HEARING RESEARCH

Hearing in American leaf-nosed bats. III: *Artibeus jamaicensis*

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Abstract

We determined the audiogram of the Jamaican fruit-eating bat (Phyllostomidae: *Artibeus jamaicensis*), a relatively large (40–50 g) species that, like other phyllostomids, uses low-intensity echolocation calls. A conditioned suppression/avoidance procedure with a fruit juice reward was used for testing. At 60 dB SPL the hearing range of *A. jamaicensis* extends from 2.8 to 131 kHz, with an average best sensitivity of 8.5 dB SPL at 16 kHz. Although their echolocation calls are low-intensity, the absolute sensitivity of *A. jamaicensis* and other 'whispering' bats does not differ from that of other mammals, including other bats. The high-frequency hearing of *A. jamaicensis* and other Microchiroptera is slightly higher than expected on the basis of selective pressure for passive sound localization. Analysis suggests that the evolution of echolocation may have been accompanied by the extension of their high-frequency hearing by an average of one-half octave. With respect to low-frequency hearing, all bats tested so far belong to the group of mammals with poor low-frequency hearing, i.e., those unable to hear below 500 Hz.
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Key words: Audiogram; Chiroptera; Echolocation; Evolution; Mammal

1. Introduction

With over 150 species, the family of American leaf-nosed bats (Phyllostomidae) is one of the most successful and widely distributed families of bats, ranging from southwestern USA, Central America, to as far south as northern Argentina (Ortega and Castro-Arellano, 2001). Their diets are similarly diverse, with different species feeding on pollen, nectar, fruit, and insects, as well as some that eat vertebrates, and true vampires that feed on blood (Gardner, 1977; Nowak, 1999). The echolocation calls of phyllostomids (usually emitted through their nostrils) consist of short, multiharmonic, and frequency-modulated sweeps. Because these sonar calls are typically 40–60 dB less intense than those of insectivorous bats that pursue insects in the open, phyllostomids are often referred to as 'whispering' bats (Grinnell and Griffin, 1958; Howell, 1974).

As part of a survey of hearing abilities in bats, we have been examining the hearing of phyllostomids (Koay et al., 2002, 2003). One purpose of these studies was to determine if the use of low-intensity echolocation calls is associated with unusual sensitivity in the bats' hearing range. Another goal was to increase the sample of bats for which audiograms are available, in an effort to determine if the specialization of bats for echolocation has affected their passive hearing abilities, particularly their ability to hear high frequencies.

In this study, we determined the audiogram of the Jamaican fruit-eating bat *Artibeus jamaicensis*, a relatively large (40–50 g) species that, like other phyllostomids, uses low-intensity echolocation calls. *A. jamaicensis* prefers figs, feeding high in the forest canopy where it is exposed to predators, which it avoids with the aid of social alarm calls (Bonaccorso and Gush, 1987). Like other frugivorous phyllostomids, *A. jamaicensis* relies primarily on olfaction to detect and locate ripe fruits, while echolocation is used primarily for obstacle avoidance and orientation to objects in the environment (Bonaccorso and Gush, 1987; Kalko et al., 1996; Morrison, 1978).

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2. Methods

2.1. Subjects

Three *A. jamaicensis* (one female, A, and two males, B and C), approximately 2–3 years old, were used in this study. They were maintained in captivity on a diet of mixed fruit (see Barnard, 1995). While being tested, the bats were individually housed in wood and plastic mesh cages (48×39×95 cm) and allowed to fly daily in the test chamber. They had free access to water and received their food in the form of fruit juice during the test sessions. Supplements of fruit were given as needed to maintain a healthy body weight. The use of animals in this study was approved by the University of Toledo Animal Care and Use Committee.

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
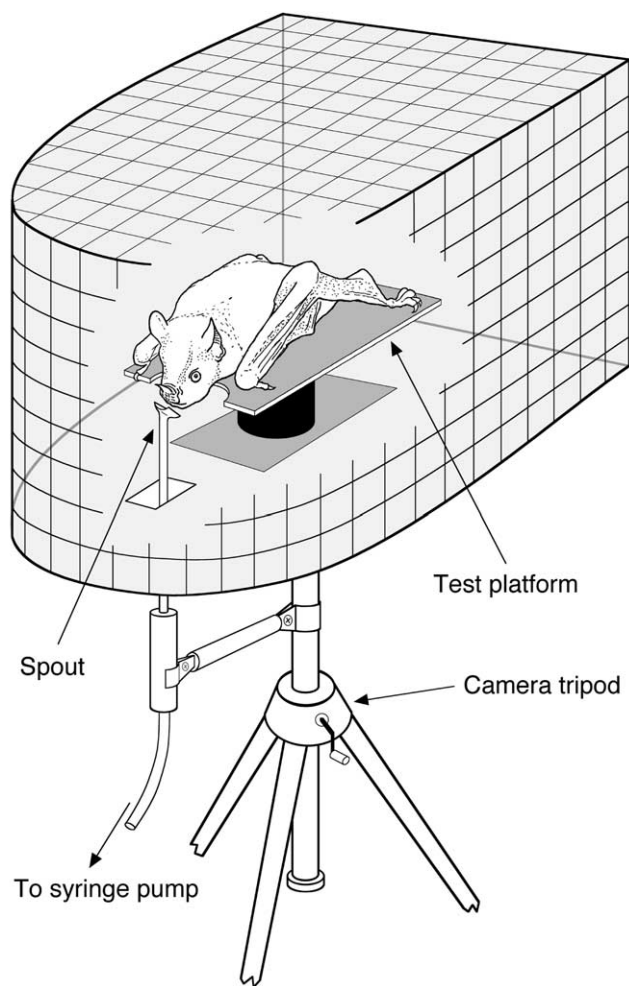

Fig. 1. Drawing of *A. jamaicensis* in the test cage.

with egg-crate foam. The equipment for stimulus generation and behavioral measurement was located outside the chamber and the bats were observed via closed-circuit television.

The bats were tested in a cage (37×22×23 cm) constructed of 0.5-in (1.26-cm) wire mesh, and raised 92 cm above the floor on a tripod (Fig. 1). A reward spout (2-mm-diameter brass tube, topped with a 4×6-mm oval lick plate attached at a 45° angle) was mounted vertically such that it projected into the front of the cage at 7 cm above the floor. The spout was attached, via plastic tubing, to a 30-cc glass syringe that served as the fruit juice reservoir. Fruit juice (consisting of a mix of cantaloupe, pear juice, and vitamin supplement, finely blended and sieved) was dispensed using a syringe pump. Both the syringe pump and food reservoir were housed in a high-density polyethylene box (64×21× 28 cm). To eliminate the noise generated when the pump was activated, the box was lined with egg-crate foam and placed on the floor behind the cage.

During testing, a bat rested on a small platform (15×8×7 cm) located directly behind the reward spout. The tip of the reward spout was placed at the same height and 1 cm in front of the platform, thus minimizing obstructions between the animal's ears and the loudspeaker while it ate from the spout. The platform was covered with a piece of dampened carpet to provide good traction and facilitate electrical contact as it ate from the spout. A contact circuit connected between the food spout and platform was used to detect when an animal made contact with the spout and to activate the syringe pump. Requiring the bat to maintain mouth contact with the spout served to keep its head in a fixed position within the sound field.

A shock generator was also connected between the reward spout and platform. The shock was adjusted for each individual to the lowest level that produced a consistent avoidance response, in the form of backing away slightly or lifting its head from the spout. Shock levels ranged from 35 V (0.18 mA) to 74 V (0.34 mA). A 25-W light, mounted 0.5 m 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 generated using a signal generator (Zonic A&D 3525 for frequencies of 100 kHz and below, or Krohn-Hite 2400 AM/FM Phase Lock Generator for frequencies above 100 kHz) and continuously monitored using a frequency counter (Fluke 1900A). The tones were pulsed (Coulbourn S53-21, 400 ms on and 100 ms off for four pulses) and routed through a rise-fall gate (Coulbourn S84-04, set to 10 ms rise-de-

cay). The signal was then bandpass filtered (Krohn-Hite 3202, 24 dB/oct rolloff starting 1/3-octave above and below the test frequency) and the intensity attenuated (Hewlett Packard 350D) as needed for threshold determination. Finally, the electrical signal was amplified (Crown D75 or Adcom GFA545), monitored with an oscilloscope (Tektronix TDS210), and routed to a loudspeaker in the test chamber. The loudspeaker was placed approximately 1 m in front of the cage directly facing the bat (at a height of 1 m) when it was eating from the spout.

Various loudspeakers were used to present the tones – for frequencies of 1–2.8 kHz either a 15-in (38-cm), 12-in (30.4-cm) or one of two 6-in (15.2-cm) woofers (Infinity RS2000) were used, whereas for frequencies from 4 to 140 kHz, one of two ribbon tweeters (Panasonic EAS-10TH400C) was used. Note that loudspeakers 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 all bats at the following frequencies: 2, 2.8, 5.6, 12, 16, 32, 40, 50, 56, 80, 90, 100, 110, and 140 kHz. Additional thresholds were also obtained for bat A at 1, 4, 8, 20, 45, 64, 71, and 125 kHz.

To detect the contribution of pinna directionality to variation in sensitivity in the mid-frequency range, thresholds for three frequencies were also obtained for bat A, with the loudspeaker placed 30° above or below the horizon in the median sagittal plane. Selection of the frequencies for testing was based on the obtained audiogram, i.e., the mid-frequency decrease in sensitivity at 40 kHz, and the most sensitive frequencies above and below that point, at 16 kHz and 56 kHz, respectively.

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 ate from the spout, and pointing it directly at the loudspeaker. The sound pressure level (SPL re 20 μN/m^2) for frequencies of 100 kHz and below was measured daily with a 1/4-in (0.64-cm) microphone (Brüel and Kjaer 4939, corrected for free-field with the protection grid on), preamplifier (Brüel and Kjaer 2669), and measuring amplifier (Brüel and Kjaer 2608). For measuring frequencies above 100 kHz, a 1/8-in (0.32-cm) microphone (Brüel and Kjaer 4138, corrected for free-field with the protection grid on) was used in place of the 1/4-in microphone. The output of the measuring amplifier was then routed to a spectrum analyzer (Zonic A&D 3525) to monitor the speaker output for harmonics or distortion. Subsequent testing demonstrated that any measurable harmonics were at least 50 dB below the fundamental fre-

quency and at least 20 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 a bat continuously licked a spout to receive a steady trickle of fruit juice. It was then trained to break contact with the spout whenever it detected a tone to avoid impending shock (Heffner and Heffner, 1995).

A hungry bat was initially trained to climb onto the platform and drink from the reward spout. Requiring the bat to maintain contact with the spout served to orient it towards the loudspeaker and also activated the syringe pump to dispense a steady trickle of juice. A train of four tone pulses was then presented at random intervals, followed at its offset by a mild electric shock (300 ms duration) delivered between the spout and platform. The bat learned to avoid the shock by breaking contact with the spout whenever it heard the tones and readily returned to the spout after the shock had been delivered (as indicated by the offset of the shock-indicator light).

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. Approximately 22% of the trial periods contained a pulsing tone (warning signal), whereas no sound was presented in the remaining trial periods (safe signal). The contact circuit was used to detect whether the bat was in contact with the spout during the last 150 ms of each trial. If the bat 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 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 proportionately reduces the hit rate by the false alarm rate associated with each intensity (i.e., each block of trials) and varies from 0 (no hits) to 1 (100% hit rate with no false alarms).

Auditory thresholds were determined by successively reducing the intensity of the tones (in blocks of 6–10 warning trials) until the bat no longer responded to the
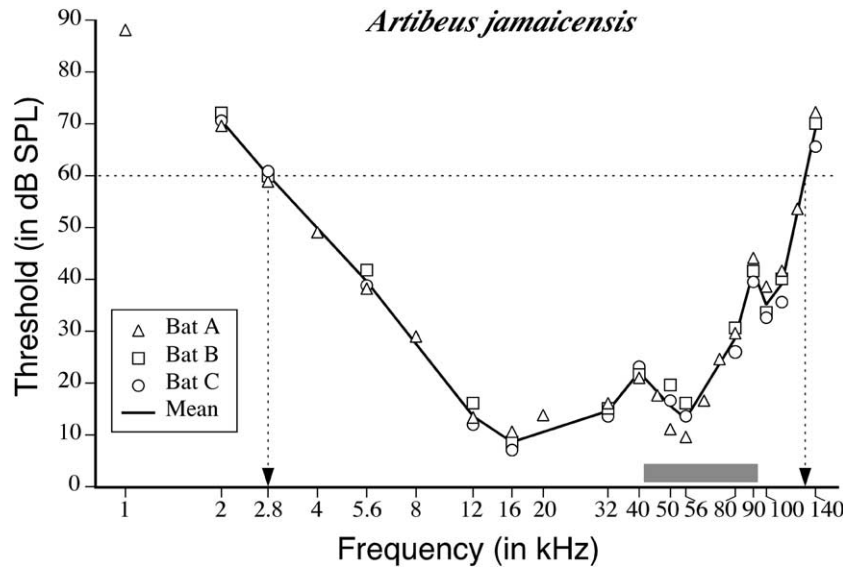
Fig. 2. Audiograms of three *A. jamaicensis*. The gray bar indicates the dominant frequencies in their echolocation call, sweeping from 92 kHz to 42 kHz (Pye, 1967; Gould, 1977); dotted lines and arrows indicate the range of frequencies audible at 60 dB SPL.

warning signal above chance (i.e., the hit and false alarm rates did not differ significantly; $P > 0.05$, 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. Once an audiogram had been completed, selected frequencies were rechecked to ensure reliability.

3. Results

In a typical test session, lasting approximately 1.5–2 h, a Jamaican fruit-eating bat can consume up to 25 ml of fruit juice and received as many as 80 warning trials (and approximately 300 associated safe trials). Because of the rapid passage of food through their digestive system, each session included at least two bouts of feeding, with 20- to 30-min pauses in between. This feeding pattern is common among frugivores because they are adapted to eating large amounts of an abundant, but protein-poor, diet (Morrison, 1978; Studier et al., 1983). With the relatively large number of trials, a threshold at a single frequency could usually be obtained in each session.

The thresholds of the three *A. jamaicensis* (Fig. 2) show good agreement between individuals. Beginning with a threshold of 88 dB at 1 kHz, sensitivity increased rapidly (approximately 20 dB per octave) as frequency increased, with the lowest mean threshold of 8.5 dB at 16 kHz. From 16 kHz to 40 kHz, hearing sensitivity gradually declined, reaching a mean threshold of 22 dB

at 40 kHz; this was followed by gradual improvement to a 13-dB mean threshold at 56 kHz. At frequencies above 56 kHz, hearing sensitivity rapidly declined to 69 dB at 140 kHz, broken only by a slight improvement at 100 kHz. At a level of 60 dB SPL, the audiogram extends from 2.8 to 131 kHz, a range of 5.5 octaves.

To explore the possibility that the decrease in sensitivity at 40 kHz, or the secondary sensitivity peak at 56 kHz, might have been due to pinna directionality, additional thresholds at 16, 40, and 56 kHz were deter-
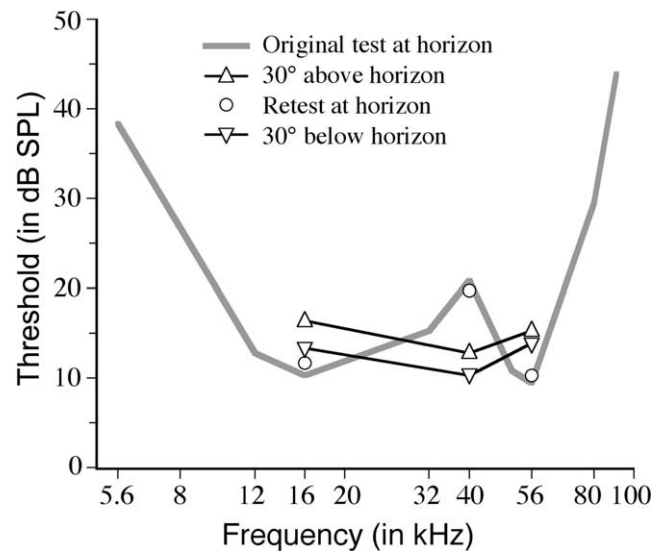

Fig. 3. Original thresholds for bat A determined with the speaker located on the horizon (0° elevation, gray line) and then with the speakers located 30° above and below the horizon, with replication at the horizon. The decrease in sensitivity at 40 kHz is apparent only at 0°, suggesting that filtering effects of the pinna influence detectability as a function of elevation.
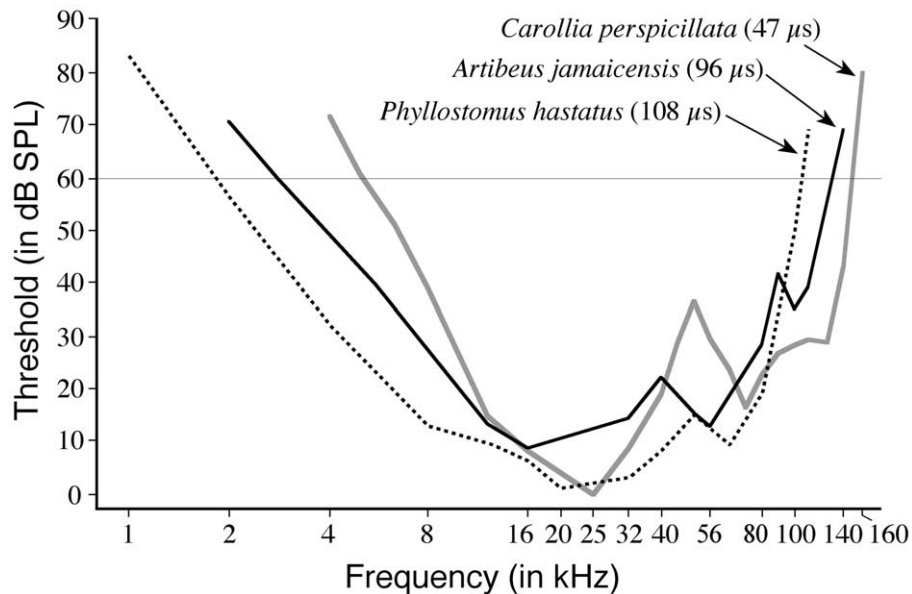
Fig. 4. Audiograms for three species of Phyllostomidae: *A. jamaicensis*, *P. hastatus* (Koay et al., 2002), and *C. perspicillata* (Koay et al., 2003). Functional interaural distance (in parentheses) was estimated for each species by measuring the shortest distance around the head from one auditory meatus to the other. This distance was then converted to the time (in μs) required for a sound to travel around a sphere of the same hemi-circumference. Note that even among closely related species, high- and low-frequency hearing vary with functional interaural distance, with the smallest species hearing the highest frequencies and the largest species hearing the lowest frequencies (see Section 4.2).

mined at 30° above and below the horizon in the median sagittal plane for bat A. As shown in Fig. 3, as the elevation of the sound source moved above or below the horizon, hearing thresholds at 40 kHz improved. In contrast, sensitivity was either unaffected or decreased slightly at the flanking frequencies. Note that replication of the thresholds at 0° elevation showed good agreement with the bat's original thresholds. Thus the changes seen at the different elevations cannot be attributed to re-test variation.

4. Discussion

4.1. Comparison with other phyllostomid bats

With the inclusion of the present audiogram, there are now five species of phyllostomids whose hearing has been studied behaviorally. However, not all of the available audiograms are directly comparable. In one study (Ryan et al., 1983), unconditioned responses of frog-eating bats (*Trachops cirrhosus*) were obtained to tape-recorded tones. However, unconditioned responses occur only to sounds that are relatively loud to the animal and do not reflect absolute threshold. In another study, thresholds were obtained for lesser spear-nosed bats (*Phyllostomus discolor*) using a Y-maze in which the bats had to crawl 1 m to the source of the sound (Esser and Daucher, 1996). The resulting thresholds were unusually high and variable, with thresholds at each frequency varying over a range averaging about 28 dB, most likely due to the difficulty of the task. Thus, we have chosen to limit our comparison to phyllostomids whose thresholds were determined with techniques that were both valid and reliable.

Fig. 4 illustrates the audiograms for three phyllostomid bats, all of which emit low-intensity echolocation calls – the greater spear-nosed bat (*Phyllostomus hastatus*, Koay et al., 2002), the short-tailed fruit bat (*Carollia perspicillata*, Koay et al., 2003), and the Jamaican fruit-eating bat (*A. jamaicensis*, current report). There is no indication of unusual sensitivity among these three species. Indeed, their best hearing is very close to the 2.9-dB mean (S.D. 9.8 dB) for 67 surface-dwelling mammals. The typical sensitivity of these 'whispering' bats makes it clear that the use of low-intensity echolocation calls is not associated with unusually good or poor sensitivity in this family.

The frequencies to which the three phyllostomids are most sensitive lie in a relatively narrow range, well below the dominant frequencies of their echolocation calls. Frequencies in this range are used in communication, especially between mother and infant (e.g., Bohn et al., 2001; Gould, 1975; Sterbing, 2002). The fact that communication calls often fall in the frequency range of an animal's best sensitivity may be due either to the calls conforming to the audiogram, or to the audiogram adjusting to accommodate the calls, or both. On the other hand, the secondary peak(s) of sensitivity closely corresponds to the dominant frequencies in the bats'

echolocation calls. In *A. jamaicensis*, the strongest components are the second and third harmonics, sweeping from 92 kHz to 42 kHz (Gould, 1977; Pye, 1967). These are also the frequencies that seem to be selectively filtered by the pinnae as a function of elevation and may be especially useful in localizing the sources of sound-reflecting and sound-emitting objects (Jen and Chen, 1988; Wotton et al., 1995; Wotton and Jenison, 1997). Of particular interest for comparative hearing is the variation in high- and low-frequency hearing, which is discussed below.

4.2. Comparisons with mammals

4.2.1. High-frequency hearing

The ability of mammals to hear frequencies above 10 kHz enables them to use the spectral cues for sound locus, namely the binaural spectral-difference cue and monaural pinna cues. To use these spectral cues, mammals must hear frequencies high enough to be effectively shadowed by their heads and pinnae (Heffner and Heffner, 1998; Masterton et al., 1969). The smaller its functional interaural distance and pinnae, the higher the frequencies a mammal must hear in order to obtain useable binaural spectral-difference and pinna cues. The relationship between functional interaural distance and high-frequency hearing is illustrated in Fig. 5, where functional interaural distance is defined as the time required for sound to travel around the head from one ear to the other (or, in the case of marine mammals, through the head; Masterton et al., 1969). As can be seen, animals with functionally small heads generally have better high-frequency hearing than those with functionally larger heads ($r = -0.79$, $P < 0.0001$). This relationship is evident even among closely related species, as seen in the three Phyllostomidae (Fig. 4) and Sciuridae (Heffner et al., 2001). Different hearing in closely related species that differ in functional interaural distance suggests that high-frequency hearing is not an evolutionarily conservative trait, but that it changes rapidly in response to the need to localize sound. Thus, given their small interaural distance, it comes as no surprise that the most notable feature of the three phyllostomid bats (Fig. 4) is their excellent high-frequency hearing.

4.2.2. Allometry and high-frequency hearing

An alternative explanation of the relationship between high-frequency hearing and the size of an animal's head is that it is simply due to allometric scaling. Because the size of an animal's middle ear is determined by the size of its head, and because small middle ears are better able to transduce high frequencies than larger middle ears, small mammals have better high-frequency hearing than large mammals (for discussions of middle

ear transduction, see Nummela, 1995, and Rosowski, 1992). However plausible this hypothesis may appear from an engineering standpoint, the notion that high-frequency hearing might be determined by allometric scaling without regard for its adaptive value has little appeal from a biological perspective.

If high-frequency hearing is determined by the size of the middle ear, then we should expect members of the same species to have different high-frequency hearing limits depending on their size. However, this does not appear to be the case, as the high-frequency hearing of dogs is not linked to head size, body size, or to the area of the tympanic membrane, despite wide variation in these physical parameters (Heffner, 1983). Similarly, variation in human high-frequency hearing has not been linked to size in humans even though the area of the adult tympanic membrane ranges from 50 to 90 mm^2 (von Bekesy and Rosenblith, 1951). Allometric scaling also cannot explain the observation that pocket gophers, blind mole rats, and naked mole rats – small mammals with small middle ears (Mason, 2001) – do not hear high frequencies (see Fig. 5). On the other hand, this observation is consistent with the hypothesis that mammals use high-frequency hearing for sound localization because, being subterranean dwellers, these three rodents do not localize sound and are no longer under selective pressure to hear high frequencies for that use (Heffner and Heffner, 1990, 1992, 1993). Finally, from a biological standpoint, the idea that the hearing range of an animal is passively determined by its head size is, to say the least, surprising, as no similar occurrence has been suggested for other sensory systems. For example, there is widespread variation in the resolution and frequency response of the eye that is attributable to selective pressure, with no indication that this variation is imposed by the size of the animal (Marshall and Oberwinkler, 1999; Reymond, 1985).

In summary, the best available explanation for the variation in mammalian hearing is that it is the result of selective pressure, with the requirements of sound localization exerting the most pressure on high-frequency hearing. The idea that the variation in mammalian high-frequency hearing might simply be due to allometric scaling addresses *how* questions but not *why* questions: the size of the middle ear is a likely determinate of *how* a mammal is able to hear high frequencies, but it is selective pressure, probably for sound localization, that determines *why* it hears them. Contributing to the confusion is the fact that small middle ears transduce high frequencies quite well and many small mammals have small middle ears; but this is not because their heads are small, since small mammals are certainly capable of having large ears when necessary, as demonstrated by the enlarged bullae of many Heteromyid and Gerbilline rodents (Lay, 1972; Web-
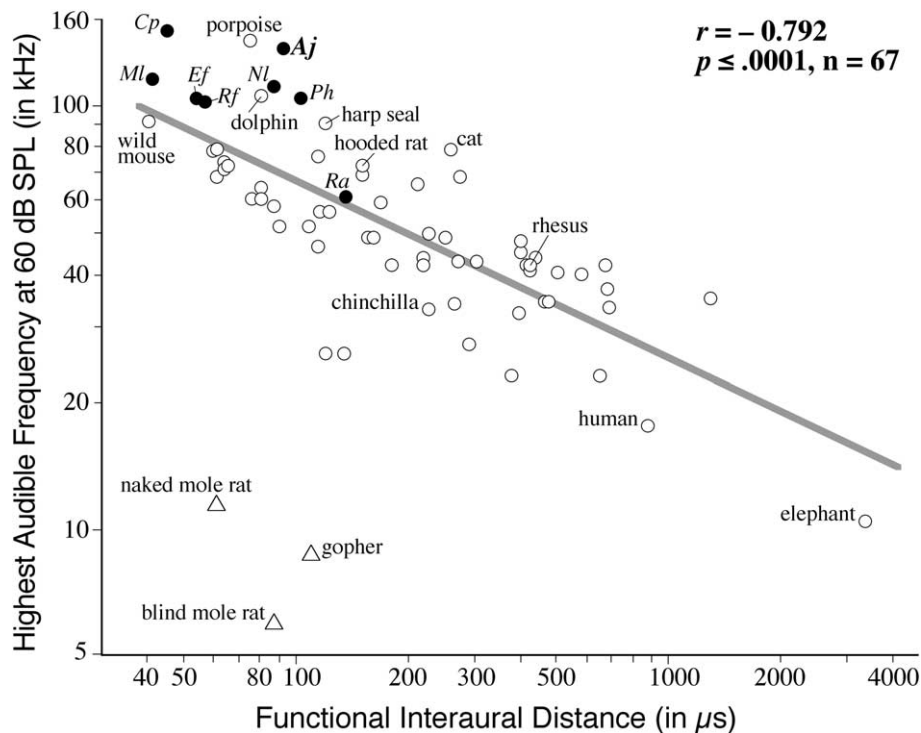
Fig. 5. Relationship between functional interaural distance and high-frequency hearing (highest audible frequency at 60 dB SPL) for mammals. Aj, *A. jamaicensis*; Cp, *C. perspicillata* (Koay et al., 2003); Ef, *Eptesicus fuscus* (Dalland, 1965; Koay et al., 1997); Ml, *Myotis lucifugus* (Dalland, 1965); Nl, *Noctilio leporinus* (Wenstrup, 1984); Ph, *P. hastatus* (Koay et al., 2002); Ra, *Rousettus aegyptiacus* (Megachiroptera; Koay et al., 1998); Rf, *Rhinolophus ferrumequinum* (Long and Schnitzler, 1975); some familiar species are labeled for comparison; subterranean species (open triangles) are not included in the correlation.

ster and Webster, 1984). Rather small mammals have small middle ears because small ears are well-suited to transducing the sounds important for survival.

4.2.3. Echolocation and high-frequency hearing

Although bats no doubt require good high-frequency hearing for passive sound localization, it is nonetheless possible that selective pressure for echolocation may have caused bats to evolve slightly better high-frequency hearing than necessary for passive sound localization. With the additional audiograms available for bats, we can now attempt to address this possibility.

First, we can estimate how much selective pressure for sound localization has extended the high-frequency hearing of bats. This can be done by comparing them with subterranean mammals that do not localize sound and therefore are not under selective pressure to hear high frequencies for sound localization. Specifically, the pocket gopher, naked mole rat, and blind mole rat have 60-dB high-frequency hearing limits of 8.7, 11.5, and 5.9 kHz, respectively, for an average of 8.4 kHz (Fig. 5; Heffner and Heffner, 1990, 1992, 1993). Using 8.4 kHz as an average high-frequency limit for a species not under selective pressure to localize sound, we can use the regression line in Fig. 5 to estimate how much higher a mammal with the functional interaural distance of

each bat would be predicted to hear. This value ranges from 3.0 octaves for *P. hastatus* to 3.6 octaves for *Myotis lucifugus*, with a mean of 3.3 octaves for the seven microchiropteran species. Thus, we suggest that approximately 3.3 octaves of the high-frequency hearing of bats may be attributable to selective pressure for passive sound localization.

To address whether echolocation has exerted additional selective pressure on high-frequency hearing, we note that although no single species of Microchiroptera hears significantly higher than predicted, they are not evenly distributed about the regression line (Fig. 5), but instead each hears somewhat higher frequencies than predicted for a mammal with its interaural distance. As a group, Microchiroptera differ reliably from mammals in general ($t = 3.5$, $P = 0.0009$, one-tailed) showing a mean deviation of 0.475 octaves from the regression line. Thus, we conclude that although Microchiroptera are subject to the same selective pressures for passive sound localization that apply to other mammals, their high-frequency hearing has increased by an average of approximately one-half octave to meet the demands of echolocation. An exception among bats is the megachiropteran, *Rousettus aegyptiacus*. The suborder Megachiroptera diverged early in the evolution of bats and is composed almost entirely of non-echolocators.

Although *R. aegyptiacus* is one of the few species that has re-acquired echolocation (in a rudimentary form using tongue clicks; Springer et al., 2001), like other mammals, its high-frequency hearing is very close to that predicted by its functional interaural distance (Fig. 5; Koay et al., 1998). This suggests that the additional high-frequency hearing observed in our sample of Microchiroptera is associated with their use of highly structured echolocation calls.

4.2.4. Low-frequency hearing

Low-frequency hearing limits in mammals, defined as the lowest frequency audible at 60 dB SPL, are distributed over nine octaves, from 17 Hz in the elephant (*Elephas maximus*; Heffner and Heffner, 1982) to 10.3 kHz in the little brown bat (*M. lucifugus*; Dalland, 1965). An important factor in understanding the variation in low-frequency hearing is that low-frequency hearing limits in mammals are bimodally distributed (Heffner et al., 2001). Specifically, the low-frequency hearing limits of terrestrial mammals fall into two distinct groups separated by a gap of nearly two octaves. About two-thirds of the 60 species examined so far hear below 125 Hz, and the mean low-frequency limit for this group is 55 Hz. The remaining one-third do not hear below 500 Hz, and their group mean is 2.3 kHz. All of the bats tested so far belong to the latter group, and *A. jamaicensis* is no exception. At a level of 60 dB,

A. jamaicensis hears only down to 2.8 kHz, and responses could not be elicited to tones below 1 kHz.

As discussed in detail elsewhere (Heffner et al., 2001), we know of no simple ecological or morphological factors that are good predictors of low-frequency hearing in mammals. For example, size is not a distinguishing feature of the species that do, or do not, hear low frequencies. Although most of the mammals that do not hear below 500 Hz are small, there are at least 16 small species that do hear low frequencies, including chipmunks, mole rats, kangaroo rats, gerbils, hamsters, tree shrews, and least weasels – all of which are smaller than some of the species that do not hear low frequencies, such as the Virginia opossum (Heffner and Heffner, 1998).

On the other hand, there is a relationship between low-frequency hearing and high-frequency hearing. In general, the better the high-frequency hearing of a species, the worse is its low-frequency hearing. As shown in Fig. 6, this relationship differs somewhat in the two groups. Mammals with good low-frequency hearing give up relatively little low-frequency hearing (0.72 octaves) to extend their high-frequency hearing by one octave. On the other hand, species in the group with poor low-frequency hearing lose approximately 1.7 octaves of low-frequency hearing for every octave of high-frequency hearing gained. One consequence is that species in this group, including all bats studied so far, have
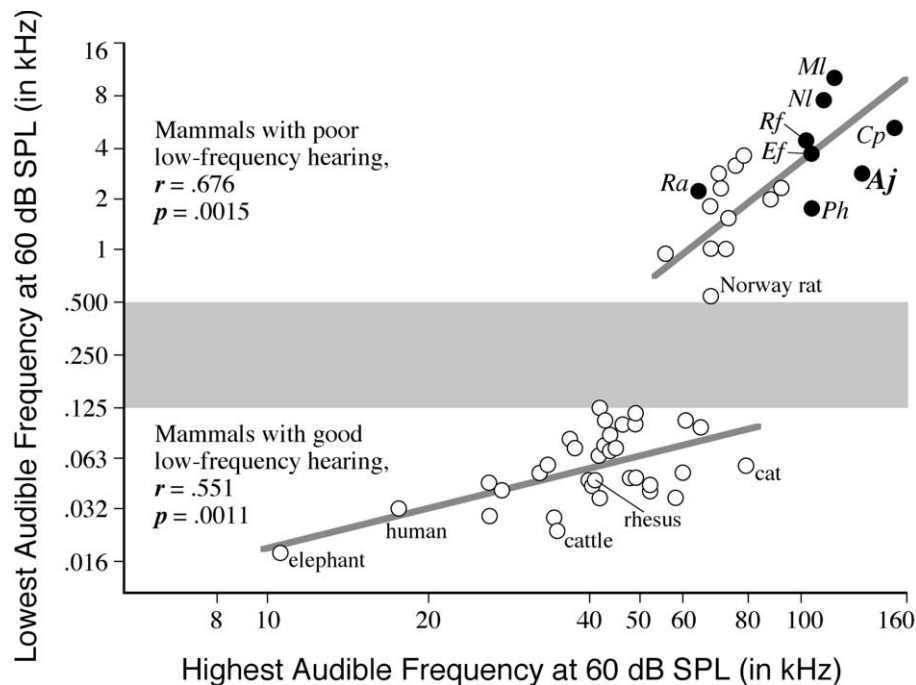

Fig. 6. Relationship between highest and lowest frequencies audible at 60 dB SPL. Note that mammals are divided into two discontinuous groups: the upper group has poor low-frequency hearing and the lower group has good low-frequency hearing. The regression line for the group with poor low-frequency hearing (containing all bats tested so far) has a steeper slope indicating that more low-frequency hearing is lost for each octave of high-frequency gained than in the group with good low-frequency hearing. For abbreviations see Fig. 5; some familiar species are labeled for comparison.

narrower hearing ranges than species in the group with good low-frequency hearing (mean 5.2 versus 9.6 octaves, respectively).

There are three potential explanations for the poor low-frequency hearing in a subset of mammals: (1) low-frequency hearing could be lost because it is incompatible with another feature that is highly adaptive; (2) it could become no longer useful and thus allowed to vary and drift without selective pressure; and (3) it could be detrimental and thus under negative selective pressure.

The influence of physiological and physical constraints on hearing range is an example of the first type of explanation. The finite length of the basilar membrane and the mechanical limitations of the middle ear would seem to limit the ability to detect low frequencies in species that hear very high frequencies (e.g., Fleischer, 1978; Nummela, 1995; Rosowski, 1992; Ruggero and Temchin, 2002; West, 1985). However, although middle and inner ears impose some constraints, these may not be as severe as sometimes thought since there are species, most notably domestic cats and cattle, that can hear 10.5 octaves without sacrificing excellent sensitivity to sound (as low as −10 dB SPL; Heffner and Heffner, 1983, 1985b). Broad hearing ranges also occur in small mammals, with the least weasel that weighs only 45 g and has a functional interaural distance approximately one-quarter that of a cat, hearing over a 10.2-octave range and detecting intensities as low as −8 dB SPL (Heffner and Heffner, 1985a).

The second possibility considers that there might be little benefit to hearing low frequencies in some mammals. However, among vertebrates, hearing low frequencies is nearly universal (Heffner and Heffner, 1998). Low frequencies attenuate less over long distances, making them useful for long-distance communication and for detection at greater distances. The low-frequency hearing that first appeared in fish has been retained in amphibians, reptiles, birds, and in most mammals (Heffner and Heffner, 1998), suggesting that it has strong adaptive value. At this time we cannot suggest any reason why the ability to hear below 500 Hz would not be of use to the mammals with poor low-frequency hearing.

Finally, there may exist some circumstances in which low-frequency hearing could be detrimental. For example, sensitivity to low frequencies could be a disadvantage if low frequencies mask or in some way interfere with the neural analysis of higher frequencies essential for communication or sound localization. It is well established that sounds have greater masking effects on higher frequencies than lower (e.g., Wegel and Lane, 1924). Thus one possibility is that reduced low-frequency hearing prevents low-frequency ambient sounds from masking vocal communications. With regard to sound localization, we have observed that both cats (unpublished observations) and chinchillas (Heffner et al., 1995) localize high-pass noise better than broadband noise when relying on pinna cues.

We suggest that it is important to ask why some animals *do not hear low frequencies* as well as why they hear high. We raise these possibilities to show that investigating the basis for the extraordinary distribution of low-frequency hearing in mammals may lead to important advances in our understanding, not only of the evolution of hearing in mammals, but also of the mechanisms involved.

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