's central nervous system must receive information about wing position at least once per wing cycle. Since motor control of the indirect flight muscles of Lepidoptera is synchronous (Roeder, 1950) this information could be extracted from the patterning of motor nerve impulses dispatched to the indirect flight muscles. Furthermore, the wings and thorax contain numerous proprioceptors that might transmit this information. However, a more intriguing possibility is that this information is provided by the B cell, a large proprioceptor located within the tympanic cavity. The B cell can be driven at various discharge frequencies by metathoracic deformations of an amplitude commensurate with that occurring during normal flight movements (Treat & Roeder, 1959). On two occasions during the present study the B cell was observed to discharge once per wing stroke when the wings of the subject were made to oscillate by being brought into contact with the vibrating wings of another intact moth in stationary flight.

So far, this analysis has been based on the assumption that moths fly a straight course except when making definite turns, and it is probably too idealized and complex. The finer detail of a moth's flapping progress in free flight (Pl. 1) is marked by a series of minor yaws, pitches, and rolls. The gross course taken by free-flying moths is marked by circling and other manoeuvres. A relatively straight course is most frequently observed in moths flying at high speed away from a distant source of ultrasonic pulses (Roeder, 1962).

This erratic progress being the normal rule, a direct course away from a bat could be achieved if a moth merely began 'hunting' randomly on becoming exposed to a source of faint ultrasonic pulses. If the moth continued to do this until the signals were balanced from both ears and were unmodulated by its own wing movements it would end up on a course away from the source. Since flapping flight inevitably causes minor perturbations of the course the only course the moth could consistently follow under these circumstances is one with the sound source behind it, since it is only from this angle that the moth's sound field is fairly uniform and gentle in contour. By contrast, the steep contours in sound fields in front of and above the line of
flight might merely serve to alert the moth to sounds not coming from behind and thereby to trigger abrupt and random changes of direction.

An added complication to the assessment of the situation is the fact that the bat repeats its echo-locating cries from 10 to well over 100 times a second, and the moth flaps its wings perhaps 30 to 40 times a second. There is presumably no synchrony between these signals, so their interaction must be quite complex. The present study indicates that a moth, flying in complete darkness, has at its disposal the structural and sensory mechanisms necessary to take it on a flight path directly away from a still distant but vociferous bat. At the moment one can only speculate how or whether these mechanisms are actually used.

SUMMARY

1. Noctuid moths of several species were mounted at the tip of a tower of fine tubing in acoustic 'free space'. Recordings were made of the intensity of a brief pulse of ultrasound necessary to produce a constant tympanic nerve response for any angle of sound presentation relative to the moth's body axis. Such plots of intensity versus angle were made with the wings held in several postures approximating those assumed in normal flight.

2. The data indicate that sound intensity reaching the tympanic organ can vary by as much as 40 db. depending upon: (a) the position of a sound source relative to the moth's body axis, and (b) the position of its wings.

3. With wings above the horizontal plane each ear reports sounds c. 20-40 db. louder on the ipsilateral side than on the contralateral side. With wings below the horizontal, the lateral asymmetries are replaced by a dorsoventral asymmetry in which each ear reports sounds coming from below the body c. 10-25 db. louder than sounds coming from above.

4. Directional sensitivity plots at 60 kcyc./sec. are more complex than plots at 30 kcyc./sec.—as expected.

5. A theory is presented to explain how a moth could determine the direction of a sound source in three-dimensional space by comparing the intensity reports of both tympanic organs during a complete wing cycle.

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REFERENCES


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Directional sensitivity of the ears of noctuid moths


EXPLANATION OF PLATES

PLATE 1
Multiple-exposure photograph of a free-flying *Catocala* (sp.) taken in the field, showing a sampling of the wing positions assumed during normal flight.

PLATE 2
Directional sensitivity of the left ear of a single specimen of *Catocala palaeogama*. Sensitivity to the same 30 kcyc./sec. pulse coming from all points on the surface of an imaginary sphere enclosing the moth is shown by using different shades of grey for each 5 db. change in sensitivity. The darker the shade, the less intense would the sounds arriving from those directions (relative to the moth’s body axis) be reported by the moth’s tympanic organ (from white, 35-40 db.; to black, 0-5 db.). The sphere is shown here in Mercator projection. A silhouette of the moth flying out of the plane of the paper towards the reader shows the angle at which the moth’s wings were held during collection of data for this sphere.

The settings of the loudspeaker in the vertical plane are indicated by dashes along the vertical borders of the picture. Similar dashes along the horizontal borders merely indicate 10° intervals and do not necessarily show all horizontal readings entered on the chart (readings at intermediate points were entered when brief changes occurred that would otherwise be lost). A, Wings up; B, wings down; C, wings removed.

PLATE 3
Explanation as in Pl. 2 but with a test frequency of 60,000 cyc./sec. Three wing positions are shown and all data are from a single specimen of *Catocala palaeogama* (not the same individual used in Pl. 2).

PLATE 4
Explanation as in Pl. 2 but with a test frequency of 60,000 cyc./sec. and with the right ear being tested. All data from a single specimen of *Catocala unijuga*. 