# Audiogram of the big brown bat (*Eptesicus fuscus*)

Gimseong Koay *, Henry E. Heffner, Rickye S. Heffner

*Department of Psychology, University of Toledo, Toledo, OH 43606, USA*

Received 10 August 1996; revised 21 November 1996; accepted 22 November 1996

## Abstract

The audiograms of three big brown bats (*Eptesicus fuscus*) were determined using a conditioned avoidance procedure. The average audiogram ranged from 0.850 kHz at 106 dB to 120 kHz at 83 dB SPL, with a best threshold of 7 dB at 20 kHz and a distinct decrease in sensitivity at 45 kHz. The results confirm those of a previous study by Dalland (1965a) that the big brown bat has good high-frequency hearing coupled with poor low-frequency hearing. Comparative analysis suggests that the bat's good high-frequency hearing initially evolved for passive sound localization and that it was later coopted for use in echolocation. In addition, the restricted low-frequency hearing of the big brown bat is typical of mammals with good high-frequency hearing.

*Keywords:* Chiroptera; Evolution; Hearing; Mammal

## 1. Introduction

The fascination of auditory researchers with echolocation has led to the widespread study of auditory processing in echolocating bats (cf., Popper and Fay, 1995). Of those bats that have been studied, one of the most popular has been the big brown bat, *Eptesicus fuscus*. Two factors have contributed to this species' popularity — its abundance throughout much of North America and the relative ease with which it adapts to captivity.

A large number of studies have appeared concerning the auditory mechanisms of the big brown bat. Most of these have focused on the nature and acuity of its echolocation capabilities and the anatomical and physiological mechanisms underlying them (e.g., Obrist et al., 1993; Dear et al., 1993; Covey and Casseday, 1991; Moss and Schnitzler, 1989; Moss and Simmons, 1993; Masters et al., 1991). In contrast, little is known about the passive hearing abilities of the big brown bat, specifically its audiogram and sound localization ability. Indeed, our knowledge of its hearing range is based on the audiogram of a single animal (Dalland, 1965a).

* Corresponding author. Tel.: +1 (419) 530 2684; fax: +1 (419) 530 8479; e-mail: fac2622@uoft01.utoledo.edu

Moreover, there is some disagreement concerning its low-frequency hearing ability (Poussin and Simmons, 1982), a disagreement that is of theoretical significance.

The only complete audiogram of a big brown bat was obtained by Dalland (1965a) using a go/no–go procedure. The resulting audiogram, which ranged from 2.5 to 100 kHz, displayed two distinct regions of best sensitivity: first, a broad frequency range around 20 kHz and, second, a more sharply tuned region at 60 kHz. Hearing sensitivity then rapidly decreased for frequencies above 60 kHz and below 10 kHz. Of particular interest was the animal's low-frequency sensitivity — the lowest frequency audible to the bat at a level of 60 dB SPL (i.e., its 60-dB low-frequency hearing limit) was 3.7 kHz, making it notably insensitive to low frequencies when compared with other mammals (e.g., Heffner and Heffner, 1997).

More recently, however, it has been suggested that the big brown bat has better low-frequency hearing than was previously believed. Using a two-choice procedure, Poussin and Simmons (1982) determined the absolute thresholds for two bats for frequencies from 0.2 to 5 kHz. The results of their tests suggested that the big brown bat has a third region of sensitivity centered at 0.9 kHz and that their 60-dB low-frequency

limit is 0.2 kHz — over 4 octaves lower than that found by Dalland (1965a).

The low-frequency hearing ability of the big brown bat is of theoretical interest for three reasons. First, field observations have suggested that this bat uses the relatively low-frequency sounds of katydids (3.5–6 kHz) and frogs (3.2–4.5 kHz) as cues to areas containing prey (Buchler and Childs, 1981). However, the big brown bat's ability to seek out prey on the basis of such sounds obviously depends on its ability to hear them and knowledge of its low-frequency hearing is necessary to evaluate this possibility.

Second, the low-frequency hearing ability of the big brown bat has implications regarding the selective pressures involved in the evolution of hearing. Specifically, it has been shown that there is a general relationship between high- and low-frequency hearing, such that many animals with good high-frequency hearing show poor low-frequency hearing, and vice versa (Masterton et al., 1969; Heffner and Heffner, 1992a, 1997). Because the big brown bat can hear above 100 kHz (Dalland, 1965a), it would be expected to lack good low-frequency hearing.

Third, the shape of the audiogram obtained by Poussin and Simmons is unique in that it shows a large low-frequency peak of sensitivity centered at 0.9 kHz — a peak which occurs after thresholds increased by approximately 50 dB from the bat's best hearing at 20 kHz. Although peaks of sensitivity have been found in the high-frequency hearing range, no other mammal shows a low-frequency peak (Heffner and Heffner, 1992a, 1997). Thus, the presence of this peak would suggest that the big brown bat is under unusual selective pressure to hear frequencies around 0.9 kHz and that the mechanism for improving its low-frequency sensitivity may differ from that of other mammals.

In order to resolve the issue of low-frequency hearing in the big brown bat, as well as to verify other aspects of the big brown bat's audiogram, we assessed the absolute sensitivity of three animals using a conditioned avoidance procedure. Our results support the findings of Dalland (1965a).

## 2. Methods

The bats were tested using a conditioned avoidance procedure in which a hungry animal was trained to make continuous mouth contact with a reward spout in order to receive a steady flow of food paste (Heffner and Heffner, 1995). Signals were then presented at random intervals and followed by a mild electric shock delivered via the spout. To avoid the shock, the bat had to break contact with the spout. More importantly, this action indicated that the animal had detected the signal.

### 2.1. Subjects

Three wild-caught male big brown bats (*Eptesicus fuscus*) were used. The animals were individually housed with free access to water (supplemented with vitamins) and received a meal worm food paste during their daily test session. Additional supplements of meal worms were given as needed to maintain adequate body weight.

### 2.2. Behavioral apparatus

Testing was conducted in a carpeted, double-walled acoustic chamber (IAC model 1204; 2.55×2.75×2.05 m), the walls and ceiling of which were lined with egg-crate foam. The equipment for behavioral control and stimulus generation was located outside the chamber.

The animals were tested in a cage (37×22×23 cm) constructed of 0.5″ (1.26 cm) hardware cloth, mounted 70 cm above the floor on a tripod (Fig. 1). A food spout (2-mm-diameter brass tube topped with a 4×6 mm 'lick' plate) was mounted vertically so that it projected up through the bottom of the cage 6 cm above the cage floor. The spout was attached to a 10-ml syringe located below the cage that served as the food reservoir. A meal worm paste (consisting of a mixture of 40 meal worms, 1 tablespoon cottage cheese, and 2 tablespoons water, finely blended) was dispensed through the spout by a syringe pump similar to that described by Thompson et al. (1990).

During testing, the bats were placed on a small platform (10×6.5×6.5 cm) located directly behind the spout (see Fig. 1). The platform was covered with a 2-mm-thick dampened cellulose sponge to facilitate electrical contact. The tip of the food spout was placed approximately 5 mm below the front of the platform to minimize obstructions between the animal's ears and the loudspeaker. A contact circuit, connected between the food spout and platform, served to detect when an animal made contact with the spout and activated the syringe pump. Requiring the bat to maintain mouth contact with the spout fixed its head within the sound field. Finally, a constant current shock generator was connected between the food spout and platform, and a 15-W light mounted 0.5 m below the cage was used to signal the shock.

### 2.3. Acoustical apparatus

Sine waves were generated by a tone generator (Krohn-Hite 2400 AM/FM Phase Lock Generator) and calibrated daily with a frequency counter (Fluke 1900A). The signal was then sent to a rise-fall gate (Coulbourn S84), bandpass filtered (Krohn-Hite 3202, set 1/3 octave above and below the center frequency), and its intensity was adjusted with an attenuator
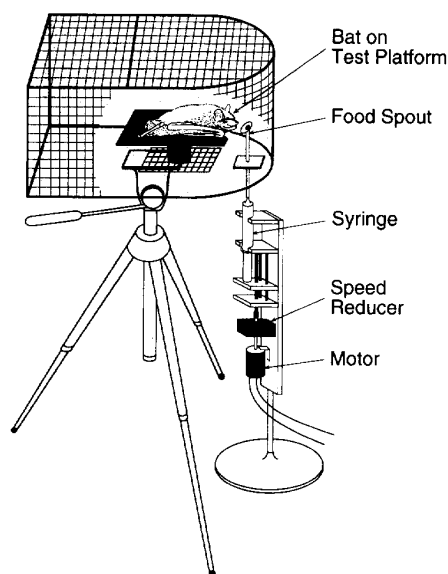
Fig. 1. Behavioral test apparatus. A meal worm food paste was dispensed from a syringe pump which was driven by a variable speed DC motor connected to a speed reducer (for details, see Thompson et al., 1990).

(Daven T-692-R). Finally, the signal was amplified (Adcom GFA545), monitored for both distortion and noise with an oscilloscope, and routed to a loudspeaker which was placed approximately 1 m in front of the cage and oriented toward the position of the bat's head (when the animal was eating from the spout) at an elevation of 0°. Four loudspeakers were used to present the different frequencies: for frequencies of 2 kHz and below, one of two 15″ (38-cm) woofers were employed, whereas one of two Foster ribbon tweeters were used to present frequencies of 4 kHz and higher. The loudspeakers were rotated on a regular basis to check for the possibility that a threshold might be influenced by the peculiarities of a particular speaker.

The tones were pulsed, 400 ms on and 100 ms off for 4 pulses, with a rise-decay of 10 ms for frequencies 2 kHz and above, and 20 ms for frequencies 1 kHz and below. In addition, thresholds for bats A and B were repeated at 500 Hz, 850 Hz, 1 kHz, 2 kHz, and 4 kHz using rapid tone bursts (100 ms on, 21 ms off, and 10 ms rise/fall for a duration of 2 s) as used by Poussin and Simmons (1982).

The sound pressure level (SPL re 20 μNewtons/m²) was measured daily with a 1/4″ (6.4 mm) microphone (Brüel and Kjaer 4135), microphone amplifier (Brüel and Kjaer 2608), and filter (Krohn-Hite 3202) set to pass 1 octave above and below the test frequency. The measuring system was calibrated with a pistonphone (Brüel and Kjaer 4230). Sound measurements were taken by placing the microphone in the position

occupied by the animal's head and pointing it directly toward the loudspeaker (0° incidence). Care was taken to produce a homogeneous sound field (within ± 1 dB) in the area occupied by the animal's head and ears when it was in contact with the spout. In addition, the linearity of the attenuator was checked by examining both the electrical and acoustical signals over the range of attenuations used in the tests.

As a precaution against the transmission of vibrations to the animals through the floor, both the 15″ woofer and the base of the tripod that held the test cage rested on 8-cm-thick acoustical foam. Furthermore, each frequency was examined daily for the presence of overtones using a spectrum analyzer (Zonic 3535). Care was taken to insure that any harmonics present were at least 40 dB below the fundamental frequency and at least 20 dB below the animal's threshold. This procedure was of particular importance when testing at 4 kHz and below.

### 2.4. Behavioral procedure

A hungry bat was trained to maintain mouth contact with the spout in order to receive a steady flow of food paste. Tones, presented at random intervals, were followed by a mild electric shock delivered between the spout and platform. The animal learned to avoid the shock by breaking contact with the spout whenever it heard a tone. The shock was adjusted for each animal to the lowest level that would reliably elicit an avoidance response. The mildness of the shock was attested by the fact that none of the animals developed a fear of the spout and readily returned to it after a shock had been delivered.

The bats were tested daily during the early evenings when they were normally active. Test sessions were divided into 2-s trials, separated by 1.5-s intertrial intervals. Each trial contained either a pulsing test tone or silence. The contact circuit was used to determine whether an animal was in contact with the spout during the last 150 ms of each trial. If an animal broke contact for more than half of the 150-ms period, a response was recorded. This response was classified as a hit if the trial had contained a test tone or as a false alarm if no tone had been presented. Each trial had a 22% probability of containing a test tone.

Both the hit rate and false alarm rate were determined for each block of 6–8 tone trials (which included ≈ 30 silent trials) for each intensity. The hit rate was corrected for false alarms to produce a performance measure according to the formula: Performance = Hit rate − (False alarm rate × Hit rate). This measure proportionately reduces the hit rate by the false alarm rate observed for each block of trials and varies from 0 (no hits) to 1 (100% hit rate with no false alarms).

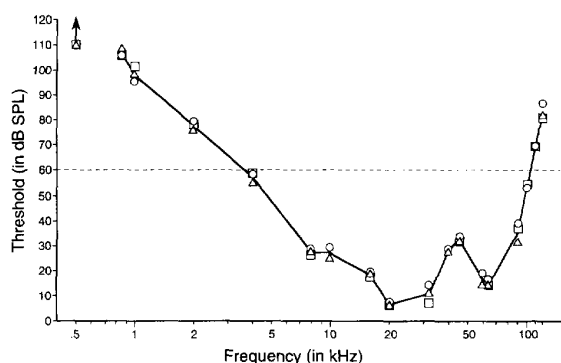Auditory thresholds were determined by reducing the

Fig. 2. Absolute thresholds of three big brown bats (symbols represent individual bats). Solid line indicates average thresholds for the three animals. Arrow indicates that the bats were unable to hear 500 Hz at an intensity of 110 dB SPL.

intensity of the test tone in successive blocks of 6–8 tone trials until the animal no longer responded to it above the level expected by chance ($P < 0.01$, binomial distribution). Once a preliminary threshold had been obtained for a frequency, final threshold determination was conducted by presenting test tones varying in intensity by 5 dB increments, extending from approximately 10 dB below to 10 dB above the estimated threshold. Threshold was defined as the intensity at which the performance measure equalled 0.50. For a particular frequency, testing was considered complete when the thresholds obtained in at least three different sessions were within 3 dB of each other. Once a complete audiogram had been obtained, each threshold was then rechecked to ensure reliability.

## 3. Results

The bats required approximately 30 sessions to adapt to the test procedure and learn to listen for low-intensity tones before they were producing reliable thresholds. In the course of training, we noticed that they would often freeze momentarily when the test tone was presented, but fail to break contact with the food spout. Learning to withdraw their mouths from the spout when the test tone was presented was perhaps the most time consuming aspect of training and required precise adjustment of the position of the food spout relative to the animal. Once trained, however, the bats were very reliable and a complete threshold for a single frequency could be achieved in a 1-h session.

Curiously, the bats had difficulty generalizing their performance to frequencies several octaves removed from the previous day's test frequency. That is, a bat would perform well on a new test frequency if that frequency was within an octave or two of the frequency it had been tested on the day before, but not if it differed by several octaves. This failure to generalize per-

sisted throughout testing and occurred during retesting in spite of the fact that the animal had been previously tested on each frequency. As a result, most testing was done by moving between adjacent frequencies. However, even when the change in frequency was large, an animal rarely required more than two practice sessions before it was once more producing reliable data.

Absolute thresholds were obtained at octave points from 1 to 64 kHz, with additional thresholds obtained at 0.850, 10, 20, 25, 35, 40, 50, 55, 60, 70, 90, 100, 110, and 120 kHz. The bats were unable to respond to 500 Hz at 110 dB SPL (the highest intensity which did not produce significant distortion).

The audiograms of the three bats show good agreement (Fig. 2). Beginning with an average threshold of 106 dB at 0.850 kHz, the three animals show a gradual improvement in sensitivity with their lowest threshold of 7 dB occurring at 20 kHz. Sensitivity declines rapidly above 32 kHz with a reversal occurring above 45 kHz resulting in a secondary peak of best hearing at 64 kHz. Above 64 kHz, sensitivity declines rapidly to a threshold of 86 dB at 120 kHz. At a level of 60 dB SPL, the hearing range of the bat extends from 3.7 to 104 kHz.

Once the audiogram had been completed, bats A and B were retested at 0.500, 0.850, 1, 2, and 4 kHz with rapidly pulsing 100-ms tone bursts in order to replicate the stimulus parameters used by Poussin and Simmons (1982). The thresholds obtained are shown in Table 1 where it can be seen that they did not differ from those for the 400-ms tone pulses used to obtain the complete audiogram.

It should be noted that special care was taken during low-frequency testing (2 kHz and below). First, the acoustic signal was examined with the spectrum analyzer before and after each session to ensure that there was no significant distortion. This ruled out the possibility that the animals were responding to overtones. Second, if an animal was unable to respond to a particular frequency, tones were presented at the next higher frequency to verify that the bat was still reliably responding to audible sounds. Despite a considerable amount of time spent testing at low frequencies, all three bats were unable to respond to 500 Hz, even at an intensity of 110 dB SPL.

Table 1
Average thresholds of bats A and B for two pulse durations

| Frequency (Hz) | Pulse length | |
|---|---|---|
| | 400 ms[a] | 100 ms[b] |
| 500 | No response | No response |
| 850 | 106 dB | 106 dB |
| 1k | 102 dB | 98 dB |
| 2k | 76 dB | 78 dB |
| 4k | 60 dB | 58 dB |

[a]400 ms on, 100 ms off, 20 ms rise-decay.
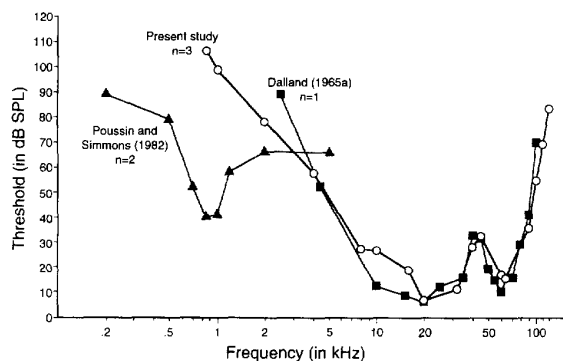[b]100 ms on, 21 ms off, 10 ms rise-decay.

Fig. 3. Average audiogram of the animals in this study (○) compared with audiograms obtained by Dalland (1965a) (■) and Poussin and Simmons (1982) (▲). n = number of animals tested in each study.

## 4. Discussion

Bats have a reputation for being more difficult to train than other mammals (e.g., Dalland, 1965a,b; Suthers and Summers, 1980; Riquimaroux et al., 1992), and compared with other animals we have tested, the big brown bats took longer to train to become reliable observers. For example, whereas rodents, such as the laboratory rat, naked mole rat, and fox squirrel can be trained within five to seven sessions (Heffner et al., 1994; Heffner and Heffner, 1993; Jackson et al., 1997), the bats took about 30 sessions before their thresholds became reliable.

Two factors may have resulted in the extra time needed to train the bats with the avoidance procedure. First, the initial response of a bat to a test tone was to freeze, that is, to stop eating without breaking contact with the food spout. Although this is not unusual, bats are not as mobile on the ground as rodents with the result that it took longer than usual to train them to retract their mouths from the spout. Second, it is a common observation that animals that have learned to respond to easily audible sounds still must be trained to respond to low-intensity sounds, i.e., they have to learn to listen. In this respect, the bats appeared to take longer than other animals before they began to respond to sounds within 20 dB of their eventual thresholds. Thus, the question arises as to whether the specialization of big brown bats for echolocation has somehow rendered them less responsive to other sounds in their environment.

In spite of the need for extra training, the results proved to be very reliable — the animals' thresholds were stable and easily replicated from day to day. Moreover, as noted below, the thresholds agree closely with those of a previously published audiogram (Dalland, 1965a).

### 4.1. Hearing in big brown bats

The audiogram obtained by the present study is compared in Fig. 3 with the complete audiogram obtained by Dalland (1965a) for a single big brown bat and the partial audiogram obtained for two bats by Poussin and Simmons (1982). As can be seen, our audiogram agrees with that of Dalland in all major respects. First, the hearing range of both audiograms is quite similar. Using the highest and lowest frequencies audible at a level of 60 dB SPL, our audiogram indicates a hearing range extending from 3.7 to 104 kHz while Dalland's showed 4.4–97 kHz — a difference of 1/4 octave at the low-frequency end and less than 1/8 octave difference at the high-frequency end. Although our audiogram shows slightly better sensitivity below 4 kHz than Dalland's, the difference is not large. Second, both audiograms show a frequency of best hearing at 20 kHz with thresholds for the individual animals ranging from 6 to 7 dB. Finally, both audiograms show a decrease in sensitivity at 40–45 kHz resulting in a second region of best hearing at 60–64 kHz. In short, there is good agreement between the two audiograms despite the fact that they were conducted in different laboratories, decades apart, and used different procedures.

Although we found slightly better low-frequency hearing than did Dalland, we were unable to replicate the low-frequency sensitivity found by Poussin and Simmons (1982) (see Fig. 3). Moreover, the difference could not be accounted for by the way in which the tones were presented as we obtained the same thresholds when the tones were pulsed rapidly, as was done by Poussin and Simmons (see Table 1). Although it is not possible to determine the reason for this discrepancy with certainty, we believe that it might be explained by the presence of overtones. Generating low frequencies at high intensities may result in distortion in the form of overtones that are audible to an animal even though the fundamental frequency is inaudible. Although the overtones are less intense than the fundamental frequency, an animal's hearing sensitivity is increasing sharply with frequency such that the overtones may be above threshold while the fundamental is below threshold.

Furthermore, we found that a loudspeaker that previously produced a relatively pure signal could develop significant overtones over time. Indeed, we began checking the spectrum of the sound both before and after each session when one bat showed a sudden improvement in sensitivity which turned out to be due the appearance of overtones — replacing that loudspeaker caused the animal's thresholds to return to their previous levels. Moreover, because no individual overtone was found to be above the animal's thresholds, it appeared that it was the combination of the near-threshold overtones that was audible to the bat. Although

Poussin and Simmons checked for the possibility of overtones, their results may have been affected by overtones which, individually, may have been just below threshold, but which taken together were audible to their animals. Whether or not that was the case, our ability to avoid such a problem is due largely to recent technical advances in spectrum analysis.

In conclusion, the big brown bat does not appear to hear well below 5 kHz, a fact which should be taken into consideration when assessing its use of environmental sounds to locate areas containing prey (Buchler and Childs, 1981).

### 4.2. Bats compared with other mammals

There are three questions regarding the hearing of big brown bats that can be answered by comparing it with that of other mammals. These are (1) whether its good high-frequency hearing is due to the use of echolocation or whether it is typical of mammals of its size, (2) whether its low-frequency hearing is unusually poor, and (3) whether the decrease in sensitivity at 45 kHz followed by a secondary peak of sensitivity at 60 kHz is unusual.

#### 4.2.1. High-frequency hearing

The high-frequency hearing ability of mammals exceeds that of any other group of vertebrates and, among mammals, bats have the best high-frequency hearing for airborne sounds (for a review, see Heffner and Heffner, 1997). However, the superiority of bats is one of degree, rather than kind, as a number of other mammals have high-frequency hearing limits which approach those of bats. Common examples are the Norway rat (*Rattus norvegicus*), domestic cat (*Felis domesticus*), and wild house mouse (*Mus musculus*), which have 60-dB upper limits of 72, 79, and 92 kHz, respectively, placing them within less than 1/2 octave of the big brown bat's 60-dB cutoff of 104 kHz (Heffner et al., 1994; Heffner and Heffner, 1985b; Heffner and Masterton, 1980). Moreover, high-frequency hearing in mammals, which ranges over more than 4 octaves, is not random, but appears to be determined by the requirements for sound localization.

The explanation for the variation in high-frequency hearing is that small mammals need to hear higher frequencies than larger mammals in order to localize sound using the binaural spectral difference and pinna cues (for reviews, see Heffner and Heffner, 1992a, 1997; Heffner et al., 1995; Masterton et al., 1969). Briefly, there are two binaural sound-localization cues, the difference in the time of arrival and the difference in the frequency-intensity spectrum of a sound reaching the two ears. For both cues, the magnitude of the binaural difference depends on the functional size of an animal's head. That is, the further apart the ears, the larger will

be the time and spectral differences in the sound reaching the two ears. Although both binaural locus cues are readily available to animals with large heads, their effectiveness is diminished in animals with close-set ears. However, a small animal can increase the magnitude of the spectral difference cue available to it if it is able to hear frequencies that are high enough to be effectively shadowed by its head and pinnae. Thus, the smaller an animal's head, the higher it must hear in order to obtain a usable binaural spectral-difference cue.

High-frequency hearing is equally important for using the pinnae to localize sound. Briefly, a pinna acts as a directional filter which modifies the spectrum of a sound reaching the ear drum as a function of the location of the sound source (e.g., Musicant et al., 1990; Phillips et al., 1982). This directional effect is not only useful in enhancing an animal's ability to pick out signals embedded in a noisy world (e.g., Middlebrooks and Pettigrew, 1981), but it also provides an important cue for localizing sound. Indeed, the pinnae provide the main cues for localizing sound sources that are away from an observer's midline and for preventing front-back reversals (Heffner et al., 1996). However, the effectiveness of the pinna depends on the wavelength of the sound relative to the size of the pinna. Because low frequencies are not attenuated by the pinnae, it is necessary for animals to hear high frequencies in order to use pinna cues (e.g., Jen and Chen, 1988; Musicant and Butler, 1984; Obrist et al., 1993). Just how high they must hear depends on the size of the animal's head and pinnae. Thus, small mammals need to hear higher frequencies than larger mammals in order that their pinnae may provide useable locus cues.

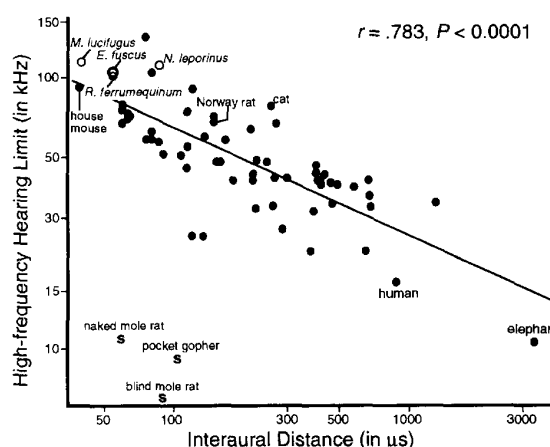The existence of a relationship between the size of an



Fig. 4. High-frequency hearing limit (highest frequency audible at 60 dB SPL) as a function of interaural distance (the number of μs required for a sound to travel from one auditory meatus to the other) for 63 mammals. Mammals with small interaural distances, including bats, hear higher frequencies than larger mammals. Subterranean rodents (s) are not included in the correlation (see text).

animal's head and high-frequency hearing was first described nearly 30 years ago (Masterton et al., 1969) and has remained strong as the sample size has tripled in the ensuing decades. This relationship is illustrated in Fig. 4, in which head size, or, more precisely, interaural distance, is defined as the time it takes for sound to travel around the head from one ear to the other. As can be seen, mammals with small heads and close-set ears are able to hear higher frequencies than species with large heads and generally larger pinnae ($r = -0.78$, $P < 0.0001$, excluding subterranean species). That mammals use their high-frequency hearing to localize sound is indicated by the fact that removing frequencies above 10 kHz (the maximum upper hearing limit of non-mammalian vertebrates) can degrade the ability of an animal to use binaural spectral difference and/or pinnae locus cues (Heffner and Heffner, 1992b; Heffner et al., 1995).

The high-frequency hearing of bats does not differ significantly from that expected based on their functional head size. Although the big brown bat falls above the regression line, indicating that it hears slightly higher than predicted, the deviation is not significant ($t = 1.38$, $P = 0.1712$). Indeed, the four bats in Fig. 4 help make the correlation as deleting them from the sample lowers the correlation from 0.783 to 0.755. Thus, it can be argued that the ancestors of bats evolved good high-frequency hearing for use in passive sound localization and that this ability was then coopted for use in echolocation.

Although the high-frequency hearing of bats is not unusual, it can be seen in Fig. 4 that there is one group of mammals that do not hear as high as predicted by

their functional head sizes. These are the subterranean species, the pocket gopher, blind mole rat, and naked mole rat, all of which lack good high-frequency hearing. However, not only have these animals lost the ability to hear high frequencies, but they have also lost virtually all ability to localize brief sounds (e.g., Heffner and Heffner, 1997). Evidently, animals that have adapted to the one-dimensional world of an underground habitat have little use for sound localization and are thus released from the selective pressure to hear high frequencies. The observation that animals that no longer localize sound lose their high-frequency hearing supports the idea the primary function of high-frequency hearing in mammals is to localize sound.

### 4.2.2. Low-frequency hearing

The variation in mammalian low-frequency hearing is even greater than the variation in high-frequency hearing. As indicated in Fig. 5, the 60-dB low-frequency limits for mammals ranges from 17 Hz for the Indian elephant (Heffner and Heffner, 1982) to over 10,000 Hz for the little brown bat (*Myotis lucifugus*; Dalland, 1965a), a range of over 9 octaves. By comparison, mammalian high-frequency hearing varies by less than 5 octaves.

There appear to be a number of factors related to low-frequency hearing, the most obvious being high-frequency hearing (Heffner and Heffner, 1985a). Specifically, there is a correlation between high- and low-frequency hearing such that mammals with good high-frequency hearing have poor low-frequency hearing and vice versa ($r = 0.793$, $P < 0.0001$). However, this relationship does not seem to apply to marine mammals
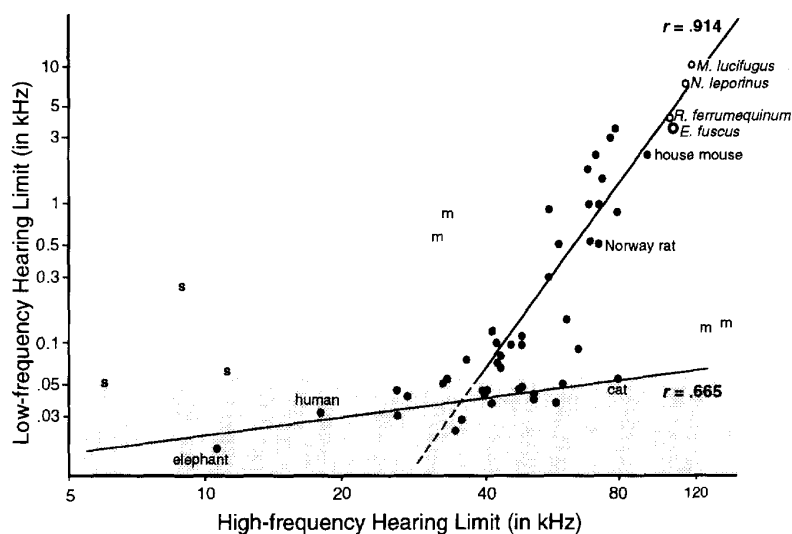


Fig. 5. Low-frequency hearing limit (lowest frequency audible at 60 dB SPL) as a function of high-frequency hearing limit (highest frequency audible at 60 dB) for 50 mammals. Correlation coefficient for all animals except marine mammals (m) and subterranean rodents (s) is $r = 0.793$ ($P < 0.0001$). Removing animals with low-frequency limits below 60 Hz (shaded area) raises the correlation to $r = 0.914$ ($P < 0.0001$, $n = 30$). The correlation for species with low-frequency limits below 60 Hz is $r = 0.665$ ($P = 0.0014$, $n = 20$).

and subterranean rodents, species that are adapted to acoustic environments very different from the aboveground environments of most mammals. Moreover, there appears to be a floor effect which changes the slope of the relationship for animals with very good low-frequency hearing (Fig. 5). Thus, when only animals with a 60-dB low-frequency hearing limit above 60 Hz are considered, the correlation coefficient rises to $r = 0.914$ ($P < 0.0001$). However, low-frequency hearing is still significantly related to high-frequency hearing in animals that hear below 60 Hz ($r = 0.665$, $P = 0.0014$). The main difference is that the slope of the relationship is much shallower suggesting the possibility that there is limited value in hearing 'infrasound'.

Bats are a good example of the relationship between high- and low-frequency hearing for animals with low-frequency limits above 60 Hz. As shown in Fig. 5, bats have extremely good high-frequency hearing coupled with comparatively restricted low-frequency hearing. Thus, the poor low-frequency hearing of the big brown bat is not unusual for a mammal with good high-frequency hearing.

### 4.3. Sensitivity at 45 kHz

Both the present results and those of Dalland indicate that the audiogram of the big brown bat has a distinct decrease or dip in sensitivity centered at 40–45 kHz (Fig. 3). Recent work by Simmons and his colleagues has indicated that the source of this dip may be the bat's external ear. Specifically, measurement of the transfer functions of the external ear of the big brown bat demonstrates a decrease in amplitude, i.e., a spectral notch, the center frequency of which varies from 30 to 50 kHz (Wotton et al., 1995). Because the center frequency of the notch varies systematically as a function of the elevation of the sound source, it is believed to play an important role in sound localization. Of particular relevance to the present study is the fact that behavioral results indicate that the frequency of this notch for a loudspeaker elevation of 0° is 45 kHz (Wotton et al., 1996). As our audiograms were conducted with the loudspeaker located at 0° elevation, our finding of a 45-kHz dip in sensitivity is entirely consistent with these results.

A survey of the audiograms of other bats indicate that some species possess similar dips in sensitivity while others do not. Specifically, the audiogram of the pale spear-nose bat (*Phyllostomus discolor*) shows a dip in sensitivity while that of the greater horseshoe bat (*Rhinolophus ferrumequinum*) shows two dips (Esser and Daucher, 1996; Long and Schnitzler, 1975). Species whose audiograms do not show a dip are the little brown bat (*Myotis lucifugus*), Indian false vampire (*Megaderma lyra*), and greater bulldog bat (*Noctilio leporinus*) (Dalland, 1965a; Schmidt et al., 1983;

Wenstrup, 1984). If such dips in sensitivity are related to sound localization, then it appears that there may be variation in the ways in which different species of bats localize sound.

## References

Buchler, E.G. and Childs, S.B. (1981) Orientation to distant sounds by foraging big brown bats (*Eptesicus fuscus*). Anim. Behav. 29, 428–432.

Covey, E. and Casseday, J.H. (1991) The monaural nuclei of the lateral lemniscus in an echolocating bat: parallel pathways for analyzing temporal features of sound. J. Neurosci. 11, 3456–3470.

Dalland, J.I. (1965a) Hearing sensitivity in bats. Science 150, 1185–1186.

Dalland, J.I. (1965b) Auditory thresholds in the bat: a behavioral technique. J. Aud. Res. 5, 95–108.

Dear, S.P., Fritz, J., Haresign, T., Ferragamo, M. and Simmons, J.A. (1993) Tonotopic and functional organization in the auditory cortex of the big brown bat, *Eptesicus fuscus*. J. Neurophysiol. 70, 1988–2008.

Esser, K.-H. and Daucher, A. (1996) Hearing in the FM-bat *Phyllostomus discolor*: a behavioral audiogram. J. Comp. Physiol. A 178, 779–785.

Heffner, R.S. and Heffner, H.E. (1982) Hearing in the elephant (*Elephas maximus*): absolute sensitivity, frequency discrimination, and sound localization. J. Comp. Physiol. Psychol. 96, 926–944.

Heffner, R.S. and Heffner, H.E. (1985a) Hearing range of the domestic cat. Hear. Res. 19, 85–88.

Heffner, R.S. and Heffner, H.E. (1985b) Hearing in mammals: the least weasel. J. Mamm. 66, 745–755.

Heffner, H.E. and Heffner, R.S. (1992a) Auditory perception. In: C. Phillips and D. Piggins (Eds.), Farm Animals and the Environment, C.A.B. International. Wallingford, UK, pp. 159–184.

Heffner, R.S. and Heffner, H.E. (1992b) Evolution of sound localization in mammals. In: D.B. Webster, R.R. Fay, and A.N. Popper (Eds.), The Evolutionary Biology of Hearing. Springer, New York, pp. 691–715.

Heffner, R.S. and Heffner, H.E. (1993) Degenerate hearing and sound localization in naked mole rats (*Heterocephalus glaber*), with an overview of central auditory structures. J. Comp. Neurol. 331, 418–433.

Heffner, H.E. and Heffner, R.S. (1995) Conditioned Avoidance. In: G.M. Klump, R.J. Dooling, R.R. Fay and W.C. Stebbins (Eds.), Methods in Comparative Psychoacoustics, Birkhäuser, Basel, Switzerland, pp. 79–93.

Heffner, H.E. and Heffner, R.S. (1997) Hearing. In: G. Greenberg and M. Haraway (Eds.), The Comparative Psychology: A Handbook. Garland, New York, in press.

Heffner, H. and Masterton, B. (1980) Hearing in glires: domestic rabbit, cotton rat, feral house mouse, and kangaroo rat. J. Acoust. Soc. Am. 68, 1584–1599.

Heffner, H.E., Heffner, R.S., Contos, C. and Ott, T. (1994) Audiogram of the hooded Norway rat. Hear. Res. 73, 244–247.

Heffner, R.S., Heffner, H.E. and Koay, G. (1995) Sound localization

in chinchillas. II. Front/back and vertical localization. Hear. Res. 88, 190–198.

Heffner, R.S., Koay, G. and Heffner, H.E. (1996) Sound localization in chinchillas. III. Effect of pinna removal. Hear. Res. 99, 13–21.

Jackson, L.L., Heffner, H.E. and Heffner, R.S. (1997) Audiogram of the fox squirrel (Sciurus niger). J. Comp. Psychol. 111, in press.

Jen, P.H.-S. and Chen, D. (1988) Directionality of sound pressure transformation at the pinna of echolocating bats. Hear. Res. 34, 101–118.

Long, G.R. and Schnitzler, H.-U. (1975) Behavioral audiograms from the bat, Rhinolophus ferrumequinum. J. Comp. Physiol. 100, 211–219.

Masters, W.M., Jacobs, S.C. and Simmons, J.A. (1991) The structure of echolocation sounds used by the big brown bat Eptesicus fuscus: some consequences for echo processing. J. Acoust. Soc. Am. 89, 1402–1413.

Masterton, B., Heffner, H. and Ravizza, R. (1969) The evolution of human hearing. J. Acoust. Soc. Am. 45, 966–985.

Middlebrooks, J.C. and Pettigrew, J.D. (1981) Functional classes of neurons in primary auditory cortex of the cat distinguished by sensitivity to sound location. J. Neurosci. 1, 107–120.

Moss, C.F. and Schnitzler, H.-U. (1989) Accuracy of target ranging in echolocating bats: acoustic information processing. J. Comp. Physiol. A 165, 383–393.

Moss, C.F. and Simmons, J.A. (1993) Acoustic image representation of a point target in the bat Eptesicus fuscus: evidence for sensitivity to echo phase in bat sonar. J. Acoust. Soc. Am. 93, 1553–1562.

Musicant, A.D. and Butler, R.A. (1984) The influence of pinnae-based spectral cues on sound localization. J. Acoust. Soc. Am. 75, 1195–1200.

Musicant, A.D., Chan, J.C.K. and Hind, J.E. (1990) Direction dependent spectral properties of cat external ear: new data and cross-species comparisons. J. Acoust. Soc. Am. 87, 757–781.

Obrist, M.K., Fenton, M.B., Eger, J.L. and Schlegel, P.A. (1993) What ears do for bats: a comparative study of pinna sound pressure transformation in Chiroptera. J. Exp. Biol. 180, 119–152.

Phillips, D.P., Calford, M.B., Pettigrew, J.D., Aitkin, L.M. and Semple, M.N. (1982) Directionality of sound pressure transformation at the cat's pinna. Hear. Res. 8, 13–28.

Popper, A.N. and Fay, R.R. (Eds.) (1995) Hearing by Bats. Springer, New York.

Poussin, C. and Simmons, J.A. (1982) Low frequency hearing in the echolocating bat, Eptesicus fuscus. J. Acoust. Soc. Am. 72, 340–342.

Riquimaroux, H., Gaioni, S.J. and Suga, N. (1992) Inactivation of the DSCF area of the auditory cortex with muscimol disrupts frequency discrimination in the mustached bat. J. Neurophysiol. 68, 1613–1623.

Schmidt, S., Turke, B. and Vogler B. (1983-1984) Behavioural audiogram from the bat, Megaderma lyra. Myotis, 21–22, 62–66.

Suthers, R.A. and Summers, C.A. (1980) Behavioral audiogram and masked thresholds of the megachiropteran echolocating bat, Rousettus. J. Comp. Physiol. 136, 227–233.

Thompson, M., Porter, B., O'Bryan, J., Heffner, H.E. and Heffner, R.S. (1990) A syringe-pump food-paste dispenser. Behav. Res. Meth. Instr. Comp. 22, 449–450.

Wenstrup, J.J. (1984) Auditory sensitivity in the fish-catching bat, Noctilio leporinus. J. Comp. Physiol. A 155, 91–101.

Wotton, J.M., Haresign, T. and Simmons, J.A. (1995) Spatially dependent acoustic cues generated by the external ear of the big brown bat, Eptesicus fuscus. J. Acoust. Soc. Am. 98, 1423–1445.

Wotton, J.M., Haresign, T., Ferragamo, M.J. and Simmons, J.A. (1996) Sound source elevation and external ear cues influence the discrimination of spectral notches by the big brown bat, Eptesicus fuscus. J. Acoust. Soc. Am. 100, 1764–1776.