Hearing Sensitivity in Bats

Abstract. *Absolute hearing thresholds for two bats were determined by an operant conditioning technique. Pure tones ranging from 2.5 to 100 kilocycles per second were perceived by a single* Eptesicus fuscus. *Its maximum sensitivity was on the order of 68 decibles below 1 dyne per square centimeter and occurred at 20 kc/sec. Maximum sensitivity for a single* Myotis lucifugus *was about 64 db below 1 dyne/cm^2 and occurred at 40 kc/sec. The* Myotis *clearly heard a tone of 120 kc/sec but gave no evidence of hearing below 10 kc/sec.*

One hundred and seventy years ago Spallanzani (*1*) showed that vision was not necessary to the bat in the exploration of its environment. Since then it has become a commonplace that the auditory sense of the bat provides a fully satisfactory basis for spatial orientation. The bat successfully pursues and captures tiny, elusive insects and, in general, behaves as if it possesses a quite accurate and detailed auditory "picture" of the external world. The precision of this spatial information has been demonstrated many times (*1, 2*). Griffin, McCue, and Grinnell (*2*) presented evidence that the bat not only detects and utilizes echoes of its own cry reflected from very thin wires placed in its flight path but also is able to utilize information from the presumably weak second harmonics of its reflected cry. The impressiveness of this feat is not lessened by the fact that it can be performed even in the presence of very loud jamming noise. One might suppose from this that the hearing acuity of the bat is of an unusual sort. The following experiment, however, seems to indicate that, for continuous pure-tones, the absolute hearing sensitivity of the bats from which data were obtained is not at all superior to that of other mammals, including man.

Two bats were conditioned to respond in a certain manner in the presence of a pure tone and to respond in a different manner in the absence of a tone. By presenting tones of various frequencies and intensities it was possible to ascertain the signal intensity at which the ability to discriminate tone from no-tone broke down. In this manner a reliable estimate of the threshold sound pressure level (SPL) for each frequency was obtained.

The experimental procedure, apparatus, and calibration methods have been fully described (*3*). Two bats, a *Myotis lucifugus* and an *Eptesicus fuscus* of the family Vespertilionidae, were used as subjects. When these bats were sufficiently starved to bring about reliable performances in the conditioning situation, the *Myotis* weighed about 6 g, the *Eptesicus* about 17 g. Each had been taken from its place of winter hibernation and had been in captivity about 2 years at the time of testing. All conditioning sessions were conducted in an ambient temperature of 27° to 32°C.

The pure-tone frequencies presented to the bats were controlled to within 3 cycles by monitoring the oscillator output with an electronic counter. For the high frequencies an electrostatic speaker was employed; this speaker was capable of producing sound intensities in excess of 10 dyne/cm^2 over a range extending to 120 kc/sec when it was polarized with 300 volts and tuned with a variable inductor.

Continuous tones from the speaker, which was mounted outside an Industrial Acoustics double-walled, soundproof room, were led into the room by a plastic tube (inside diameter, 1.8 cm). Within the soundproof room, testing was conducted in a wire cage about 46 cm long. The open end of the sound tube was butted against one end of the cage. On the cage floor, about 8 cm from the end of the sound tube, was a small 0.9-cm-high metal platform, the listening platform.

To determine whether a given tone was heard, the following procedure was used. The bat was trained to place its front paws upon the listening platform in such a manner that it broke a photobeam from a light located above. This beam normally proceeded through a small hole in the platform to a photocell below. When the bat was in the "listening position," with its head or body breaking the beam, two conditions were fulfilled. (i) A test trial was initiated by means of an automatic programming system. (ii) The bat's position within the sound field was fixed. This permitted an accurate specification of the sound pressure level of the signal to which the bat was exposed.

Conditioning was accomplished by making reinforcement (a meal worm) contingent upon the bat's remaining in the beam for an unpredictable period of time while awaiting onset of the signal. At onset, and for 5 seconds thereafter, the bat could obtain a worm by leaving the listening position and crossing to the opposite end of the test cage to an automatic feeder. At other times food was not available in the feeder. The animal thus learned to wait and listen for a signal, and signified that it had detected the signal by responding only during a brief interval after onset of the signal. If

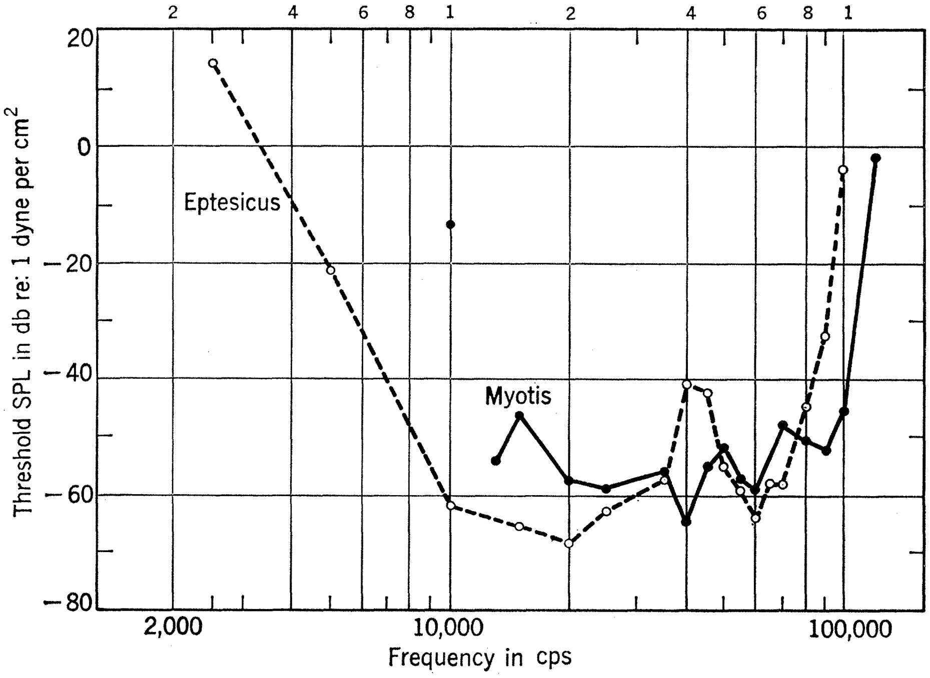

Fig. 1. Pure-tone thresholds for two bats. See text for explanation of unconnected point. *SPL,* sound pressure level.

the bat failed to leave the listening platform within the 5-second interval following onset of the tone, this signified that the tone intensity on that trial was below threshold. The conditioning method was used in conjunction with a descending method-of-limits psychophysical procedure. In this method the signal was presented in a series of decreasing steps ranging from "clearly detectable" to "undetectable." That is, the tone SPL was decreased by 10 db after each successful detection until a signal intensity was finally reached which was undetected. At this point, the SPL midway between the undetected signal and the immediately preceding detected signal was taken as an estimate of threshold for the series. The median of the threshold estimates obtained from six such series generally sufficed to determine the computed threshold for a daily session. Two daily sessions were usually sufficient to provide a reliable estimate of threshold SPL (*3*) for a given frequency.

Figure 1 represents data from two individual bats. The *Eptesicus* responded to tones of nondestructive intensity (that is, less than 15 db above 1 dyne/cm^2) between 2.5 and 100 kc/sec. The smaller *Myotis* responded to tones of less than 1 dyne/cm^2 from 120 down to 10 kc/sec. The data point representing 10 kc/sec is not connected to the other data points because the true threshold value at this frequency is uncertain. It was very difficult to obtain stable results from *Myotis* for frequencies below 15 kc/sec. The bat's responses became erratic in this frequency range, and many sessions were required to obtain usable data. For instance, at 10 kc/sec, 12 sessions were required to get two reliable data points. On ten of these sessions the bat's performance did not appear to be systematically related to sound intensity—that is, a histogram of within-session threshold estimates failed to peak sufficiently (*3*) at any central value. Peculiarities in the experimental system do not appear to be implicated, for no such difficulties occurred with *Eptesicus* in identical situations, or for that matter, with *Myotis* at higher frequencies.

An examination was made of the harmonic pattern present for a 10-kc/sec tone at a sound pressure level of 13 db below 1 dyne/cm^2 (the apparent 10-kc/sec threshold value). It was found that the SPL's of the second, third, and fourth harmonics were equal to, or slightly greater than, the respective threshold SPL's for these frequencies. This situation seems to imply that the bat may have been responding to the overtones and not to the fundamental frequency. Thus the true threshold value at 10 kc/sec may be even higher than that shown in Fig. 1. In an early conditioning session an attempt was made to determine the threshold for *Myotis* at 8 kc/sec, but there was no evidence that the bat could hear even at sound pressure levels up to 45 db above 1 dyne/cm^2.

These results indicate a sensitivity decrease of 40 db in approximately 1/7 of an octave—a rate of decrease of 266 db per octave. One might conjecture that the bat possessed some sort of "cut-off filter" of considerable sharpness. Unfortunately, the bat died before its cochlear potential sensitivity could be obtained, and, therefore, no accurate statement concerning its receptor capabilities can be made. However, if it is assumed that the functioning of the hair-cells of this bat is not very different from that of the bats in the *Myotis* population tested by Vernon and Wever (*4*), the evidence suggests a neural rather than a receptor origin for the presumed "filter action." This conclusion follows because Vernon and Wever clearly showed that the hair cells of *Myotis* respond to frequencies lower than 1 kc/sec.

The curve for *Eptesicus*, as shown in Fig. 1, displays two separate minimum threshold regions. One is a broad frequency range around 20 kc/sec, and the other is a fairly sharply tuned region around 60 kc/sec. The role of sharply tuned sensitivity maxima has been discussed (*4*); the chief utility of this tuning presumably resides in its capacity to diminish the masking effects of "noise" components from adjacent frequencies.

According to Griffin (*5*), the cry of *Eptesicus* during echo-location sweeps from 45 to 22 kc/sec while the bat is cruising and from 35 to 15 kc/sec during pursuit. Thus it is quite plausible that the maximum hearing acuity of *Eptesicus* should appear at about 20 kc/sec. The second sensitivity peak at 60 kc/sec may serve to maximize reception of a second harmonic component in the reflected echo. Although no data regarding the role of harmonics exist for *Eptesicus*, it has been shown (*2*) that another bat, *Plecotus townsendii*, does indeed utilize such information during echo-location.

The minimum threshold level for *Myotis* was obtained at 40 kc/sec. This is in accord with electrophysiologically determined sensitivity maxima previously reported (*4, 6*).

For both bats the absolute hearing threshold, over a very broad frequency range, was between 50 and 60 db below 1 dyne/cm^2. Within the margin of experimental error, this is of approximately the same order of magnitude as has been measured for man and other mammals over their respective regions of maximum sensitivity. If any difference exists it is in the direction of lesser sensitivity for the bats.

Grinnell (*6*) presented electrophysiological sensitivity data for *Myotis*. These measurements represented the N_4 sensitivity as recorded by gross electrodes in the posterior colliculus. The threshold sound intensities required to produce neural responses corresponded closely to the hearing thresholds for *Myotis* shown in Fig. 1.

Similarly, Vernon and Wever (*4*) presented measurements of the hair-cell sensitivity of *Myotis* as recorded by electrodes placed on the round window membrane. Here again, when compared with similarly derived data for several other mammals (*7*), the data for *Myotis* indicate a generally lesser absolute sensitivity at the receptor level.

Taken together, all these results provide little support for the notion that the precision of the bat's acoustically based orientation abilities is in any way related to superior absolute hearing acuity.

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References and Notes

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