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Hearing in a Megachiropteran Fruit Bat (*Rousettus aegyptiacus*)

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The Egyptian fruit bat (*Rousettus aegyptiacus*) is one of the few megachiropteran bats capable of echolocation. However, it uses rudimentary tongue clicks rather than laryngeally produced echo calls. We determined the audiogram of 2 bats using a conditioned avoidance procedure with fruit puree reward. At an intensity of 60 dB sound pressure level, the bats' hearing extended from 2.25 kHz to 64 kHz, with a region of good sensitivity between 8 kHz and 45 kHz. A dip in sensitivity at 32 kHz appears to be due to pinna directionality. The hearing of Egyptian fruit bats is typical for a mammal of that size and is not as limited as previously reported. Methodological issues, specifically training an animal to listen for low-intensity signals and imposing a significant cost for failing to report signals (i.e., misses), are discussed as the basis for the discrepancy between our results and earlier reports.

The Egyptian fruit bat, *Rousettus aegyptiacus*, is a megachiropteran bat from the Middle East and sub-Saharan Africa. Unlike other megachiropterans that do not echolocate, Egyptian fruit bats, as well as other members of its genus, roost in caves and possess an echolocation system that uses tongue clicks. Such a system is quite different from the laryngeally produced echolocation calls of microchiropterans and is believed to have evolved independently (Griffin, Novick, & Kornfield, 1958; Kulzer, 1956). Thus, Egyptian fruit bats provide an interesting contrast to the microchiropteran bats with their more sophisticated echolocation abilities.

Given the differences between the tongue click echolocation system of Egyptian fruit bats and the specialized constant-frequency and frequency-modulated echolocation calls of microchiropteran bats, the question arises as to whether such differences might also be reflected in their passive hearing abilities such as absolute thresholds. That this might be so was suggested by a behavioral audiogram showing this species to have an extremely narrow hearing range: for tones at 60 dB sound pressure level (SPL), the animals could only hear from approximately 4 kHz to 25 kHz (Suthers & Summers, 1980). Not only is such a narrow audiogram unprecedented among mammals, but it was accompanied by the poorest overall sensitivity yet observed in any mammal; even at the frequency of best sensitivity, 10 kHz, the threshold was no better than 44 dB.

Although such an audiogram has never before been seen in mammals, physiological evidence appeared to provide some support for the poor hearing reported by Suthers and Summers (1980). In particular, both the general insensitivity and the absence of good hearing above 30 kHz were supported by cochlear microphonic recordings (A. Brown, 1973) and by subsequent brain stem auditory evoked responses (Belknap & Suthers, 1982). On the other hand, recordings from the inferior colliculus of a closely related species (*R. amplexicaudatus*), although supporting the relative insensitivity, indicated much better high-frequency hearing and a region of maximum sensitivity at 50 kHz (Grinnell & Hagiwara, 1972).

Nevertheless, Suthers and Summers (1980) expressed concern regarding the validity of their audiogram for three reasons. First, the go/no-go procedure that they used was successful with only one of the six bats they attempted to train, suggesting that it was a difficult and perhaps inappropriate method for this species. Second, the authors noted that preliminary studies in their laboratory indicated electrophysiological responses in Egyptian fruit bats to frequencies above 30 kHz, responses that they were not able to elicit behaviorally. Finally, they suggested that the results, based on a single individual, could be anomalous.

The present study is a reexamination of the audiogram of Egyptian fruit bats using a conditioned avoidance procedure that has proved successful with a wide variety of mammals, including bats. The results of this study indicate that the reservations expressed by Suthers and Summers (1980) regarding the validity of their audiogram for Egyptian fruit bats were well founded; the two animals examined by us showed much better sensitivity and high-frequency hearing than previously reported. The following is a description of our results and a discussion of the factors that we believe account for the differences between the previous audiogram of Egyptian fruit bats and our audiogram. In addition, we address the question of how the decrease (or dip) in sensitivity of the bats at 32 kHz varies with loudspeaker elevation, an effect that could be due to the directional properties of the external ear that permit discrimination of the elevation of sound sources (Wotton, Haresign, & Sim-

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mons, 1995). Finally, we compare the hearing of Egyptian fruit bats with that of mammals in general.

Method

Two bats were tested using a conditioned avoidance procedure in which a hungry animal was trained to make continuous mouth contact with a reward spout to receive a steady flow of food puree. Signals were then presented at random intervals, followed by a mild electric shock delivered via the spout. To avoid the shock, the bat had to break contact with the spout, thereby also indicating that it had detected the signal. The audiogram was determined with a loudspeaker at 0° elevation throughout the animal's audible range. Absolute thresholds were determined at octave points ranging from 1 to 64 kHz; additional thresholds were obtained at 2.8, 5.6, 10, 12.5, 20, 25, 40, 45, 50, 56, and 71 kHz. Finally, thresholds for one bat were also obtained at an observed midfrequency dip, or decrease, in sensitivity centered at 32 kHz and two flanking frequencies (25 and 45 kHz); loudspeaker elevations ranged from 15° below to 30° above the horizon (at 0° azimuth).

Subjects

Two female Egyptian fruit bats (*Rousettus aegyptiacus*) were used in this study (an additional male bat was trained but failed to give reliable thresholds and was not subsequently tested). The animals were housed together in a flight cage and given free access to vitamin-supplemented water. While serving as subjects, the bats received their daily ration of food during the test sessions. Additional supplements of mixed fruit (cf. Barnard, 1995) were given as needed to maintain adequate body weight.

Behavioral Apparatus

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

The animals were tested in a cage (50 × 30 × 40 cm) constructed of 1-in. (2.5 cm) hardware cloth and raised 93 cm above the floor (Figure 1). A food spout (3-mm-diameter brass tube, topped with a 1 × 1.5-cm oval lick plate) was mounted vertically on an adjustable camera tripod so that it projected approximately 7.5 cm above the cage floor. The spout was attached to a 50-ml syringe (which served as the food reservoir) using an 80-cm long flexible tubing. Fruit puree (which consisted of a mix of banana, cantaloupe, grape juice, and vitamin supplement, finely blended and sieved) was dispensed with the 50-ml syringe using a syringe pump similar to that described by Thompson, Porter, O'Bryan, Heffner, and Heffner (1990). To eliminate the noise generated when the syringe pump was activated, both the syringe pump and food reservoir were housed in a plastic box (high-density polyethylene, 64 × 212 × 28 cm) lined with egg crate foam.

During testing, a bat mounted a small platform (31 × 14 × 8 cm) located directly behind the food spout. The tip of the food spout was approximately 0.5 cm below the front of the platform to minimize obstructions between the animal's ears and the speaker while it was eating from the spout. The platform was covered with a piece of carpet turned upside down and dampened to provide good traction for the animal and facilitate electrical contact as it ate from the spout. 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 also served to maintain its head in a fixed position within the sound field. In addition, a shock generator was connected between the food spout and platform. A 15-W light bulb, mounted 0.5 m below the cage, was turned on and off with the shock to signal a successful avoidance and to indicate when it was safe to return to the food spout.

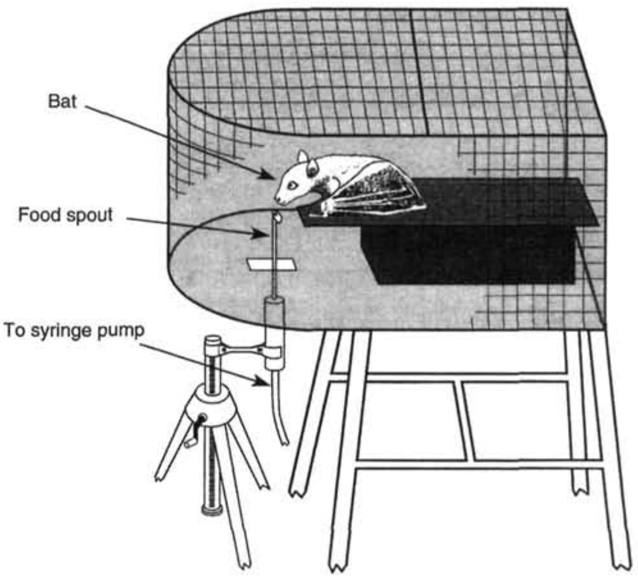


Figure 1. Test cage for *Rousettus aegyptiacus,* illustrating the position of a bat while listening for sounds and licking the food spout. To minimize reflective surfaces, the entire cage, including its floor, was constructed of wire mesh and supported on four thin legs.

Acoustical Apparatus

Sine waves were generated by a tone generator (Krohn-Hite 2400 AM/FM Phase Lock Generator, Krohn-Hite, Avon, MA) and continuously monitored using a frequency counter (Fluke 1900A, John Fluke Manufacturing, Seattle, WA). The tones were pulsed, 400 ms on and 100 ms off for four pulses. The signal was routed through a rise–fall gate (Coulbourn S84-04, Coulbourn, Lehigh Valley, PA) with rise–decay durations of 10 ms for frequencies of 2 kHz and above and 20 ms for the 1-kHz tone. The signal was then band-pass filtered (Krohn-Hite 3202, 24-dB/octave roll-off starting one-third octave above and below the center frequency) and its intensity adjusted with an attenuator (Hewlett Packard 350D, Hewlett Packard, Loveland, CO). Finally, the signal was amplified (Crown D75, Crown International Inc., Elkart, IN), monitored for distortion and noise with an oscilloscope (B & K Precision 1476A, Dynascan Corp., Japan), and sent to a loudspeaker. The loudspeaker was placed approximately 1 m in front of the cage at an elevation of 0° and oriented toward the animal's head when it was eating from the spout.

To determine the effect of elevation of the sound source and thus pinna directionality, thresholds for three frequencies—25 kHz, 32 kHz, and 45 kHz—were obtained at loudspeaker elevations of 0°, 20°, and 30° relative to the animal. Additional thresholds at 15° below and 15° above the horizon were also obtained at 32 kHz. Selection of the three frequencies for elevation thresholds were based on the obtained audiogram (i.e., the dip in sensitivity at 32 kHz and a frequency on either side of the dip at 25 and 45 kHz).

Various loudspeakers were used to present the tones: For frequencies 2.8 kHz and below, either a 12-in. (30.4 cm) or one of two 6-in. (15.2 cm) woofers (Infinity RS2000, Infinity Systems, Inc., Chatsworth, CA) were used, whereas for frequencies from 4 to 8 kHz, one of two ribbon tweeters (Foster 110T02, The Rank Organisation, London, England) or a piezoelectric tweeter (Motorola KSN1005A) were used. Frequencies above 8 kHz were presented using one of the two ribbon tweeters. The loudspeakers were rotated on a regular basis to eliminate any possibility that a threshold might be influenced by the peculiarities of a particular speaker.

The sound pressure level (SPL re 20 $\mu N/m^2$) was measured daily with a ¼-in. (0.64-cm) microphone (Brüel & Kjaer 4135, Brüel & Kjaer, Naerum, Denmark), preamplifier (Brüel & Kjaer 2619), filter (Krohn-Hite 3202, set to pass one octave above and below the test frequency, a two-octave band), and measuring amplifier (Brüel & Kjaer 2608). The measuring system was calibrated with a pistonphone (Brüel & 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.

Output from the speaker was examined daily for the presence of overtones or distortion by routing the output of the measuring amplifier to a spectrum analyzer (Zonic A&D 3525, Zonic Corp., Tokyo, Japan). When checking for harmonics, the filter (Krohn-Hite 3203) in the measuring system was opened to pass from 1 to 100 kHz. Special care was taken to reduce the possibility of significant harmonics, which often occur when generating low-frequency tones of high intensity, by choosing loudspeakers that produced signals relatively free from distortion. Subsequent testing demonstrated that any measurable harmonics were at least 40 dB below the fundamental frequency and at least 20 dB below the animals' thresholds and were, therefore, not a factor.

For calibrating the 25-, 32-, and 45-kHz tones at positions above and below the horizon, sound level measurements were taken with the microphone pointed directly at the loudspeaker. It should be noted that with the measuring microphone fixed and pointing at 0° elevation, moving the loudspeaker from $-15°$ to $+30°$ elevation resulted in a maximum intensity change of only 1 dB, as expected based on the directionality of the measuring microphone.

Behavioral Procedure

A hungry bat was initially trained to mount the platform and eat from the food spout. Requiring the bat to make mouth contact with the spout served to align it in the proper orientation to the loudspeaker directly in front of it at ear level and was necessary to activate the food pump to dispense a steady trickle of food puree. A train of four tone pulses (400 ms on, 100 ms off) was then presented at random intervals, followed at its offset by a mild electric shock (300 ms duration, $\leq$1.25 mA) 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 produce an avoidance response. Note that the animals did not develop a fear of the spout as they readily returned to it after the shock had been delivered.

The bats were tested daily during the early evening hours when they were normally active. Test sessions were divided into 2-s trials, separated by 1.5-s intertrial intervals. The intertrial intervals were interposed to slow the rate of trial presentation. Approximately 22% of the trial periods contained a pulsing tone (warning signal), whereas the remaining trial periods consisted of silence (safe signal). The contact circuit was used to detect 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 response period, a detection response was recorded. This response was classified as a hit if the trial had contained a tone (i.e., a warning signal) or as a false alarm if the trial had been silent (i.e., a safe signal). The hit rate and false alarm rate were then determined for each block of six to eight warning trials (and the approximately 30 associated safe trials) for each stimulus condition. The hit rate was then corrected for false alarms to produce a performance measure (H. E. Heffner & Heffner, 1995) according to the following formula: performance = hit rate − (false alarm rate × hit rate). This measure proportionately reduces the hit rate by the false alarm rate observed under each stimulus condition (i.e., 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 intensity of the tone in successive blocks of six to eight warning trials until the animal no longer responded to the warning signal above the level expected by chance (i.e., the hit and false alarm rates did not differ significantly; $p > .05$, binomial distribution). Once a preliminary threshold had been obtained for a frequency, final threshold determination was conducted by presenting tones varying in intensity by 5-dB increments, extending from 10 dB above to 10 dB below the estimated threshold. Threshold was defined as the intensity at which the performance measure equaled 0.50, which was usually obtained by linear interpolation. 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 an audiogram had been completed, each threshold was rechecked to ensure reliability.

Results

The bats, which had been trained to listen to broadband sounds in a previous localization test (Koay, Heffner, & Heffner, 1996), learned to respond to low-intensity tones and produced reliable thresholds after approximately 3 weeks of practice. Because of their feeding pattern, their 2-hr test session included pauses between bouts of feeding. In a typical session, they consumed 50 ml of pureed fruit (an amount equal to nearly half their body weight) and received approximately 70 to 80 warning tones and approximately 300 associated safe (i.e., silent) signals. Two threshold determinations for a single frequency were usually obtained per session.

The audiograms of the two bats are in good agreement with each other and show the same basic shape as other mammalian audiograms (Figure 2). Beginning with an average threshold of 81.5 dB at 1 kHz, the thresholds gradually improve to a point of maximum sensitivity of 4 dB at 10 kHz. The animals showed a relatively broad region of good sensitivity with average thresholds below 10 dB between 8 kHz and 25 kHz. Both bats demonstrated reduced sensitivity at 32 kHz (25-dB threshold) and a second region of good sensitivity centered at 45 kHz (13-dB threshold). Above 45 kHz, their hearing declined rapidly, reaching an average threshold of 78.5 dB at 71 kHz. At a level of 60 dB SPL, the hearing of Egyptian fruit bats extends from 2.25 kHz to 64 kHz, a range of 4.8 octaves.

The decrease in sensitivity at 32 kHz was reliable and quite marked; the thresholds at that frequency were 12 to 18 dB higher than thresholds at adjacent frequencies. Because it has been suggested that this reduction in sensitivity is due to the filtering characteristics of the pinnae (Wotton et al., 1995; Wotton, Haresign, Ferragamo, & Simmons, 1996), we obtained additional thresholds for one of the bats (Bat B) for

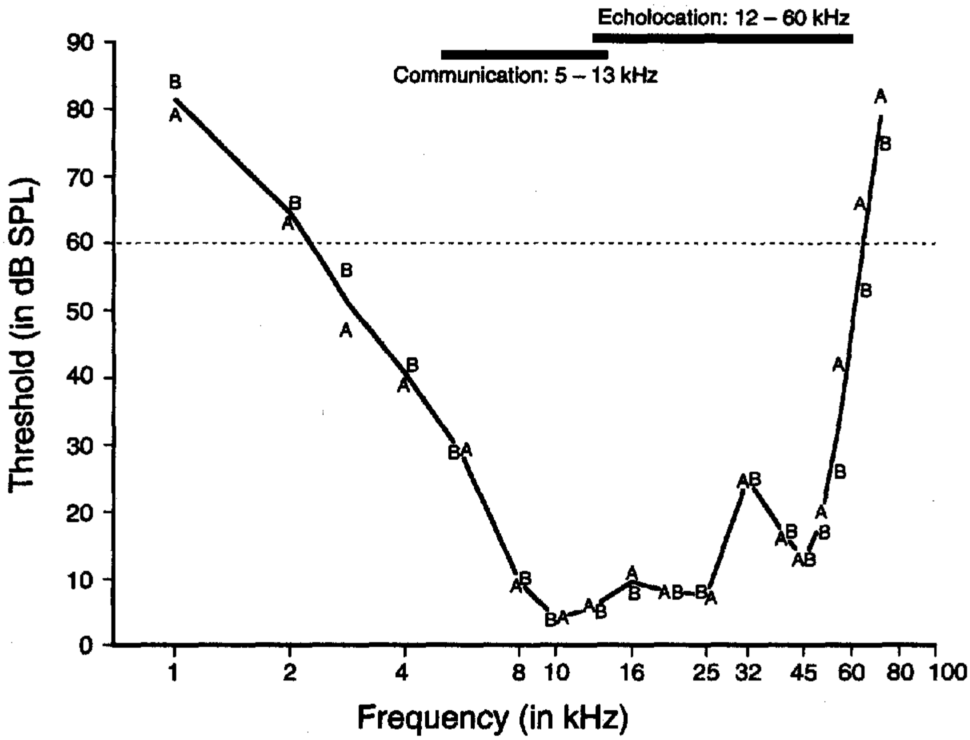


Figure 2. Audiogram for two Egyptian fruit bats (A and B represent individual bats, and the line indicates the average thresholds). The animals have good sensitivity between 8 and 50 kHz but show a region of reduced sensitivity at 32 kHz. Note that their communication and echolocation signals span most of their audible range (Suthers & Summers, 1980). SPL = sound pressure level.

25, 32, and 45 kHz at elevations of 15° below to 30° above the horizon. As shown in Figure 3A, hearing sensitivity at 32 kHz improved as the loudspeaker was raised from 15° below to 30° above the horizon. In contrast, the thresholds one-third octave below or one-half octave above 32 kHz showed little change with elevation. As a result, as the speaker elevation was raised from 0° to 30°, the magnitude of the difference between the thresholds at 32 kHz and 25 kHz fell from 18 dB to 9.5 dB; similarly, the magnitude of the difference between thresholds at 32 kHz and 45 kHz fell from 12 dB to 1.5 dB. In short, the apparent dip in sensitivity at 32 kHz largely disappeared (Figure 3B). As discussed later, these results suggest that the 32-kHz dip is a result of the directionality of the bats' pinnae.

Discussion

Hearing in Egyptian Fruit Bats

Behavioral measures. The audiogram obtained in the present study is compared in Figure 4 with the behavioral audiogram for the one Egyptian fruit bat obtained previously using a go/no-go procedure (Suthers & Summers, 1980). Although there is agreement regarding the best frequency of hearing (10 kHz), there is a 40-dB difference in best sensitivity and more than an octave difference in high-frequency hearing.

In accounting for the differences between the two audiograms, we concur with the suggestion made by Suthers and Summers (1980) that the lack of sensitivity of their audiogram for the Egyptian fruit bat may be due to the conditioning method. In particular, we believe that the greater sensitivity of the present audiogram is a result of two features of the conditioned avoidance procedure that are designed to elicit the maximum detection of which an animal is capable (H. E. Heffner & Heffner, 1995): First, the conditioned avoidance procedure includes a clear penalty for misses in the form of a mild shock that accompanies the offset of the tone. This contingency applies even for signals that eventually prove to be below threshold, because the animals must be trained to be vigilant for low-level signals. Thus, the animals in the conditioned avoidance test are punished for misses, as well as rewarded for hits, such that the failure to respond to any audible signal is discouraged. In contrast, the procedure used by Suthers and Summers (1980) was a go/no-go procedure in which the bat was trained to hang from the ceiling of the test cage and then move to an opening at the other end when it heard a tone to receive a food reward. Thus, whereas their bat received a reward for detecting a tone, there was no penalty for failure to respond other than postponement of the next reward. Because the postponement of the reward was brief and unsignaled, it may not even have been noticed by the bat and thus would not

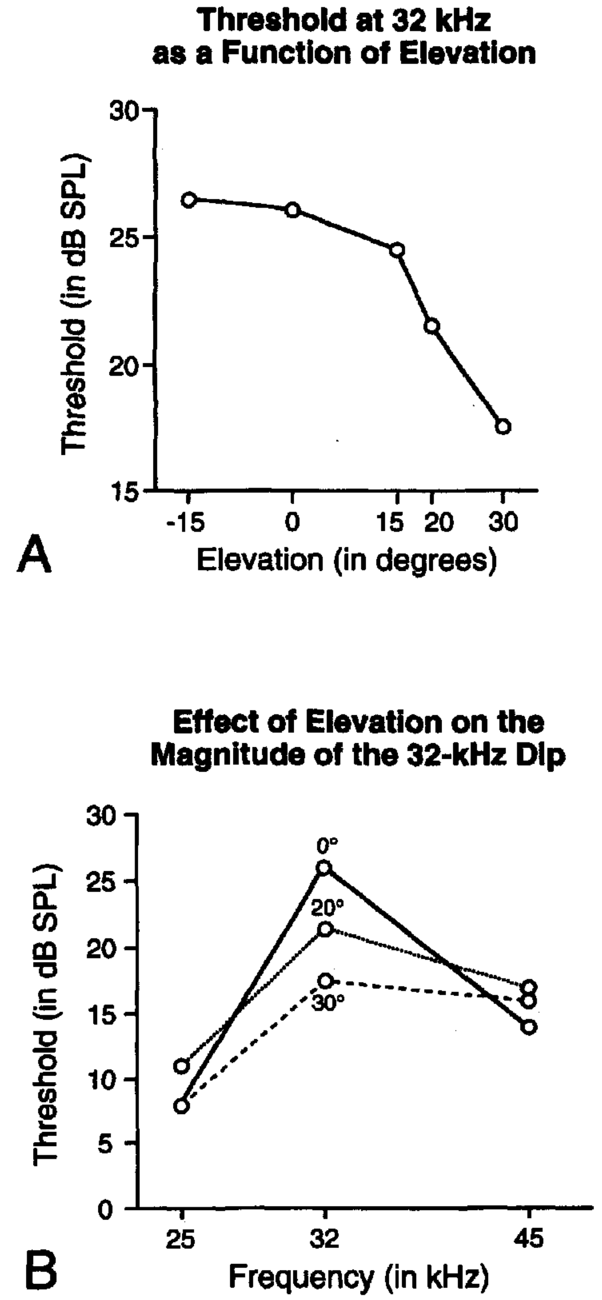


Figure 3. The effect of elevation of the sound source on thresholds for Bat B. (A) As the elevation of the sound source of a 32-kHz tone was raised from 15° below the horizon to 30° above the horizon, thresholds improved by 9 dB. (B) As speaker elevation was raised to 30°, the dip in sensitivity at 32 kHz became considerably less pronounced. In contrast, thresholds for 25 and 45 kHz changed by no more than 3 dB throughout this range. SPL = sound pressure level.

have had any effect. Moreover, the investigators increased the intensity of the tone after a failure to respond so that any miss was followed by a more readily detectable signal and thus an easier opportunity for reward.

The second important procedural difference was the extended training at low-intensity sounds that the bats received in the conditioned avoidance procedure because most of the testing was conducted near threshold. It is a common observation that early in training, after they have learned to respond to clearly audible signals, animals show thresholds that are at least 20 dB higher than their final thresholds. It is at this stage that the penalty for missing near-threshold sounds is especially important for eliciting maximum performance. Without a cost for misses, an animal can simply wait for an easily detectable signal to obtain adequate rewards, as long as it can tolerate a slightly lower density of rewards. Suthers and Summers (1980) presented signals of decreasing intensity and stopped at the first level at which a response was not elicited, defining threshold as halfway between the first miss and the previous hit. Thus, there was no extended practice with low-intensity signals and no penalty for ignoring them. In short, specific training to listen for low-intensity sounds as well as a clear and effective penalty for misses are necessary to obtain a valid audiogram.

Electrophysiological measures. Auditory thresholds have been estimated for bats of the genus *Rousettus* using several electrophysiological measures. As illustrated in Figure 4, the brain stem auditory evoked potential audiogram for the Egyptian fruit bat (Belknap & Suthers, 1982) underestimates the behavioral hearing thresholds reported here in both overall sensitivity and hearing range, although for frequencies of 10 kHz and higher it resembles the audiogram by Suthers and Summers (1980). Evoked potentials have also been recorded from the inferior colliculus of a closely related species with nearly identical echolocation signals, *Rousettus amplexicaudatus* (Grinnell & Hagiwara, 1972). This electrophysiological audiogram agrees with our behavioral audiogram at the highest frequencies, but sensitivity at 50 kHz and below is grossly underestimated, and nearly three octaves of hearing below 10 kHz were not detected. In general, the electrophysiological measures underestimate both the sensitivity and range of functional hearing and do not present consistent estimates of hearing.

Comparisons With Other Bats

Figure 5 shows the audiogram of the Egyptian fruit bat with comparable audiograms of five microchiropteran bats (audiograms obtained using behavioral procedures incorporating a penalty for misses, practice at low intensities, and good control over the acoustic stimuli). The bats included in this comparison are the big brown bat (*Eptesicus fuscus;* Koay, Heffner, & Heffner, 1997), greater horseshoe bat (*Rhinolophus ferrumequinum;* Long & Schnitzler, 1975), fish-catching bat (*Noctilio leporinus;* Wenstrup, 1984), little brown bat (*Myotis lucifugus;* Dalland, 1965), and Indian false vampire (*Megaderma lyra;* Schmidt, Turke, & Volger, 1983). The following sections compare five aspects of the audiogram of the Egyptian fruit bat with those of the microchiropteran bats and other mammals.

High-frequency hearing. The Egyptian fruit bat does not hear as high as the microchiropteran bats shown in Figure 5. At a level of 60 dB SPL, the Egyptian fruit bat

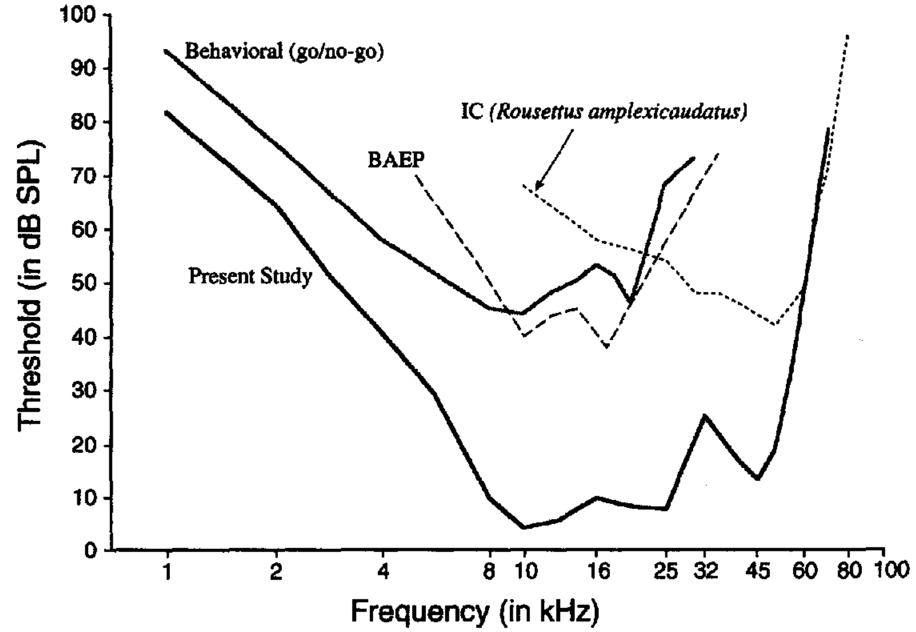


Figure 4. Audiogram of the Egyptian fruit bat obtained in the present study compared with earlier behavioral and electrophysiological estimates for the Egyptian fruit bat and another species in the same genus. All of the prior reports seriously underestimate both the range and sensitivity for this species. Behavioral audiogram was obtained using a go/no-go testing procedure (Suthers & Summers, 1980); IC = evoked potentials from the inferior colliculus of *Rousettus amplexicaudatus* (Grinnell & Hagiwara, 1972); BAEP = brain stem auditory evoked potential audiogram (Belknap & Suthers, 1982); SPL = sound pressure level.

hears up to 64 kHz, whereas all five microchiropterans hear above 100 kHz. Such a difference is not unexpected, however, because high-frequency hearing in mammals is known to vary as a function of head size or, more precisely, functional interaural distance (the time required for a sound to travel around the head from the opening of one auditory meatus to the other). Specifically, species with small functional interaural distances hear higher frequencies than those with larger interaural distances ($r = -.787$, $p = .0001$; see Figure 6). This relationship is based on the need to localize sound, such that animals with smaller heads and pinnae must hear higher frequencies to make use of interaural and pinna-based spectral cues to support sound localization (e.g., Koay et al., 1997; Masterton, Heffner, & Ravizza, 1969). The only exceptions to this relationship are underground mammals, such as gophers and mole rats, which have lost the ability to localize sound and also have reduced high-frequency hearing (R. S. Heffner & Heffner, 1993).

Just how bats fit the relationship between functional interaural distance and high-frequency hearing is shown in Figure 6. As can be seen, the functional interaural distance of Egyptian fruit bats is noticeably larger than that of the microchiropteran bats, thus leading to the expectation that they would have a lower high-frequency hearing limit. For all bats, however, the upper limit of hearing is within the range expected based on their functional head size (for a detailed discussion, see Koay et al., 1997). Thus, the more limited high-frequency hearing of Egyptian fruit bats is not unexpected, given their larger head size, which reduces their need to hear high frequencies for sound localization.

Low-frequency hearing. At an intensity of 60 dB SPL, Egyptian fruit bats can hear as low as 2.25 kHz. Although such a low-frequency hearing limit is high when compared with the 53 other nonaquatic mammals, which have a median low-frequency hearing limit of 87 Hz (for references, see Figure 6), it is low compared with that of the microchiropteran bats. Moreover, whereas the low-frequency sensitivity of the microchiropteran bats declines below 16 kHz, as shown in Figure 5, the low-frequency sensitivity of Egyptian fruit bats does not decline until well below 10 kHz.

Using the lowest frequency audible at a level of 60 dB SPL as a measure for comparison, Egyptian fruit bats have better low-frequency sensitivity than any of the microchiropterans, with the possible exception of the Indian false vampire (*Megaderma lyra;* Schmidt et al., 1983). However, close examination of this species' audiogram suggests that its low-frequency sensitivity might be overestimated. This is because the audiogram shows an unusual pattern of low-frequency hearing, specifically a sharp decline in low-frequency sensitivity below 16 kHz but a leveling off to a shallow decline in sensitivity below 7 kHz. Such a pattern is rarely seen in mammalian audiograms and, when closely examined, has been found to be due to the presence of high-frequency artifacts in the signal (see Koay et al., 1997). This is because special care is required to produce low-frequency pure tones at high intensities (above 80 dB in this

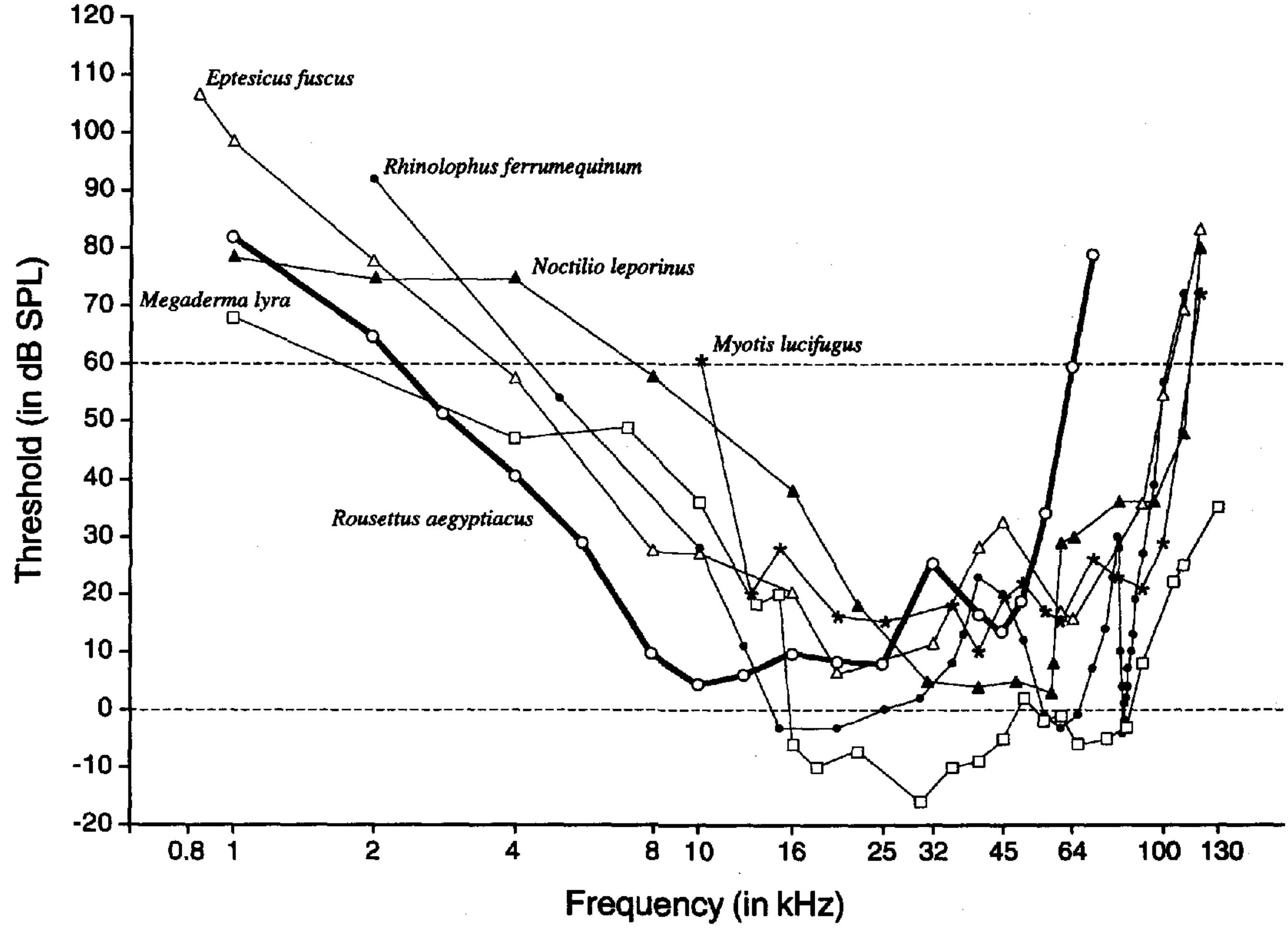


Figure 5. Behavioral audiograms for six species of bats: *Rousettus aegyptiacus* (present report), *Eptesicus fuscus* (big brown bat; Koay et al., 1997), *Megaderma lyra* (Indian false vampire; Schmidt et al., 1983), *Myotis lucifugus* (little brown bat; Dalland, 1965), *Noctilio leporinus* (fish-catching bat; Wenstrup, 1984), and *Rhinolophus ferrumequinum* (greater horseshoe bat; Long & Schnitzler, 1975). SPL = sound pressure level.

case) without introducing audible harmonics. This same point might be applicable to the audiogram of fish-catching bats (*Noctilio leporinus*) below 4 kHz.

Because the Indian false vampire has been thought to locate its ground-dwelling prey with passive localization (Fiedler, 1979), it has been tempting to conclude that the flattening of the low-frequency end of its audiogram is a specialization for accurate sound localization. However, it is difficult to see how such a specialization could enhance localization, because their thresholds below 7 kHz are above 50 dB SPL, making them sensitive only to relatively loud sounds. Moreover, it has been demonstrated that the Indian false vampire relies on low-intensity echolocation calls for the capture of ground-dwelling prey (Schmidt, Hanke, & Pillat, 1998). Thus, given the lack of evidence for a direct relation between low-frequency hearing and sound localization, together with the unusual flattening of the low-frequency portion of an audiogram that is known in other species to be due to artifacts (e.g., Koay et al., 1997), there is reason to believe that the audiogram by Schmidt et al. (1983) may have overestimated the Indian false vampire's low-frequency sensitivity. Accordingly, we have concluded that the Egyptian fruit bat probably has better low-frequency sensitivity than any of the microchiropterans shown in Figure 5.

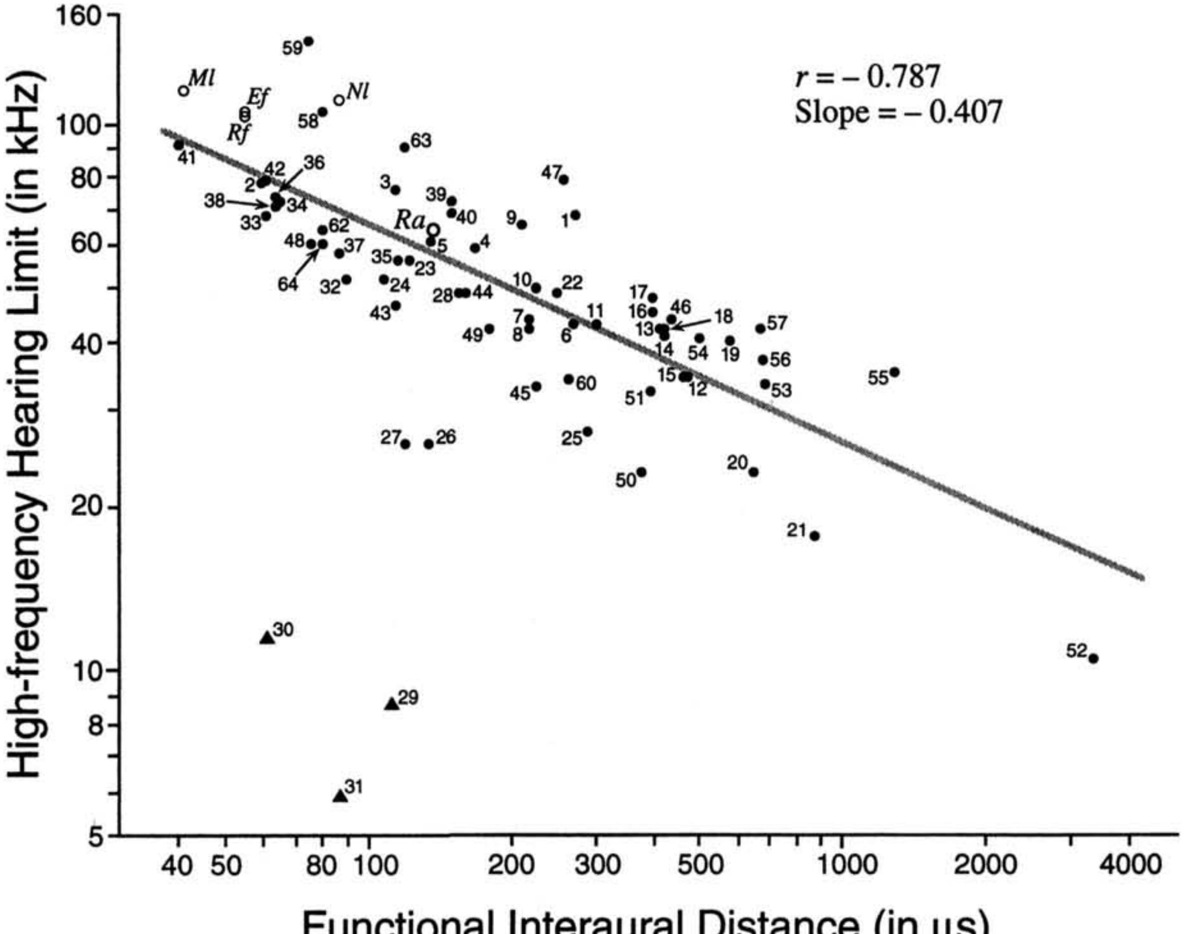
The better low-frequency hearing of Egyptian fruit bats compared with the microchiropterans is not unexpected, because mammals show a relationship between high- and low-frequency hearing such that low-frequency hearing improves as high-frequency hearing declines. However, as shown in Figure 7, this relationship is not a simple one, because there seems to be a "floor" of approximately 20 Hz below which low-frequency sensitivity (at 60 dB SPL) does not extend. Moreover, the subterranean mammals (with their degenerate hearing) and the marine mammals do not conform to this pattern (for a detailed discussion, see Koay et al., 1997). Suffice it to say that Egyptian fruit bats resemble the microchiropteran bats in their consistency with the relation between high- and low-frequency hearing.

Best frequency and best sensitivity. Although all bats tested so far, including Egyptian fruit bats, have their best hearing at frequencies well above the mammalian mean of 6.2 kHz (for references to audiograms, see Figure 6), the 10-kHz best frequency of Egyptian fruit bats is lower than the best frequencies of the microchiropterans, which range between 20 kHz and 80 kHz (see Figure 5). At their frequency of best hearing, Egyptian fruit bats have an average threshold of 4 dB, essentially identical to the 3.7-dB mean best sensitivity for mammals as a whole and well within the range for bats of −16 dB to 10 dB. Thus, whereas Egyptian fruit bats are unexceptional among bats in terms of their best sensitivity, the frequency of their best hearing is lower than that of the microchiropteran bats so far examined.

Hearing range. One notable point about bats is that they have a relatively restricted hearing range. At a level of 60 dB, their hearing ranges extend over as few as 3.5 octaves in the little brown bat (Dalland, 1965) to as many as 4.8 octaves in the Egyptian fruit bat (with the possibility that the Indian false vampire, *Megaderma lyra,* might have a wider hearing range, should a complete audiogram confirm the current estimates for its low- and high-frequency hearing). In contrast, the hearing ranges for other terrestrial mammals span from 4.3 octaves in elegant opossums (*Marmosa elegans;* Frost & Masterton, 1994) to 10.5 octaves for domestic cats, cattle, and gerbils (R. S. Heffner & Heffner, 1983, 1985b; Ryan, 1976); more than 80% have ranges greater than 6 octaves (R. S. Heffner, 1998). The reason for the restricted hearing ranges of bats and a few other species is the relationship between high- and low-frequency hearing. As noted, there is a trade-off among many species, including bats, such that 4.6 octaves of low-frequency hearing are lost for each octave of high-frequency hearing gained (solid line in Figure 7). Thus, in this group, the species with the most extensive high-frequency hearing appears to have given up the most low-frequency hearing. Among other mammals (those represented by the dashed line in Figure 7), only 0.44 octave of low-frequency hearing is sacrificed to add 1 octave of high-frequency hearing, resulting in especially broad hearing ranges. Thus, the variation in hearing range is a product of the selective pressure for high- and low-frequency hearing and is not an independent parameter itself.

Midfrequency Dip in Sensitivity

It has long been noted that animals may show one or more decreases or dips in sensitivity in the midrange of their



audiogram (seen as peaks in the audiograms in Figure 5). Indeed, early studies of primates reported a decrease in sensitivity in the 4-kHz region, which was referred to as the "4096 dip" (e.g., Harris, 1943; Wendt, 1934). As can be seen in Figure 5, not only do Egyptian fruit bats have a midfrequency dip, but most of the microchiropterans do as well.

Measurements in big brown bats have indicated that these dips are due to the directional filtering properties of the pinnae and the selective interference induced by the tragus

Figure 6 (*opposite*). High-frequency hearing limit (highest frequency audible at 60 dB sound pressure level) as a function of interaural distance (the number of µs required for a sound to travel from one auditory meatus to the other). Mammals with small interaural distances, including bats, hear higher frequencies than larger mammals. Note that subterranean species (indicated by filled triangles) were not included in the correlation. Open circles signify bat species. Key to species: *Ef* (*Eptesicus fuscus;* Koay, Heffner, & Heffner, 1997); *Ml* (*Myotis lucifugus;* Dalland, 1965); *Nl* (*Noctilio leporinus;* Wenstrup, 1984); *Ra* (*Rousettus aegyptiacus;* present report); *Rf* (*Rhinolophus ferrumequinum;* Long & Schnitzler, 1975); 1, Virginia opossum (*Didelphis virginiana;* Ravizza, Heffner, & Masterton, 1969a); 2, mouse opossum (*Marmosa elegans;* Frost & Masterton, 1994); 3, short-tailed opossum (*Monodelphis domestica;* Frost & Masterton, 1994); 4, hedgehog (*Hemiechinus auritus;* Ravizza, Heffner, & Masterton, 1969b); 5, tree shrew (*Tupaia glis;* H. E. Heffner, Ravizza, & Masterton, 1969a); 6, brown lemur (*Lemur fulvus;* Sutherland, Granger, & Masterton, 1988); 7, slow loris (*Nycticebus coucang;* H. E. Heffner & Masterton, 1970); 8, potto (*Perodicticus potto;* H. E. Heffner & Masterton, 1970); 9, bushbaby (*Galago senegalensis;* H. E. Heffner, Ravizza, & Masterton, 1969b); 10, owl monkey (*Aotus trivirgatus;* Beecher, 1974a); 11, squirrel monkey (*Saimiri sciureus;* Beecher, 1974b; Green, 1975); 12, pigtailed macaque (*Macaca nemestrina;* Stebbins, Green, & Miller, 1966); 13, crab-eating macaque (*Macaca irus;* Stebbins et al., 1966); 14, rhesus macaque (*Macaca mulatta;* Pfingst, Laycock, Flammino, Lonsbury-Martin, & Martin, 1978); 15, Japanese macaque (*Macaca fuscata;* Jackson & Heffner, 1997); 16, vervet (*Cercopithecus aithiops;* Owren, Hopp, Sinnott, & Petersen, 1988); 17, blue monkey (*Cercopithecus mitis;* C. H. Brown & Waser, 1984); 18 DeBrazza monkey (*Cercopithecus neglectus;* Owren et al., 1988); 19, yellow baboon (*Papio cynocephalus;* Heinz, Turkkan, & Harris, 1982); 20, chimpanzee (*Pan troglodytes;* Farrer & Prim, 1965); 21, human (*Homo sapiens;* R. S. Heffner & Heffner, 1991); 22, domestic rabbit (*Oryctolagus cuniculus;* H. E. Heffner & Masterton, 1980); 23, eastern cottontail (*Sylvilagus floridana;* R. S. Heffner & Koay, 1995); 24, eastern chipmunk (*Tamias striatus;* R. S. Heffner & Contos, 1989); 25, groundhog (*Marmota monax;* Conesa, Heffner, & Heffner, 1991); 26, black-tailed prairie dog (*Cynomys ludovicianus;* R. S. Heffner, Heffner, Contos, & Kearns, 1994); 27, white-tailed prairie dog (*Cynomys leucurus;* R. S. Heffner et al., 1994); 28, fox squirrel (*Sciureus niger;* Jackson, Heffner, & Heffner, 1997); 29, pocket gopher (*Geomys bursarius;* R. S. Heffner & Heffner, 1990b); 30, naked mole rat (*Heterocephalus glaber;* R. S. Heffner & Heffner, 1993); 31, blind mole rat (*Spalax ehrenbergi;* R. S. Heffner & Heffner, 1992); 32, kangaroo rat (*Dipodomys merriami;* H. E. Heffner & Masterton, 1980); 33, grasshopper mouse (*Onychomys leucogaster;* H. E. Heffner & Heffner, 1985); 34, cotton rat (*Sigmodon hispidus;* H. E. Heffner & Masterton, 1980); 35, wood rat (*Neotoma floridana;* H. E. Heffner & Heffner, 1985); 36, Darwin's leaf-eared mouse (*Phyllotis darwini;* Mooney, Heffner, & Heffner, 1990); 37, gerbil (*Meriones unguiculatus;* Ryan, 1976); 38, spiny mouse (*Acomys cahirinus;* Mooney et al., 1990); 39, Norway rat, albino (*Rattus norvegicus;* Kelly & Masterton, 1977); 40, Norway rat, hooded (*Rattus norvegicus;* H. E. Heffner, Heffner, Contos, & Ott, 1994); 41, house mouse, wild (*Mus musculus;* H. E. Heffner & Masterton, 1980); 42, house mouse, domestic (*Mus musculus;* Markl & Ehret, 1973); 43, hamster (*Mesocricetus auritus;* R. S. Heffner & Koay, 1993); 44, guinea pig (*Cavia porcellus;* R. S. Heffner, Heffner, & Masterton, 1971); 45, chinchilla (*Chinchilla laniger;* R. S. Heffner & Heffner, 1991); 46, dog (*Canis familiaris;* H. E. Heffner, 1983); 47, domestic cat (*Felis catus;* R. S. Heffner & Heffner, 1985b); 48, least weasel (*Mustela nivalis;* R. S. Heffner & Heffner, 1985a); 49, ferret (*Mustela putorius;* Kelly, Kavanagh, & Dalton, 1986); 50, harbor seal in air (*Phoca vitulina;* Mohl, 1968); 51, sea lion in air (*Zalophus californianus;* Schusterman, Balliet, & Nixon, 1972); 52, elephant (*Elephas maximus;* R. S. Heffner & Heffner, 1980); 53, horse (*Equus caballus;* R. S. Heffner & Heffner, 1983); 54, pig (*Sus scrofa;* R. S. Heffner & Heffner, 1990a); 55, cattle (*Bos taurus;* R. S. Heffner & Heffner, 1983); 56, goat (*Capra hircus;* R. S. Heffner & Heffner, 1990a); 57, sheep (*Ovis aries;* Wollack, 1963). The following species were tested underwater. Note that the functional interaural distance in water is smaller than that in air because of the faster speed of sound in water and the direct path of the sound from one ear to the other through the head: 58, dolphin (*Inia geoffrensis;* Jacobs & Hall, 1972); 59, porpoise (*Tursiops truncatus;* Johnson, 1967); 60, killer whale (*Orcina orca;* Hall & Johnson, 1972); 61, beluga whale (Figure 7 only, *Delphinapterus leucas;* Awbrey, Thomas, & Kastelein, 1988; White, Ljungblad, Norris, Baron, & diSciara, 1977); 62, harbor seal (*Phoca vitulina;* Mohl, 1968); 63, harp seal (*Pagophilus groenlandicus;* Terhune & Ronald, 1972); 64, ringed seal (*Pusa hispida;* Terhune & Ronald, 1975).

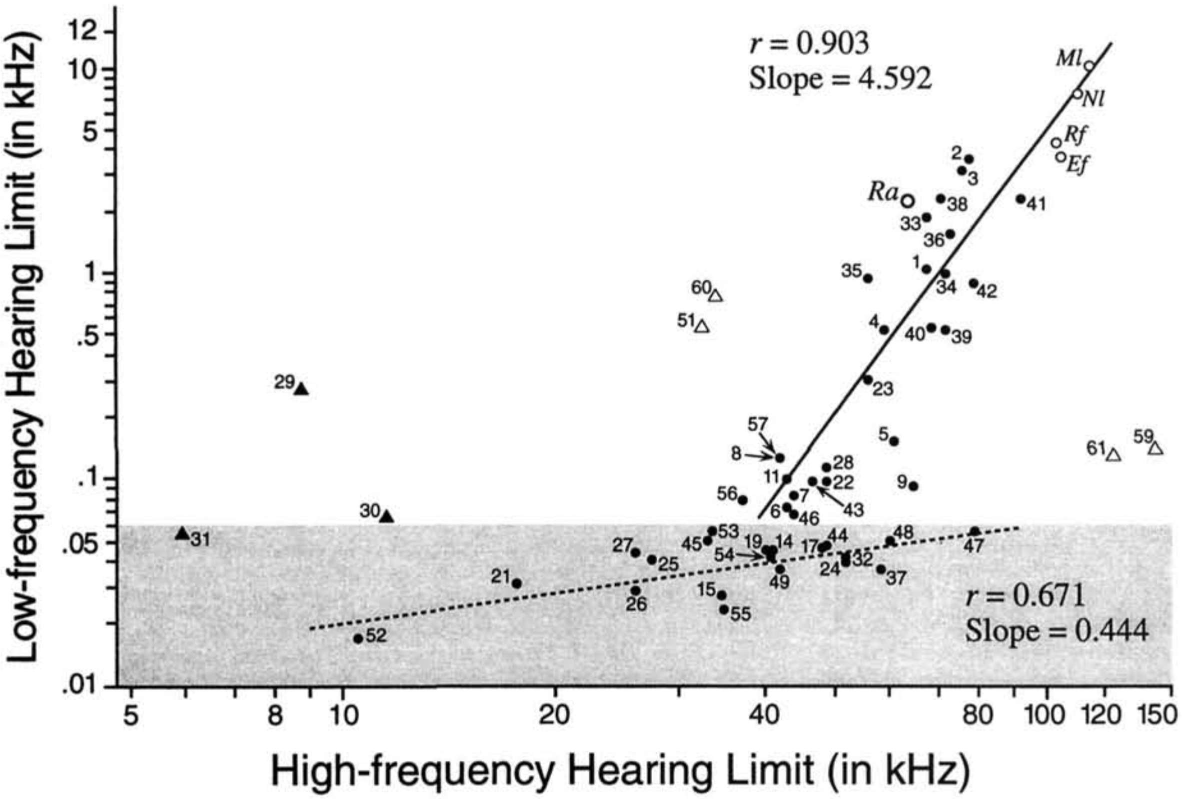


Figure 7. Relation between the highest and lowest frequencies audible at 60 dB for 58 species of mammals. As discussed in detail elsewhere (Koay et al., 1997), there appears to be a floor effect such that species with the most extensive low-frequency hearing (i.e., those capable of hearing 60 Hz and below, included in the shaded area and represented by the dashed line) seem to be able to achieve good low-frequency hearing without the sacrifice of high-frequency hearing that occurs in other mammals (those represented by the solid line). Note that neither the subterranean species (filled triangles) nor the marine mammals (open triangles) were included in the calculation of the regression lines. Open circles signify bat species. (See Figure 6 caption for the key to species.)

(Wotton et al., 1995). Because the directionality of the pinna varies with the elevation of a sound source—indeed, this property of the pinna provides the cues used to discriminate elevation (e.g., R. S. Heffner, Koay, & Heffner, 1996; Lawrence & Simmons, 1982)—we tested the notion that the 32-kHz dip of Egyptian fruit bats was due to their pinnae by obtaining thresholds at 32 kHz and adjacent points at various elevations in the median sagittal plane (see Figure 3b). Our results support the findings of Wotton and her colleagues that the dip in sensitivity in big brown bats appears to be due to the directional filtering properties of the pinnae, which they showed to be important to that species for discriminating the elevation of sound sources (Wotton et al., 1996; Wotton & Jenison, 1997).

An alternative explanation of midfrequency dips in sensitivity, with the associated apparent peaks of sensitivity flanking them on either side, is that they are the result of neural specializations. One such specialization is the "acoustic fovea," in which a substantial portion of the basilar membrane is devoted to a very narrow range of frequencies, such as echo call reception. This expanded frequency representation is often accompanied by other morphological and neural specializations as well (Kossl & Vater, 1995), and it is usually proposed as a basis for enhanced frequency resolution for echolocation in constant-frequency bats (e.g., Bruns & Schmieszek, 1980; Kossl & Vater, 1996). However, the acoustic fovea is not associated with detection more sensitive than that achieved at lower frequencies represented in unspecialized parts of the cochlea (for a review, see Kossl & Vater, 1995). Indeed, similar cochlear specializations have been found that do not appear to be associated with functional specializations, and it seems that frequency expansion in the cochlea is not consistently related to either enhanced frequency tuning or sensitivity (Kossl, Grank, Burda, & Muller, 1996; Kossl & Vater, 1995). Thus, the multiple peaks observed in audiograms of other bats (cf., *M. lucifugus* and *R. ferrumequinum* in Figure 5) may result, at least in part, from the directional filtering characteristics of their elaborate pinnae.

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