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Echolocation in Bats: The External Ear and Perception of the Vertical Positions of Targets

Abstract. *Echolocating bats (*Eptesicus fuscus*) can perceive changes of as little as 3° of arc in the vertical angles separating pairs of horizontal rods. This acuity depends upon modification of sounds entering the external ear canal by the structures of the external ear. Deflection of the tragus degrades the acuity of vertical-angle perception from 3° to about 12° to 14°. The pinna-tragus structure produces a strong secondary echo of sounds entering the external ear canal, and the delay of this echo after the time when the sound directly enters the ear canal apparently encodes the vertical direction of a sound source.*

Bats (Microchiroptera) use a form of biological sonar called echolocation for orientation in the environment (*1*). They can perceive the size, shape, direction, distance, and velocity of objects by using acoustic images as a substitute for vision (*2, 3*). Acoustic information in sonar echoes (intensity, frequency, and time of occurrence) represents various target features to the bat (*3*) and the bat's auditory system processes these echoes to reconstitute spatial images of objects within the bat's brain (*4*). The perceptual operating range of echolocation by various species of insectivorous bats extends out to roughly 1 to 10 m for targets comparable in size to the flying insects on which these bats prey (*5*). Because perception of auditory space is such an important part of the bat's use of hearing, the mechanisms of sound localization in echolocation are likely to be highly developed and correspondingly more clearly observed in bats than in other kinds of animals where spatial perception is only one aspect of the use of hearing. We report here the results of experiments which show that echolocating bats can perceive the locations of sonar targets in the vertical plane with exceptional accuracy. Furthermore, the acoustic cues for vertical localization by bats may be more distinguishable and more experimentally separable than has been demonstrated in other mammals, including humans, perhaps as a consequence of their heightened significance in the bat's life.

Echolocating bats of the species *Eptesicus fuscus* (the big brown bat; family Vespertilionidae) were trained with the use of methods described in (*6*) to discriminate between two simultaneously presented pairs of horizontal brass rods (4 mm in diameter and 22 cm long) separated by vertical angles of different sizes. The rods were suspended in a plane located 44 cm from the bat by nylon monofilament wires 0.15 mm in diameter and the rods in the pairs were oriented to be perpendicular to the bat's "line of sight" from its observing position on an elevated platform. Each bat was trained to approach the pair of horizontal rods separated by the smaller vertical angle (positive stimulus) by moving forward a few centimeters onto one of two other elevated platforms located in the same directions as the pairs of rods. The bat received a piece of a mealworm (*Tenebrio* larva) offered in forceps as a food reward for its correct choice. Responses to the other pair of rods, separated by the larger vertical angle (negative stimulus), were not rewarded.

The smaller vertical angle was kept constant at 6.5°, and the larger angle was varied from an initial 40° down to 35°, 30°, 25°, 20°, 16°, 13°, 11°, 9.5°, 8.5°, 7.5°, and 6.5°. When each bat had learned to respond correctly to the 6.5° angle at a criterion of better than 90 percent correct responses for 50 consecutive trials, the larger angle was reduced to 35° and the experiment begun. For the larger vertical angles (negative stimuli) down to 13°, 30 trials were conducted for each bat before the arrangement was changed to the next smaller angle. For negative stimuli of 11° and smaller, 50 trials were conducted for each value. By pairing an angle of 6.5° with successively smaller angles from 40° to 6.5°, we could assess psychophysically the acuity of the bat's discrimination of vertical angles by the descending method of limits (*6*). Of the two bats which completed the entire experiment, one (bat a) had been blinded (enucleated) to prevent the possible use of visual cues in the discrimination.

The graph in Fig. 1 shows the performance of two bats on discriminations of a vertical angle of 6.5° versus angles from 16° to 7.5° (angular differences from 9.5° to 1.0°). The bats readily discriminated larger angular differences and proceeded smoothly through the descending method-of-limits procedure to the region near threshold performance indicated in Fig. 1. If we use 75 percent correct responses as an index of the limits of the bat's performance, we find that *Eptesicus fuscus* can discriminate vertical angles with an acuity of 3° to 3.5°. This compares well with an acuity of about 1.5° for discrimination of horizontal angles in a similar experimental procedure (*7*).

The mechanisms for perception of the vertical position of a sound source by humans appear to involve modifications imposed upon sounds entering the external ear canal by the external ear acting as a receiving antenna (*8*). Sound reflects in different ways from the ridges and folds of the external ear, depending upon the vertical angle of incidence of the sound.

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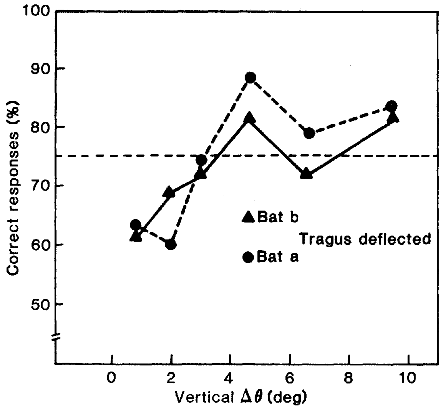

Fig. 1. A graph of the performance of two *Eptesicus fuscus* (bats a and b) discriminating a vertical angle of 6.5° from vertical angles from 16° to 7.5°. Using 75 percent correct responses as a threshold criterion, we find that the acuity of vertical angle discrimination is 3° to 3.5° of arc. The separated data points indicate the performance of the bats when the tragus of each of the external ears was deflected away from its normal position (see text and Fig. 2).

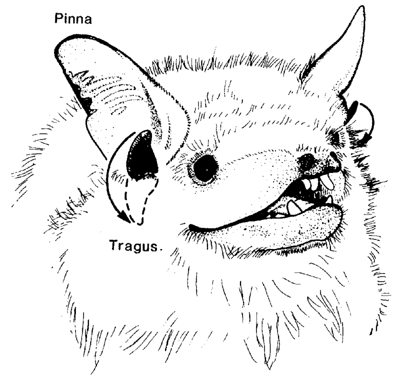

Fig. 2. Head of the bat *Eptesicus fuscus*, showing the pinna and the tragus of the external ear. The external ear canal is located behind the tragus, at the base of the horn-shaped pinna. In this experiment the tragus of each ear was deflected forward and down (arrow and dotted line) and then glued to the fur on the side of the head. The glue was dissolved and each tragus restored to its normal position for the last part of the experiment.

The time delays of these reflections at present seem to encode vertical direction in stimuli at the eardrum. It is not known, however, whether the time delay itself or the associated spectral modification of sounds actually comes to represent vertical direction within the auditory system. The external ear of *Eptesicus fuscus* appears much simpler in structure than the human ear; the multiple folds and ridges of the human ear are replaced by a large, horn-shaped pinna and a smaller blade-shaped tragus in this species of bat (Fig. 2). If the external ear contributes to vertical localization of sound sources by generating secondary reflections with angle-dependent delays that appear in stimuli at the eardrum, then it seems likely that pinna-to-tragus reflections serve this purpose in *Eptesicus*.

To assess the potential role of the external ear system in the vertical localization of targets by these bats, the tragus of each ear was bent forward, out of its normal position in front of the external ear canal, and glued with a cyanoacrylate adhesive (Duro Super Glue) to the fur on the side of the bat's head (Fig. 2). This deflection affected the entire length of the tragus and removed it as an obstacle that might otherwise slightly impede the arrival of sound at the external ear canal from a frontal direction, the only acoustic effect of the bat's tragus that, as far as we know, has yet been demonstrated (*9*). In this experiment we placed a few drops of the adhesive on the fur near the tragus and left it there for 1 day (to ascertain whether the glue itself was irritating and disturbed the bat's performance); we deflected and glued the tragus on the second day and again placed glue on the bat's fur with the tragus restored to normal on the third day. Each day we conducted 50 to 90 discrimination trials for each bat, using vertical angles of 6.5° (positive stimulus) and 11° (negative stimulus). After each day's experiment, the glue was removed with solvent (acetone). This discrimination task, at 4.5° angular difference, was chosen to be readily discriminable to the bat (Fig. 1) but near enough to the threshold of performance for any action that might adversely affect the acuity of vertical discrimination to yield noticeable changes in performance.

Figure 1 shows the performance obtained from each bat when the tragus of each ear was deflected forward. For bat a, 80 trials were conducted, yielding 59 percent correct responses with the tragus folded; for bat b, 65 trials were conducted, yielding 65 percent correct responses. On the day before the tragus was folded, bat a achieved 85 percent correct responses (89 trials) and bat b achieved 82 percent correct responses (50 trials). On the day after the tragus was folded, bat a achieved 84 percent correct responses (57 trials) and bat b achieved 78 percent correct responses (60 trials). From the curves in Fig. 1, bat a achieved 88 percent correct responses in the 50 trials carried out at an angular difference of 4.5° in the descending method-of-limits procedure and bat b achieved 82 percent correct responses. Using the threshold criterion of 75 percent correct responses (halfway between chance and perfect performance), deflection of the tragus substantially impairs vertical discrimination, whereas the presence of adhesive and general "poking around" on the tragus region just prior to conducting the discrimination trials had no observable effect upon performance. On the basis of statistical tests for two-choice data (*10*), the probability that bat a would score 58 percent correct by chance instead of 85 percent correct is less than 10^{-6}, and the probability that bat b would score 65 percent correct instead of 82 percent correct is less than 10^{-3}. If performance at an angular difference of 4.5° is depressed from about 85 percent to approximately 60 percent as a result of disturbance of the tragus, then the bat's acuity (75 percent correct threshold) would be altered from about 3° to approximately 12° to 14°, if we assume a simple straight-line extrapolation of the data. The bat's acuity is thus roughly four times worse. This may represent the ability of the bat to discriminate vertical directions of targets using echo cues other than those supplied by the tragus, such as the directional sensitivity of the ear caused by the pinna (*9*). It seems reasonable to conclude that the tragus functions to generate acoustic cues for determining the direction of a sonar target in the vertical plane. No more dramatic effect of its dislocation hitherto has been found, as far as we are aware.

We investigated the properties of the external ear of *Eptesicus fuscus* as a receiving antenna that introduces into sounds arriving at the eardrum acoustic information which represents the vertical direction of a target. The external ear of a bat that had died was separated from the bat's head along the plane of the eardrum and mounted on a condenser microphone (Brüel and Kjaer model 4135). The sounds arriving at the location of the eardrum after passage through the external ear system were observed on an oscilloscope. When this ear was "stimulated" with a broadband acoustic impulse consisting primarily of a peak 15 μsec wide generated from a specially constructed electrostatic loudspeaker (*11*), a strong reflection of this impulse was observed at the microphone 45 to 60 μsec after the arrival of the primary impulse through the external ear. This secondary reflection was produced in the bat's external ear, was greatly attenuated by removal of the tragus, and was strongly affected by the angle of incidence of the sound in the vertical plane. The reflection's delay was shortest for elevations of horizontal to 15° below the horizontal and was greatest for elevations substantially above or below the horizontal (30° to 45°, for example).

These acoustic observations suggest that a change in the location of the sound source over a vertical angle span from horizontal to 45° above or below the horizontal is associated with a change from 45 to 60 μsec in the delay of the external ear's secondary reflection after the primary impulse. Experiments on the ability of *Eptesicus fuscus* to perceive changes in the time of occurrence of echoes of sonar signals much like those emitted in this vertical angle experiment indicate an echo delay acuity of about 1 μsec (*12*). Since vertical angles spanning 45° are accompanied by external ear echo delay changes of 15 μsec, the bat ought to be able to perceive a vertical angle change of 3° if its 1-μsec, echo delay acuity applies to external ear echoes also. Thus, there is good correspondence between the vertical angle acuity demonstrated in Fig. 1 and the acuity expected if the external ear secondary reflection is, in fact, perceived as a delayed reflection of the sonar echo arriving directly at the ear canal.

Such a correspondence suggests that the tragus functions as a reflecting surface in generating acoustic cues for vertical localization of sonar targets by *Eptesicus fuscus*. The tragus produces a second, slightly longer path for sound to travel along to the ear canal, in effect simulating a second opening leading to the tympanic membrane. The neural mechanisms of vertical localization in this bat must involve cells specialized for responding to secondary reflections with delays of 45 to 60 μsec, and they may make up one of the many nuclei of the lower auditory system. It is not entirely clear what roles time- and frequency-domain representations of echoes play in vertical localization: does the auditory system "observe" the timing of nerve spikes to evaluate these reflections, or does it observe peaks and nulls in the composite spectrum of primary and secondary signals? The echo delay discrimination experiments (*12*) indicate that the former is likely.

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Type A Behavior and Elevated Physiological and Neuroendocrine Responses to Cognitive Tasks

Abstract. *Qualitatively distinct patterns of cardiovascular and neuroendocrine responses were observed in male college students during mental work and during sensory intake task performance. During mental work, Type A (coronary-prone) subjects showed greater muscle vasodilatation and more enhanced secretion of norepinephrine, epinephrine, and cortisol than Type B subjects. During sensory intake, Type A hyperresponsivity was found for testosterone and, among those subjects with a positive family history of hypertension, for cortisol. As a demonstration of combined cardiovascular, sympathetic nervous system, and neuroendocrine hyperresponsivity to specific cognitive tasks in Type A subjects, this study breaks ground in the search for mechanisms mediating the increased coronary disease risk among Type A persons.*

It is now generally accepted that the Type A behavior pattern is an independent risk factor for acute coronary events, and there is also extensive evidence that Type A persons show more severe and extensive coronary atherosclerosis on coronary arteriography (*1*). Studies of Type A persons documenting both cardiovascular and catecholamine hyperresponsivity to a variety of behavioral challenges have led to the hypothesis that such hyperresponsivity represents a mechanism for the expression of excess coronary events and atherosclerosis among Type A persons (*2*). Rarely are both cardiovascular and catecholamine responses assessed in the same study, and the secretion of other neuroendocrine substances in response to behavioral challenge among Type A and B subjects has not been assessed at all. Although available studies lack consistency regarding which response measures are enhanced among Type A persons, they, and not the Type B's, have been the ones to show hyperresponsivity. For example, during work on an impossible jigsaw puzzle in the presence of loud noise, Type A subjects showed excessive norepinephrine but not epinephrine secretion (*3*); during a competitive television "pong" game with harassment, however, they showed hyperresponsivity only in epinephrine secretion (*4*). Some studies of cardiovascular responses to behavioral challenge have found hyperresponsivity in systolic blood pressure, heart rate, or both among Type A subjects (*5*). These studies have used a wide variety of behavioral challenges with varying types of incentive and harassment.

Mason has proposed that a given neuroendocrine substance does not respond to a behavioral challenge in isolation but as one component of a broad array of multiple, concurrent responses; in addition, different types of challenge may elicit different patterns of neuroendocrine response (*6*). On the basis of Mason's suggestions (*6*), on theorizing by Lacey and Lacey (*7*), and on our findings of muscle vasodilatation during mental work behavior and muscle vasoconstriction during sensory intake (*8*), we have proposed that these two behaviors are associated with qualitatively distinct patterns of both cardiovascular and neuroendocrine response, and that enhanced expression of these patterns could explain the increased risk of coronary heart disease among Type A persons (*9*). Accordingly, we evaluated a broad range of cardiovascular and neuroendocrine responses among Type A and B subjects during mental arithmetic (mental work) and reaction time (sensory intake) tasks. The Type A subjects were hyperresponsive on both cardiovascular and neuroendocrine measures. The pat-