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Hearing in large (*Eidolon helvum*) and small (*Cynopterus brachyotis*) non-echolocating fruit bats

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Abstract

Comparing the hearing abilities of echolocating and non-echolocating bats can provide insight into the effect of echolocation on more basic hearing abilities. Toward this end, we determined the audiograms of two species of non-echolocating bats, the straw-colored fruit bat (*Eidolon helvum*), a large (230–350 g) African fruit bat, and the dog-faced fruit bat (*Cynopterus brachyotis*), a small (30–45 g) bat native to India and Southeast Asia. A conditioned suppression/avoidance procedure with a fruit juice reward was used for testing. At 60 dB SPL, the hearing range of *E. helvum* extends from 1.38 to 41 kHz with best sensitivity at 8 kHz; the hearing range of *C. brachyotis* extends from 2.63 to 70 kHz with best sensitivity at 10 kHz. As with all other bats tested so far, neither species was able to hear below 500 Hz, suggesting that they may not use a time code for perceiving pitch. Comparison of the high-frequency hearing abilities of echolocating and non-echolocating bats suggests that the use of laryngeal echolocation has resulted in additional selective pressure to hear high frequencies. However, the typical high-frequency sensitivity of small non-echolocating mammals would have been sufficient to support initial echolocation in the early evolution of bats, a finding that supports the possibility of multiple origins of echolocation.
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1. Introduction

In bats, we are presented with an opportunity to directly compare the hearing abilities of echolocating and non-echolocating species within a taxonomic order to provide insight to auditory adaptations that might be unique to echolocation. Although most of the approximately 1000 species of bats rely largely on echolocation to detect and identify objects, there are approximately 150 species of non-echolocating bats in the family Pteropodidae that rely on vision and olfaction for orientation and foraging. Because echolocation is such a specialized use of hearing, it has been the main target of studies of audition in bats, leaving other aspects of their hearing relatively unexplored.

Accordingly, the extent to which basic auditory abilities might differ between echolocating and non-echolocating bats remains largely unexamined. Although the audiograms of several echolocating bats have been determined, including *Rousettus aegyptiacus*, an exceptional pteropid bat that does echolocate (e.g., Heffner et al., 2003; Koay et al., 1998a), the only estimates of hearing in non-echolocating bats have been physiological (Calford and McAnally, 1987; Grinnell and Hagiwara, 1972; Neuweiler et al., 1984), thus making comparison between echolocating and non-echolocating bats difficult. Recently, we have had the opportunity to study the hearing of two non-echolocating Pteropodidae: the straw-colored fruit bat (*Eidolon helvum*), a large (230–350 g) African fruit bat, and the dog-faced fruit bat (*Cynopterus brachyotis*), a small (30–45 g) species native to India and Southeast Asia. This has allowed us to address two issues regarding bat hearing.

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The first issue involves the high-frequency hearing of bats. Mammals are unique among vertebrates in that virtually all mammals hear higher than 10 kHz (Heffner and Heffner, 2003), whereas non-mammalian vertebrates that hear higher than 10 kHz are considered remarkable (e.g., Popper et al., 2004). The main source of selective pressure for this high-frequency hearing in mammals has been to enable them to use the two high-frequency sound-localization cues, namely, the pinna cues that result from the directionality of the pinnae, and the binaural spectral-difference cue, the difference in the frequency-intensity spectrum of a sound reaching the two ears. Because these cues require that an animal hear sounds of wavelengths short enough to be affected by its head and pinnae, mammals with small heads and pinnae typically hear higher frequencies than larger mammals (for a review, see Heffner and Heffner, 2003). As a result, it is not surprising that bats, with their relatively small size, hear higher frequencies than most mammals. Recently, however, we noted that echolocating bats hear slightly higher than their small head size would predict—on average, half an octave higher (Heffner et al., 2003). This raises the question whether the extended high-frequency hearing of these echolocating bats is also found in non-echolocating bats, or if it is restricted to bats that echolocate.

The second issue involves the low-frequency hearing ability of bats. We have previously noted that the distribution of mammalian low-frequency hearing is bimodal, with animals falling into two groups: those that hear below about 250 Hz, and those that do not (Heffner and Heffner, 2003; Heffner et al., 2001a). One implication of this finding is that animals whose limits do not fall below 250 Hz do not use temporal coding for the perception of pitch, but rely solely on place coding. So far, all bats whose audiograms have been determined fall into the group that does not hear below 250 Hz. Indeed, as Calford and colleagues (1985) noted in their physiological studies, even very large Pteropodidae may not hear as low as similar sized primates. Thus, we wished to verify behaviorally if non-echolocating bats have low-frequency hearing as restricted as that of echolocating bats.

2. Methods

The equipment and procedures described below are similar to those used in earlier reports from this laboratory on the hearing of a wide range of different mammals, including bats. Any modifications made were to accommodate the body size and motor abilities of particular species. (For additional detail on behavioral and acoustical apparatus and procedures suitable for testing small mammals, see Heffner et al., 2006).

2.1. Subjects

Two *E. helvum*, one adult male (bat A, 9.5 years, 350 g) and one female (bat B, 3.5 years, 260 g) were tested in this study. Two male *C. brachyotis* (bat A, 2 years, 35 g; bat B, 3 years, 32 g) were also tested. All bats were captive born and on loan from the Lubee Bat Conservancy where they had been housed in outdoor enclosures in a quiet rural setting. While on test, they were housed individually in wood and plastic mesh cages (48 × 39 × 95 cm).

The use of animals in this study was approved by the University of Toledo Animal Care and Use Committee.

2.2. Behavioral apparatus

The behavioral testing was carried out in separate custom-built wire mesh cages (Fig. 1). Each cage was sized appropriately for the species and large enough that the bats could maneuver easily. The test apparatus had the following pertinent features: the reward spouts were 3-mm brass tubing with small oval lickplates at the top (25 × 18 mm for *E. helvum*; 12 × 8 mm for *C. brachyotis*) and projected vertically through the floor at the front of the cage at a height convenient for the bats to reach while they perched on the small platform in the middle of the test cage. This configuration minimized acoustic obstructions between the bats and the loudspeakers. The platform was covered with damp carpet to provide traction and electrical contact for
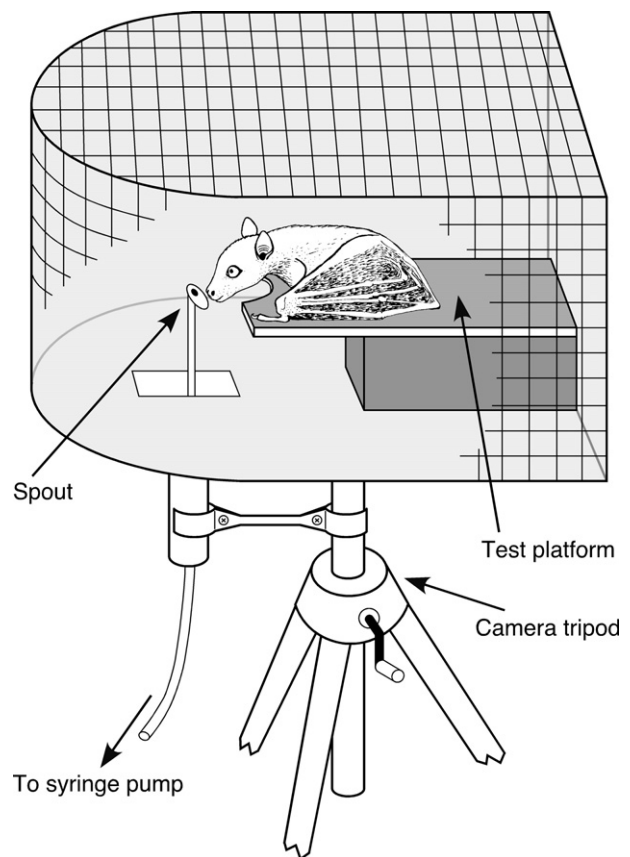

Fig. 1. Drawing of *Cynopterus brachyotis* in the test cage. The test cage was designed to minimize obstructions and reflective surfaces in the sound field.

the bat. (For specifics of cage construction see Heffner et al., 2003; Koay et al., 1998a.) Fruit juice was used as the reward and consisted of a mix of cantaloupe, pear juice, and vitamin supplement, finely blended and sieved. It was dispensed using a syringe pump housed in a foam-lined box made of high-density polyethylene and located at the back of the test chamber to eliminate dispenser noise. A bat was required to maintain mouth contact with the spout in order to receive a steady trickle of juice, thus keeping its head in a fixed position within the sound field. A shock generator was connected between the reward spout and platform, and the shock was adjusted for each bat to the lowest level that produced a consistent avoidance response (backing away slightly or lifting the head from the spout). A 25-W light, mounted below the cage, was turned on and off with the shock to provide feedback for a successful avoidance and to indicate when it was safe to return to the spout.

2.3. Acoustical apparatus

Pure tones were digitally generated (Zonic A & D 3525), pulsed (Coulbourn S53-21; 400 ms on, 100 ms off, for 4 pulses) and routed to a rise-fall gate (Coulbourn S84-04, 10 ms rise-fall). The tones were then bandpass filtered (Krohn-Hite 3202, ±1/3 octave settings, 24 dB/oct rolloff) and attenuated (Hewlett–Packard 350D) as needed for threshold determination. Finally, the signal was amplified (Crown D75 or Adcom GFA545), monitored with an oscilloscope (Tektronix TDS 210), and routed to a loudspeaker in the test chamber. The loudspeaker was placed approximately 1 m in front of the cage (0° elevation and azimuth), directly facing the bat when it was eating from the spout. Various loudspeakers were used to present the tones—for frequencies 2.8 kHz and below, either a 12-in. (30.4 cm) woofer or one of two 6-in. (15.2 cm) woofers (Infinity RS 2000) was used; tones above 2.8 kHz were produced using one of two ribbon tweeters (Panasonic EAS-10TH400C). The speakers were regularly switched to check for the possibility that a threshold might be influenced by the peculiarities of a particular loudspeaker.

Thresholds were obtained for *E. helvum* at 0.8, 1, 2, 4, 5.6, 8, 10, 12.5, 16, 20, 25, 32, 40, and 45 kHz, and for *C. brachyotis*, at frequencies of 1.4, 2, 2.8, 4, 5.6, 8, 10, 12.5, 16, 20, 25, 32, 40, 50, 64, and 80 kHz. Although harmonics were present in the 800-Hz signal at 85 dB SPL, they were at least 25 dB below the detection thresholds of the bats. No harmonics were detected in the 1.4-kHz signal, even at 90 dB SPL.

2.4. Sound level measurement

Sound level measurements were taken by placing the microphone in the position normally occupied by a bat's head and ears while it drank from the spout and pointing it directly at the loudspeaker. The sound pressure level

(SPL re 20 μN/m^2) was measured daily with a 1/4-in. (0.64-cm) microphone (Brüel & Kjaer 4939, corrected for free-field with the protection grid on), preamplifier (Brüel & Kjaer, 2669), and measuring amplifier (Brüel & Kjaer, 2608, set to 22.4 Hz high pass). The output of the measuring amplifier was then routed to a spectrum analyzer (Zonic A & D 3525) to monitor the acoustic signal for harmonics or distortion. Subsequent testing demonstrated that any measurable harmonics were at least 50 dB below the level of the fundamental frequency and at least 25 dB below the animals' thresholds and thus did not contribute unwanted cues. Care was also taken to produce a homogeneous sound field (within ±1 dB) in the area occupied by the animal's head and ears when it was eating from the spout.

2.5. Behavioral procedure

The bats were tested with a conditioned suppression/avoidance procedure in which they continuously licked the reward spout to receive a steady trickle of fruit juice. They were then trained to break contact with the spout whenever they detected a tone to avoid impending shock (Heffner and Heffner, 1995; Heffner et al., 2006).

Initially, the bats were trained to climb the platform, maintain spout contact, and keep their heads oriented toward the speaker. Auditory training was then initiated by presenting, at random intervals, brief trains of four tone pulses (400 ms on, 100 ms off) at intensities well above threshold. Each pulse train was followed at its offset by a mild electric shock (approximately 35 V at 0.18 mA to 74 V at 0.34 mA, 300 ms duration) delivered between the spout and platform. The bats learned to avoid the shock by breaking contact with the spout whenever they heard a tone and to return to the spout after the shock had been delivered (as indicated by the offset of the shock-indicator light). Initial acclimation and training to respond reliably to pure tones required about 35–50 days for *E. helvum* and 38 days for *C. brachyotis*.

Test sessions were divided into 2-s trials, separated by 1.5-s intertrial intervals. Approximately 22% of the trial periods contained a pulsing tone (warning signals), whereas no sound was presented in the remaining trial periods (safe signals). If a bat broke electrical contact with the spout for more than half of the last 150 ms of a trial, 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). If a bat was not in contact with the spout during the 1 s preceding a trial, the signal (safe or warning) was presented as usual, but the response of the bat was not recorded. Thus, spout contact before a trial served as a "ready response", but the occasional aborted trial resulted in slightly fewer than the maximum warning trials being obtained in a session.

The hit and false alarm rates were then determined for each stimulus intensity, with a single intensity presented

in a consecutive block of 6–10 warning trials (with approximately 24–40 associated safe trials). Finally, the hit rate was corrected for false alarms to produce a performance measure (Heffner and Heffner, 1995) according to the formula: performance = hit rate − (false alarm rate × hit rate). This measure proportionally reduces the hit rate for a block of trials by the false alarm rate associated with those trials; the performance measure can vary from 0 (no hits) to 1.0 (100% hit rate with no false alarms).

Auditory thresholds were determined by successively reducing the intensity of the tones first in 10-dB steps until threshold was approached, and then in 5-dB steps (in blocks of 6–10 warning trials) until a bat no longer responded to the warning signal above chance (i.e., the hit and false alarm rates did not differ; $p > 0.05$, binomial distribution). Threshold was defined as the intensity at which the performance measure equaled 0.50, which was usually obtained by linear interpolation. Testing was considered complete for a particular frequency when the thresholds obtained in at least three different sessions were within 3 dB of each other and were no longer showing consistent improvement. Once an audiogram had been completed, selected frequencies were rechecked to ensure reliability.

3. Results

3.1. Eidolon helvum

Both straw-colored fruit bats were tested in twice daily sessions lasting approximately 30 min each. During each session they accumulated approximately 30–45 warning trials, which were adequate to determine a reliable threshold for one frequency in each session. The bats consumed 20–35 cm³ of fruit juice per session, enough to maintain stable body weights of about 350 g (male) and the 260 g (female).

Thresholds for the two bats are shown in Fig. 2. There was good agreement between the two individual bats (mean difference 2.9 dB), with thresholds differing by 4 dB or less except at the lowest frequency tested where the difference was 7 dB. Responses were elicited at frequencies as low as 800 Hz from both bats, with thresholds of 84.5 and 77 dB. Sensitivity improved as the frequency was increased, reaching a lowest threshold of 10 dB at 8 kHz. Thresholds remained at 25 dB or better up to 25 kHz, with slightly elevated thresholds around 16 kHz and lower thresholds at flanking frequencies. Above 25 kHz, hearing sensitivity declined steadily to an average of 75.5 dB at 45 kHz. At an intensity of 60 dB SPL, the hearing range of E. helvum extends from 1.38 to 41 kHz, a range of 4.82 octaves. Although Jones (1982) reported that E. helvum can live at least 21 years, we wondered whether the 9.5-year-old male would show some sign of age-related hearing loss. However, this animal's thresholds are so similar to those of the younger animal, including at the high frequencies, that it seems to represent typical hearing for this species.

3.2. Cynopterus brachyotis

Bat A was tested in twice daily sessions of 25–40 min, during which it accumulated approximately 50 warning trials and consumed 5–8 cm³ of fruit juice each session. Bat B was tested approximately 1 year later in 1 h daily test sessions, during which it accumulated approximately 60 warning trials and consumed 6–8 cm³ of fruit juice. Both bats maintained stable weights around 35 and 32 g, respectively. With this number of trials, a threshold could be determined for one frequency per test session.

The thresholds for the dog-faced fruit bats are illustrated in Fig. 3, again showing good agreement between the two individuals, with the mean difference being
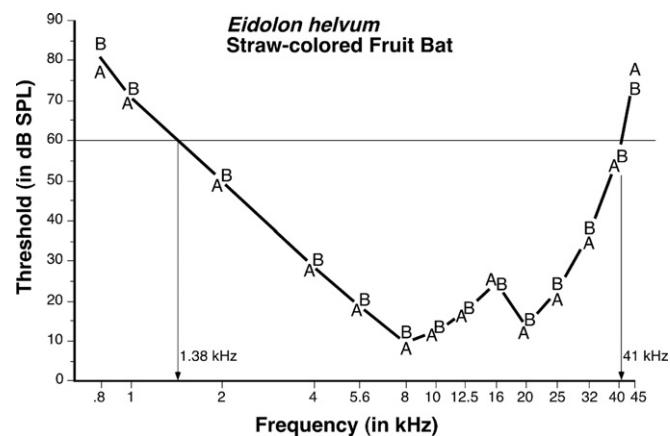

Fig. 2. Behavioral audiogram of *Eidolon helvum*. (A) represents the male, and (B) represents the female. The horizontal line at 60 dB SPL crosses the audiogram at the operationally-defined low- and high-frequency limits of the hearing range, indicated by the arrows.
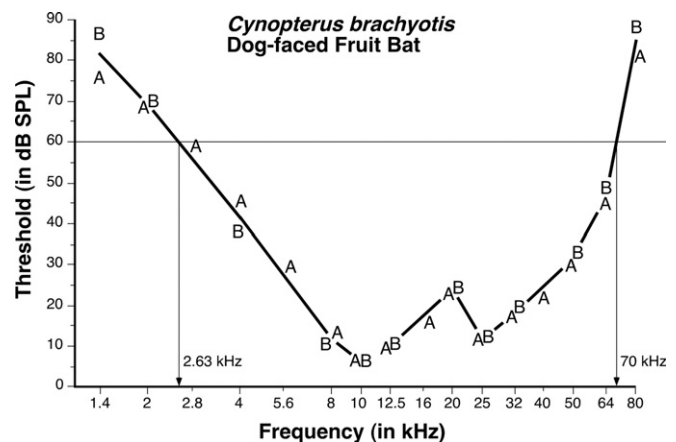

Fig. 3. Behavioral audiogram of *Cynopterus brachyotis*. (A) and (B) represent the two individuals tested, both males. The line representing the audiogram connects the mean thresholds for all frequencies at which both individuals were tested. The horizontal line and arrows indicate the hearing range at 60 dB SPL.
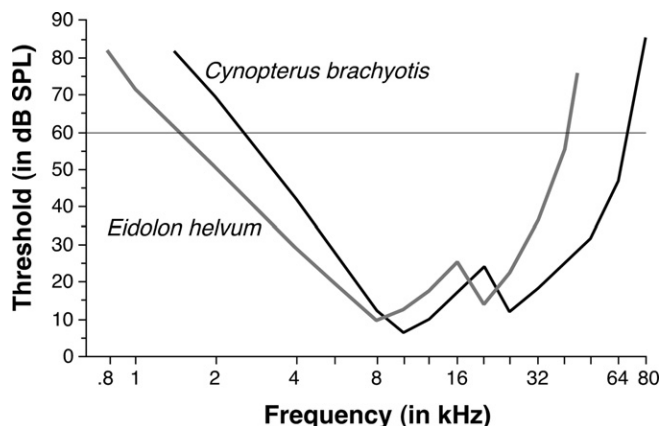
Fig. 4. A comparison of the average audiograms for *E. helvum* and *C. brachyotis*. Although similar in shape, *C. brachyotis* was slightly more sensitive than *E. helvum* and was able to hear nearly one octave higher than *E. helvum*.

3.4 dB and the majority of points within 2 dB of each other. (Note that Bat B was tested at fewer different frequencies than Bat A due to time constraints; it was used to help define the upper and lower limits of hearing and the inflection points in the midrange of the audiogram.) Responses were obtained for *C. brachyotis* at frequencies as low as 1.4 kHz. Thresholds improved with frequency, from an average of 81.5 dB at 1.4 kHz to their best sensitivity of 6.5 dB at 10 kHz (Fig. 3). Thresholds remained below 25 dB up to 40 kHz, with a region of slightly diminished sensitivity around 20 kHz. Above 40 kHz, sensitivity declined rapidly to an average threshold of 85 dB at 80 kHz. At an intensity of 60 dB SPL, the hearing range of this species extends from 2.63 to 70 kHz, a range of 4.73 octaves.

3.3. Features of E. helvum and C. brachyotis hearing

The audiograms of *E. helvum* and *C. brachyotis* are shown together in Fig. 4. Both have relatively steep slopes at the upper and lower ends of their audible range, and both show a mid-frequency region of slightly diminished sensitivity in between regions of better sensitivity. This 'midrange dip' is common in mammals, including bats (e.g., Heffner et al., 2001a, 2003), and is usually attributed to the filtering and amplification characteristics of the pinnae (Jen and Chen, 1988; Koay et al., 1998b, 2003; Heffner et al., 2003; Wotton et al., 1995). Overall, the shapes of the two audiograms are similar, but with that of the smaller *C. brachyotis* shifted almost one octave higher compared to that of the much larger *E. helvum*. This sensitivity to higher frequencies in *C. brachyotis* is not surprising given its smaller head size, as discussed further below.

4. Discussion

Although there have been no previous behavioral audiograms of non-echolocating bats, auditory responses

in several other species of Pteropodidae have been studied by recording sound-evoked neural activity in the inferior colliculus (Calford and McAnally, 1987; Calford et al., 1985; Grinnell and Hagiwara, 1972; Neuweiler et al., 1984). Despite the similarity of neural thresholds to behavioral thresholds at some frequencies and the approximately similar shape of the sensitivity curves, we have found that audiograms derived physiologically do not predict behavioral sensitivity closely enough for comparative studies (Heffner and Heffner, 2003; Koay et al., 1998a, 2003). This is not surprising because it is the behavioral responses to sound (such as detecting and locating predators and prey), rather than the neural mechanisms underlying those responses that are directly subject to evolutionary selective pressures. Accordingly, the following comparative analysis includes only behaviorally determined audiograms.
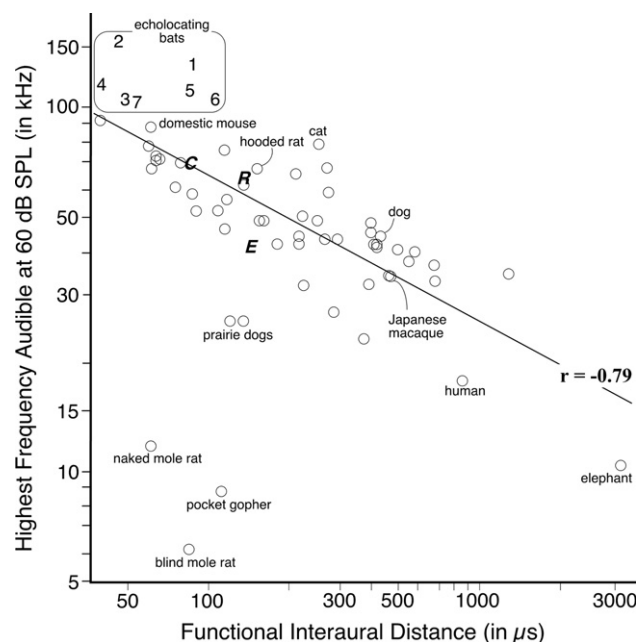

Fig. 5. Relationship between functional head size (the time required for sound to travel from one ear to the other) and the highest frequency audible at 60 dB SPL in mammals. Smaller species hear progressively higher frequencies. The regression line is based on 61 species of aerial and terrestrial mammals but excludes the three subterranean species. *C*, *Cynopterus brachyotis*; *E*, *Eidolon helvum*; *R*, *Rousettus aegyptiacus* (Koay et al., 1998a), 1 – *Artibeus jamaicensis* (Heffner et al., 2003), 2 – *Carollia perspicillata* (Koay et al., 2003), 3 – *Eptesicus fuscus* (Koay et al., 1997), 4 – *Myotis lucifugus* (Dalland, 1965), 5 – *Noctilio leporhinus* (Wenstrup, 1984), 6 – *Phyllostomus hastatus* (Koay et al., 2002), 7 – *Rhinolophus ferrumequinum* (Long and Schnitzler, 1975). A few familiar species are also named for reference. The only species to deviate significantly from the regression line, other than the subterranean rodents and prairie dogs, is the Jamaican fruit bat, *A. jamaicensis* ($p = 0.037$); no other species meets the 0.05 probability criterion (the next most deviant species being the domestic cat, $p = 0.06$).

4.1. High-frequency hearing

By hearing frequencies high enough to be shadowed by the head and amplified or attenuated by the pinnae, mammals gain access to spectral cues for sound-localization (Heffner and Heffner, 2003; Masterton et al., 1969). The smaller an animal's head and pinnae, the higher it must hear to obtain useable binaural spectral-difference cues and pinna cues. The relationship between head size (specifically *functional* head size, the time it takes sound to travel around the head from one auditory meatus to the other) and high-frequency hearing is illustrated in Fig. 5. This figure shows that the ability to hear high frequencies increases as functional head size decreases, with a correlation of $r = -0.79$ ($t = -8.26$, $p < 0.0001$). That this relationship is driven by the need to localize sound is supported by two findings. First, the importance of high frequencies for sound-localization has been demonstrated by the reduced ability to localize noise if high frequencies are filtered out (Butler, 1975; Heffner et al., 1995, 1996, 2001b). Second, subterranean mammals that have lost the ability to localize sound have also lost the ability to hear high frequencies (Fig. 5 and Heffner and Heffner, 1990a, 1992, 1993). Thus, high-frequency hearing is closely linked to sound-localization in mammals.

The relationship between functional head size and high-frequency hearing can be seen even within closely related species of bats. One example is provided by the three American leaf-nosed bats (Phyllostomidae, bats 1, 2, and 6 in Fig. 5) in which progressively smaller species hear progressively higher frequencies (Heffner et al., 2003). The two Pteropodidae in this report show a similar trend in which the smaller *C. brachyotis* hears higher frequencies than the larger *E. helvum* (C and E in Fig. 5). The observation that the hearing of closely related species differs as a direct function of head size suggests that high-frequency hearing is not highly conserved evolutionarily, and that it evolves to adjust to the contingencies of sound-localization in each species.

Bats are typically mammalian in their abilities to hear high frequencies as can be seen in Fig. 5. Further, the pteropids, *C. brachyotis*, *E. helvum* and *R. aegyptiacus*, are not exceptions as they lie close to the regression line relating high-frequency hearing to interaural distance (C, E, and R, respectively, in Fig. 5). However, all of the bats that use laryngeal echolocation lie above the regression line suggesting that an additional factor might be affecting their high-frequency hearing. Indeed, when information as to whether or not a species possesses laryngeal echolocation is added to a multiple regression analysis of high-frequency hearing, the amount of total variance explained increases significantly ($t = -4.32$, $p < 0.0001$), from 61.8% using interaural distance alone, to 71.1%, when using both interaural distance and echolocation ability. It thus appears that echolocation has influenced high-frequency hearing in bats: on average, the laryngeal echolocators (numbered 1–7 in Fig. 5) hear approximately one-half octave higher than

expected based on the selective pressure exerted by passive sound-localization alone (Heffner et al., 2003). Thus, although bats conform to the mammalian pattern, they do seem to be subject to additional selective pressure from echolocation.

Not all Pteropodidae lack the ability to echolocate. Specifically, several species within the genus *Rousettus* (*R. aegyptiacus* being the most studied) have been shown to use echolocation. Echolocation is thought to have been lost in the lineage of Pteropodidae but re-acquired relatively recently by *Rousettus* as simple tongue clicks (unlike the more specialized laryngeal echolocation pulses used by all other echolocating bats; e.g., Waters and Vollrath, 2003). *Rousettus* uses echolocation primarily for orienting in cave roosts and not for detecting and identifying small insects or for flying in cluttered environments. It is therefore of some interest that the high-frequency hearing of the echolocating *R. aegyptiacus* (R in Fig. 5) is typical of that found in non-echolocating mammals. It seems that its unspecialized echolocation has not exerted selective pressure for extended high-frequency hearing beyond that normally used for passive localization of brief sounds. Because it echolocates quite differently from the laryngeal echolocators and because it lies so close to the regression line, we are currently grouping it with the 'non-echolocators' for the purpose of the multiple regression analysis. Further tests with other click-echolocating bats and with very large laryngeal echolocators may eventually provide further insight into their most appropriate grouping.

These results have implications for the evolution of echolocation in bats. Given that *R. aegyptiacus* can use a simple form of echolocation, we know it would not have been necessary to hear higher than about 65 kHz in order to develop an useful form of echolocation. Because early bats were small, they are virtually certain to have heard frequencies at least that high for passive localization. Once they began to use the information in reflected sound, the higher resolution of high-frequency echoes would have made it advantageous to detect even higher frequencies, the result of which we now observe in the echolocating bats in both major suborders (Vespertilioniformes and Pteropodiformes). Thus, echolocation is very likely improved by sensitivity to very high frequencies, even if it began simply by taking advantage of the good high-frequency hearing bats had acquired for localizing sound passively. From this perspective, it is not difficult to conceive of a function as seemingly complex as echolocation evolving independently more than once, as is consistent with one interpretation of recent molecular phylogenies (Eick et al., 2005; Teeling et al., 2005) that reveal the traditional suborder, Microchiroptera, to be polyphyletic. The basic ingredients of high-frequency sensitivity and a neural mechanism for localizing sound were already in place, and the added advantage of perceiving objects and obstacles in the dark would be considerable for a nocturnal flyer.

4.2. Low-frequency hearing

Fig. 6[1] shows the distribution of low-frequency hearing limits in behaviorally tested mammals. The ability of *E. helvum* to hear down to 1.38 kHz at 60 dB gives it the distinction of having the best low-frequency hearing so far of any bat with a behaviorally determined audiogram. [Although it has been suggested that at least one species of bat, *Trachops cirrhosus*, can detect lower frequencies using tape recorded sounds under field conditions (Ryan
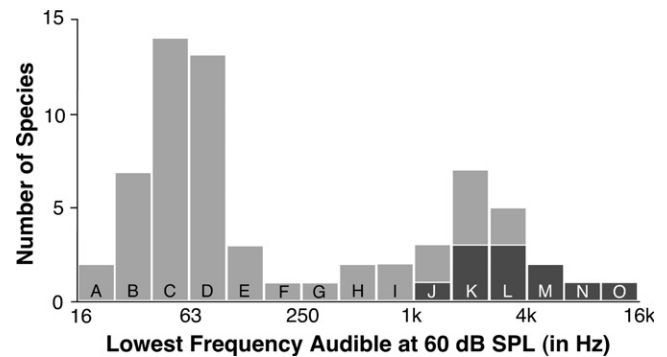

Fig. 6. Distribution among terrestrial mammals of the lowest frequency audible at 60 dB SPL (referred to as the low-frequency hearing limit). Each bar represents 2/3 octave; bats are indicated by dark shading with the non-echolocating bats falling into bins J and L (the names of the individual species can be found in footnote 1), other mammals are indicated by light shading.

et al., 1983), this possibility awaits confirmation in controlled acoustic conditions.] Yet, even the 1.38 kHz hearing of *E. helvum* is still quite limited when compared to the low-frequency hearing of other mammals, most of which can hear frequencies below 125 Hz (Heffner et al., 2001a, 2003). Even among small species, such as most rodents and small primates, good low-frequency hearing is common, as can be seen in Fig. 6.

The inability of bats and several other species to hear frequencies below about 500 Hz may have implications for their auditory processing. Specifically, these species may not use a temporal code for pitch and instead rely only on place coding on the basilar membrane (Heffner et al., 2001a, 2003). It may be worth emphasizing that, at least based on the species tested so far, non-echolocating and echolocating bats appear to be similar in their limited low-frequency hearing, in contrast to their difference in high-frequency hearing. Thus, it is quite likely that high- and low-frequency hearing evolve independently, presumably under different selective pressures.

Acknowledgements

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[1] **A, 16–25 Hz**: Indian elephant *Elephas maximus*[1], Domestic cow *Bos taurus*[2]. **B, 26–40 Hz**: Japanese macaque *Macaca fuscata*[3], Black-tailed prairie dog *Cynomys ludovicianus*[4], Human *Homo sapiens*[5], Gerbil *Meriones unguiculatus*[6], Ferret *Mustela putorius*[7], Eastern chipmunk *Tamias striatus*[8], Woodchuck *Marmota monax*[8]. **C, 41–63 Hz**: Kangaroo rat *Dipodomys merriami*[9,10], Domestic pig *Sus scrofa*[11], White-tailed prairie dog *Cynomys leucurus*[4], Rhesus macaque *Macaca mulatta*[12], Yellow Baboon *Papio cynocephalus*[13], Blue monkey *Cercopithecus mitis*[14], Guinea pig *Cavia porcellus*[15], Chinchilla *Chinchilla laniger*[16], Least weasel *Mustela nivalis*[17], Gray-cheeked mangabey *Cercopithecus mitis* (extrapolated value)[18], Blind mole rat *Spalax ehrenbergi*[19], Domestic cat *Felis domesticus*[20], Domestic horse *Equus caballus*[2], DeBrazza monkey *Cercopithecus neglectus*[21]. **D, 64–100 Hz**: Naked mole rat *Heterocephalus glaber*[22], Ring-tailed lemur *Lemus catta*[23], Domestic dog *Canis familiaris*[24], Vervet *Cercopithecus aethiops*[21], Reindeer *Rangifer tarandus*[23], Brown lemur *Lemur fulvus*[26], Domestic goat *Capra hircus*[11], Slow loris *Nyctecebus coucang*[27], Lesser bushbaby *Galago senegalensis*[28], Domestic rabbit *Oryctolagus cuniculus*[10], Golden hamster *Mesocricetus auritus*[8], Tree shrew *Tupaia glis*[29], Squirrel monkey *Saimiri sciureus*[30]. **E, 101–160 Hz**: Fox squirrel *Sciureus niger*[31], Potto *Perodicticus potto*[27], Domestic Sheep *Ovis aries*[32]. **F, 161–250 Hz**: Northern fur seal *Callorhinus ursinus*, tested in air[33]. **G, 251–400 Hz**: Pocket gopher *Geomys bursarius*, vestigial hearing[34]. **H, 401–630 Hz**: Hedgehog *Hemiechinus auritus*[35], Norway hooded rat *Rattus norvegicus*[36]. **I, 631–1000 Hz**: Wood rat *Neotoma floridana*[37], Cotton rat *Sigmodon hispidus*[10]. **J, 1–1.6 kHz**: Virginia opossum *Didelphis virginia*[38], **Straw-colored fruit bat *Eidolon helvum***, Darwin's mouse *Phylotus darwini*[8]. **K, 1.6–2.5 kHz**: Indian false vampire bat *Megaderma lyra*[39], Greater spear-nosed bat *Phylostomus hastatus*[40], Grasshopper mouse *Onychomys leucogaster*[37], Domestic mouse *Mus musculus*[41], Egyptian fruit bat *Rousettus aegyptiacus*[42], Spiny mouse *Acomys cahirinus*[8], wild House mouse *Mus musculus*[10]. **L, 2.5–4 kHz**: **Dog-faced fruit bat *Cynopterus brachyotis***, Jamaican fruit bat *Artibeus jamaicensis*[43], Gray short-tailed opossum *Monodelphis domestica*[44], Llaca *Marmosa elegans*[45], Big brown bat *Eptesicus fuscus*[46]. **M, 4–6.3 kHz**: Greater horseshoe bat *Rhinolophus ferrumequinum*[47], Short-tailed fruit bat *Carollia perspicillata*[48]. **N, 6.3–10 kHz**: Fish-eating bat *Noctilio leporinus*[49]. **O, 10–16 kHz**: Little brown bat *Myotis lucifugus*[50].

[1] Heffner and Heffner, 1982; [2] Heffner and Heffner, 1983; [3] Jackson et al., 1999; [4] Heffner et al., 1994; [5] Jackson et al., 1999; Sivian and White, 1933; [6] Ryan, 1976; [7] Kelly et al., 1986; [8] Heffner et al., 2001; [9] Webster and Webster, 1972; [10] Heffner and Masterton, 1980; [11] Heffner and Heffner, 1990; [12] Pfingst et al., 1975; [13] Hienz et al., 1982; [14] Brown and Waser, 1984; [15] Heffner et al., 1971; [16] Heffner and Heffner, 1991; [17] Heffner and Heffner, 1985a; [18] Wendt, 1934; [19] Heffner and Heffner, 1992; [20] Heffner and Heffner, 1985b; [21] Owren et al., 1988; [22] Heffner and Heffner, 1993; [23] Gillette et al., 1973; [24] Heffner, 1983; [25] Flydal et al., 2001; [26] Sutherland et al., 1988; [27] Heffner and Masterton, 1970; [28] Heffner et al., 1969a; [29] Heffner et al., 1969b; [30] Beecher, 1974; Green, 1975; [31] Jackson et al., 1997; [32] Wollack, 1963; [33] Babushina et al., 1991; [34] Heffner and Heffner, 1990; [35] Ravizza et al., 1969b; [36] Heffner et al., 1994; [37] Heffner and Heffner, 1985c; [38] Ravizza et al., 1969a; [39] Schmidt et al., 1983; [40] Koay et al., 2002; [41] Koay et al., 2002; [42] Koay et al., 1998; [43] Heffner et al., 2003; [44] Frost and Masterton, 1994; Reimer and Bauman, 1995; [45] Frost and Masterton, 1994; [46] Koay et al., 1997; [47] Long and Schnitzler, 1975.

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