HEARING
RESEARCH

Audiograms of five species of rodents: implications for the evolution of hearing and the perception of pitch

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Abstract

Behavioral audiograms were determined for five species of rodents: groundhog (*Marmota monax*), chipmunk (*Tamias striatus*), Darwin's leaf-eared mouse (*Phyllotis darwinii*), golden hamster (*Mesocricetus auratus*), and Egyptian spiny mouse (*Acomys cahirinus*). The high-frequency hearing of these animals was found to vary inversely with interaural distance, a typical mammalian pattern. With regard to low-frequency hearing, the animals fell into two groups: those with extended low-frequency hearing (chipmunks, groundhogs, and hamsters hear below 100 Hz) and those with restricted low-frequency hearing (spiny and leaf-eared mice do not hear appreciably below 1 kHz). An analysis of mammalian hearing reveals that the distribution of low-frequency hearing limits is bimodal with the two distributions separated by a gap from 125 to 500 Hz. The correspondence of this dichotomy with studies of temporal coding raises the possibility that mammals that do not hear below 500 Hz do not use temporal encoding for the perception of pitch. © 2001 Published by Elsevier Science B.V.

Key words: Audiogram; Evolution; Frequency coding; Groundhog; Chipmunk; Leaf-eared mouse; Hamster; Spiny mouse

1. Introduction

Over the last few years, we have had the opportunity to test the hearing of five species of rodents. This brings the total number of species in the order Rodentia with reasonably complete behavioral audiograms to 20. Each of the five species tested was selected to broaden the sample of mammals whose hearing is known. The eastern chipmunk (*Tamias striatus*) and the groundhog (*Marmota monax*), both sciurids, dig their own nest burrows and were tested to increase the number of burrowing rodents in the sample. In addition, the groundhog is a large rodent (7 kg) and its inclusion expands the size range of the rodents in the sample. Darwin's leaf-eared mouse (*Phyllotis darwinii*), a murid, increases the sample of very small rodents (< 50 g) to four. The golden hamster (*Mesocricetus auratus*), a

murid rodent, is the only common laboratory animal used in auditory research whose behavioral audiogram has not previously been reported. Finally, the spiny mouse (*Acomys cahirinus*), also a murid, is a precocious rodent and was tested to provide information to those interested in an animal that is well developed at birth.

In this report we describe the audiograms of these five species and compare them to those of other mammals to gain insight into the selective pressures involved in the evolution of mammalian hearing. Of particular interest is the finding that mammalian audiograms fall into two distinct groups based on whether or not they show good low-frequency hearing. Analysis of this dichotomous distribution raises the possibility that animals that do not hear below 500 Hz do not use temporal coding for the perception of pitch.

2. Methods

All of the animals were tested using a conditioned suppression/avoidance procedure in which a thirsty animal was trained to lick a water spout in order to re-

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Abbreviations: pps, pulses per second; *r*, correlation coefficient; SPL, sound pressure level re 20 μN/m²

ceive a steady trickle of water (Heffner and Heffner, 1995). Pure tones were then presented at random intervals and followed at their offset by a mild electric shock delivered through the spout. The animal learned to avoid the shock by breaking contact with the spout when a tone was presented, a response indicating that it had heard the tone. Absolute thresholds were then determined for tones throughout each species' hearing range.

2.1. Subjects

Eastern chipmunks (*T. striatus*). Three animals of undetermined sex (designated A, B, and C), weighing 85–111 g, were wild-trapped in Lucas County, OH, USA. They were housed in glass tanks ($50.8 \times 25.4 \times 30.5$ cm) with corncob bedding and provided small wooden nest boxes ($20 \times 9 \times 7.6$ cm). The nest boxes were equipped with sliding doors and were used to transfer the animals from their home cage to the test cage. They were given access to rodent blocks, sunflower seeds, and mixed nuts with occasional supplements of fruits and vegetables.

Groundhogs, also known as marmots or woodchucks (*M. monax*). Four young males (designated A, B, C, and D), weighing 2.7–5.7 kg, were wild-trapped in Lucas and Fulton Counties, OH, USA. They were housed in large glass tanks ($91 \times 32 \times 43$ cm) with corncob bedding and provided free access to rodent blocks, and monkey chow, with occasional supplements of fruits and vegetables. The groundhogs went into hibernation during the fall and winter months during which time they stopped eating and drinking and became torpid. Thus, all testing was conducted during the spring and summer months.

Hamsters (*M. auratus*). Eight male Syrian golden hamsters (designated A through H), weighing 117–140 g, were obtained from Charles River Laboratory and housed in standard solid bottom cages ($33 \times 21.6 \times 19$ cm) with corncob bedding. They were given free access to rodent blocks and occasional pieces of apple.

Darwin's leaf-eared mice (*P. darwinii*). Two females (designated A and B), weighing 35–49 g, were purchased from a local animal supplier. They were housed in the same type of glass tanks and nest boxes used for chipmunks and given free access to rodent blocks, with occasional supplements of seeds and vegetables.

Spiny mice (*A. cahirinus*). Four animals, two males (designated A and C) and two females (designated B and D), weighing 50–69 g, were obtained from a local animal supplier. They were housed and fed in the same manner as the leaf-eared mice.

The animals received water in the test sessions and were weighed before each session to monitor their dep-

rivational state. The care and use of the animals in this study were approved by the University of Toledo Institutional Animal Care and Use Committee.

2.2. Behavioral apparatus

Testing was conducted in a carpeted, double-walled chamber (IAC model 1204; Industrial Acoustics Co., Bronx, NY, USA; $2.55 \times 2.75 \times 2.05$ m). To reduce sound reflections, the walls and ceiling were lined with acoustic foam. The equipment for behavioral and stimulus control was located outside the chamber and the animals were observed over closed-circuit television.

The animals were tested in wire cages mounted approximately 1 m above the chamber floor to minimize sound-reflecting surfaces in the vicinity of the animal. The groundhogs were tested in a cage ($74 \times 38.5 \times 24$ cm) constructed of 1-inch (2.54-cm) welded wire fencing and mounted on four narrow wooden legs. The other rodents were tested in a cage ($35 \times 21 \times 24$ cm) constructed of half-inch (1.27-cm) wire mesh on a supporting frame of 1/8-inch (3.2-mm) brazing rods and mounted on a camera tripod. When testing hamsters and chipmunks, the width of the cage was restricted by a narrow (7-cm), shoulder-high wire mesh fence that ensured they were directly facing a loudspeaker when licking the water spout. The leaf-eared mice and spiny mice were positioned in front of the loudspeaker by requiring them to climb onto a narrow wire mesh platform (16 cm $\times 6 \times 6$ cm) to reach the water spout.

A water spout, consisting of 15-gauge brass tubing with a small brass oval 'lick plate' at the top, came up through the floor in the front of a cage (Fig. 1). The spout was adjusted to a level that permitted an animal to drink comfortably with its head facing towards a loudspeaker. This position placed the spout low enough
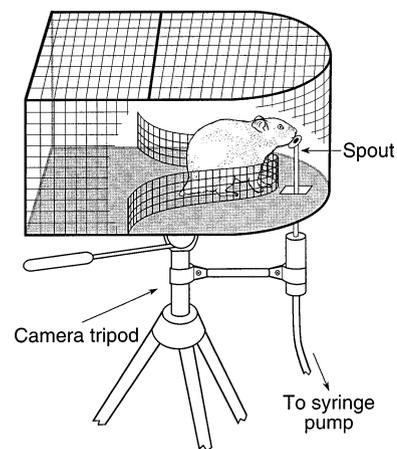

Fig. 1. Drawing of the cage used to test the hamsters and chipmunks.

that it did not interfere with the sound reaching the animal's ears. For the mice, chipmunks, and ground-hogs, water was delivered to the spout from a constant-pressure water reservoir (Marriotte bottle) through an electrically operated water valve with the flow rate controlled by varying the rate of operating pulses sent to the water valve (e.g., 2–3 per s). For the hamsters, water was delivered using a 25-ml syringe pump with an adjustable drive. The flow rate was adjusted so that an animal could obtain adequate water in a single test session lasting 30–60 min. Requiring the animals to keep their mouths on the water spout served to fix their heads in the sound field, allowing precise measurement of the intensity of the sound at their ears.

A contact circuit, connected between the water spout and cage floor, turned on the water whenever an animal touched the spout. Mild shock, which was provided by a shock generator connected between the spout and the cage floor, could be avoided or escaped by breaking contact with the spout. A 15-W light, mounted 0.5 m below the cage, was turned on whenever the shock was on and the animals learned to return to the spout following a shock as soon as the 'shock light' was turned off.

2.3. Acoustical apparatus

Sine waves from 16 to 80 000 Hz were generated by a tone generator (Hewlett Packard 209A or Krohn-Hite 2400) and the frequency verified with a frequency counter (Fluke 1900A). The signal was shaped by a rise/fall gate (Coulbourn S84-04, cosine gating) with a 10-ms rise/fall time for frequencies of 1 kHz and higher. For frequencies from 63 to 500 Hz, rise/fall times were used that allowed at least 10 cycles during signal onset and offset. For 16 and 32 Hz, rise/fall times of 270 and 160 ms, respectively, were used with the signal gated on at zero crossing (i.e., when the phase of the sine wave was at zero voltage).

For frequencies of 125 Hz and higher, four pulses of 400-ms duration each were presented, with a 100-ms interval between pulses. To accommodate the longer rise/fall times, the intertrial interval was lengthened to 160 ms for 32 and 63 Hz. For 16 Hz, the four pulses were 500 ms in duration with a 270-ms inter-pulse interval.

The intensity of the pure tones was adjusted in 5-dB steps using an attenuator (Hewlett Packard 350D), the linearity of which was calibrated throughout the range used in testing. The electrical signal was band-pass-filtered (Krohn-Hite 3550; ±1/3 octave), amplified (Crown D75), and sent to a loudspeaker. The electrical signal to the loudspeaker was monitored with an oscilloscope. One of the following loudspeakers was used each session depending on the frequency being tested:

15-inch (38-cm) or 12-inch (30.5-cm) woofer, 6-inch (15.2-cm) or 3-inch (7.6-cm) midrange, ribbon tweeter or piezoelectric tweeter. The loudspeaker was placed at ear level 1 m in front of the animal for frequencies of 63 Hz and above. At 16 and 32 Hz, the 15-inch loud-speaker, which was mounted in a 0.45-m^3 enclosure, was turned to face into a corner of the acoustic chamber. The test cage was then placed in a standing wave, which was located using the measuring microphone. This arrangement was necessary to achieve a sufficiently intense, but undistorted sound at the location of the animal. It may be noted that sound-measuring microphones are not directionally sensitive at such low frequencies and, indeed, varying the orientation of the microphone did not change the sound pressure level (SPL) reading. As a precaution against substrate-borne vibrations, 8-cm thick foam pads were placed under the woofer and the legs of the test cage when testing 16 and 32 Hz.

The SPL (re 20 μN/m^2) was measured daily using a Brüel and Kjaer 1/4-inch (0.64-cm) microphone (model 4135) or 1-inch (2.54-cm) microphone (model 4231), preamplifier (model 2618), microphone amplifier (model 2608), and filter (Krohn-Hite 3202 set to pass one octave above and below the test frequency). The measuring system was calibrated with a pistonphone (Brüel and Kjaer model 4230). Sound measurements were taken by placing the microphone in the position occupied by an animal's head when it was drinking and pointing it directly toward the loudspeaker (0° incidence). Care was taken to produce an homogeneous sound field (±1 dB) in the area occupied by the animal's head and ears. The acoustic signal was also analyzed for overtones by sending the unfiltered output of the sound level meter to a spectrum analyzer (Zonic 3525). This analysis indicated that overtones, which were present when low-frequency tones were produced at high intensity, were at least 20 dB below the animal's threshold.

2.4. Behavioral procedure

A thirsty animal was trained to make steady contact with the water spout in order to obtain a slow but steady trickle of water. A train of four tone pulses was presented at random intervals and followed at its offset by a mild electric shock (300 ms maximum duration) delivered between the spout and the platform. The animal soon 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 reliably produced an avoidance response. The mildness of the shock was confirmed by the willingness with which an animal returned to the spout after the shock had been delivered.

Test sessions were divided into trials lasting 2–3 s (depending on the frequency being tested) and separated by 1.5-s intertrial intervals. Approximately 22% of the trials contained a pulsing tone (warning signal) while the remaining trials contained only silence (safe signal). The contact circuit detected whether an animal was in contact with the spout during the final 150 ms of every trial. If an animal broke contact for more than half of the 150-ms response period, an avoidance response was recorded. This response was classified as a hit if the trial contained a tone (warning signal) or as a false alarm if the trial consisted of silence (safe signal). Typically, the same tone (i.e., same frequency and intensity) was presented for 6–8 successive warning trials and approximately 30 associated safe trials following which the hit and false alarm rates were calculated. The hit rate was then corrected for false alarms to produce a performance measure for that stimulus using the formula:

$$\text{Performance} = \text{Hit rate} - (\text{False alarm rate} \times \text{Hit rate})$$

This measure proportionately reduces the hit rate by the false alarm rate observed for a particular stimulus and can range from 0 (no hits) to 1 (100% hit rate with no false alarms, i.e., perfect performance).

Auditory thresholds were determined by reducing the intensity of the tone in successive blocks of 6–8 warning trials until the animal no longer responded to the warning signal above the 0.01 level of chance, that is, the hit rate was no longer significantly higher than the false alarm rate (binomial distribution). After a preliminary threshold had been obtained, final threshold determination was conducted by presenting tones varying in 5-dB increments from 10 dB above to 10 dB below the estimated threshold. A typical test session for a trained animal would consist of approximately 35–75 tone (warning) trials and approximately four times as many silent (safe) trials. Threshold was defined as the intensity at which the performance measure equaled 0.50, which was usually obtained by interpolation. For a particular frequency, initial testing was considered complete when the thresholds obtained in at least three different sessions were within 3 dB of each other. Once an entire audiogram had been completed for an individual animal, each frequency was retested at least once to ensure threshold reliability.

3. Results

The audiograms of the five species presented here in graphical form are available in tabular form on the Internet (http://www.utoledo.edu/psychology/animalhearing/).

3.1. Eastern chipmunk

Beginning at 16 Hz, the audiograms of the three eastern chipmunks show a gradual increase in sensitivity as frequency is increased to about 250 Hz with little change in sensitivity between 250 Hz and 45 kHz (Fig. 2). Sensitivity declines rapidly for frequencies above 45 kHz with 56 kHz being the highest frequency to which an animal responded. At a level of 60 dB SPL, the chipmunks have a broad hearing range extending from 39 Hz to 52 kHz (10.4 octaves) with an average best sensitivity of 16.7 dB at 1 kHz. Compared with other mammals, chipmunks have good low-frequency hearing, but relatively poor overall sensitivity as only 500 Hz and 1 kHz are audible at levels below 20 dB SPL.

Because it is unusual (although not unknown) for small animals to hear low frequencies (Heffner and Heffner, 1998), the chipmunk was tested down to 16 Hz. In doing this, it was necessary to rule out the possibility that the chipmunks might have been responding to extraneous cues. Because it can be difficult to generate tones below 63 Hz at high intensities without harmonics, one possibility is that the animals were responding to high-frequency harmonics in the signal. However, a spectrum analysis indicated that all harmonics were at least 20 dB below the animals' thresholds making it unlikely that the animals were responding to them. A second possibility is that the animals were responding to non-auditory cues, such as cage vibrations, air movement on the animals' facial hair or vibrissae (which could occur if the animals were in the 'near-field' portion of the sound field), or that they could see the movement of the loudspeaker diaphragm at low frequencies. However, it is unlikely that the animals were responding to air currents or that they could see the speaker vibrating because at 16 and 32 Hz the speaker was facing away from the animals. Although it is not possible to completely rule out cage vibrations, it should be noted that laboratory rats tested concurrently with the same apparatus never responded to frequencies below 250 Hz even at intensities of 100 dB SPL (Heffner et al., 1994). Thus, we are confident that the low-frequency thresholds are valid.

3.2. Groundhog

Beginning at 32 Hz, the audiograms of the four groundhogs show a gradual increase in sensitivity as frequency is increased with their best hearing occurring at 4 and 8 kHz (Fig. 2). At higher frequencies, sensitivity decreases slightly at 16 kHz, followed by a small increase in sensitivity at 22.4 kHz. Above 22.4 kHz, sensitivity declines rapidly with 32 kHz being the high-
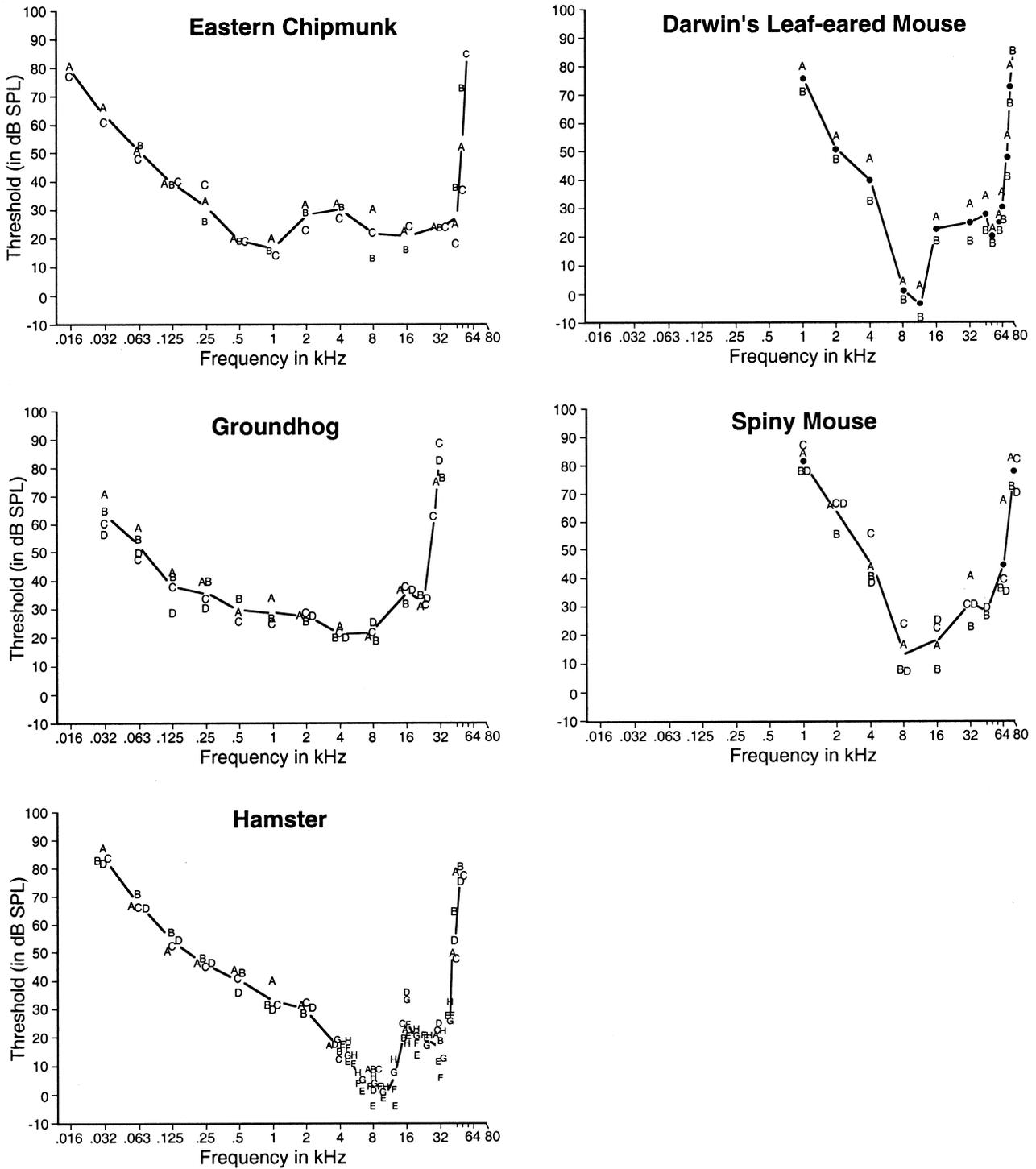
Fig. 2. Audiograms of the five species of rodents. Individual animals are designated by letters. Note that the three species in the left column have more extensive low-frequency hearing than the two species in the right column.

est frequency to which they responded. At a level of 60 dB SPL, the groundhogs have a broad hearing range extending from 40 Hz to 27.5 kHz (9.4 octaves) with an average best sensitivity of 21.5 dB at 4 kHz. Like chipmunks, groundhogs have good low-frequency hearing

and relatively poor sensitivity as they do not hear appreciably below 20 dB SPL. However, their 60-dB high-frequency limit is about one octave lower than that of the chipmunks, making them noticeably less sensitive at high frequencies.

3.3. Hamster

The complete audiograms of four hamsters (hamsters A, B, C, and D) are shown in Fig. 2 along with the partial audiograms of four additional animals (hamsters E–H). Beginning at 32 Hz, the audiograms show a gradual increase in sensitivity as frequency increases up to a comparatively well-defined point of best hearing at 10 kHz. Sensitivity declines noticeably at 16 kHz followed by improvement from 20 to 32 kHz. Above 32 kHz, sensitivity declines rapidly to 50 kHz, the highest frequency to which they responded. At a level of 60 dB SPL, the hamsters show a broad hearing range extending from 96 Hz to 46.5 kHz (8.9 octaves) with an average best sensitivity of 1 dB at 10 kHz. Although the hamsters' low-frequency hearing is not quite as good as that of chipmunks and groundhogs, they have much better sensitivity in their range of best hearing with frequencies from 4 to 12.5 kHz audible at a level below 20 dB SPL.

3.4. Darwin's leaf-eared mouse

Beginning at 1 kHz, the audiograms of the two leaf-eared mice show a comparatively sharp increase in sensitivity as frequency is increased with a well-defined point of best hearing around 11 kHz (Fig. 2). Sensitivity declines at 16 kHz followed by a plateau and an improvement in sensitivity at 45 kHz. Above 64 kHz, sensitivity declines rapidly to 80 kHz, the highest frequency to which one animal responded. At a level of 60 dB SPL, their hearing range extends from 1.55 kHz to 73.5 kHz (5.5 octaves) with an average best sensitivity of −3.5 dB at 11 kHz. Compared with the previous three rodents, Darwin's leaf-eared mice have better high-frequency sensitivity and much poorer low-frequency sensitivity. In addition, they have superior best sensitivity although their ability to hear below 20 dB SPL is limited to a narrow range around 8–11 kHz.

3.5. Spiny mouse

Beginning at 1 kHz, the audiograms of the four spiny mice, like those of Darwin's leaf-eared mice, show a sharp increase in sensitivity as frequency is increased to 8 kHz, their frequency of best sensitivity (Fig. 2). Sensitivity then declines gradually to 32 kHz with a small improvement at 45 kHz. Above 45 kHz, sensitivity declines rapidly to 80 kHz, the highest frequency to which the animals responded. At a level of 60 dB SPL, their hearing range extends from 2.3 kHz to 71 kHz (4.9 octaves) with an average best sensitivity of 14 dB at 8 kHz. Spiny mice are able to hear below 20 dB SPL at two frequencies, 8 and 16 kHz.

4. Discussion

The audiograms of these rodents and those of other mammals are discussed with respect to five issues: (1) the variation in high-frequency hearing and its relation to sound localization, (2) the occurrence of secondary peaks of sensitivity that are apparently due to the pinnae, (3) a dichotomy in the distribution of mammalian low-frequency hearing that suggests species differences in the mechanisms used in the perception of pitch, and (4) the variation in low-frequency hearing and its relation to high-frequency hearing.

4.1. Variation in high-frequency hearing

Rodents show more variation in high-frequency hearing than any other order of mammals. Using the highest frequency audible at 60 dB SPL as a standard for comparison, rodent high-frequency hearing limits extend from 5.9 kHz for the blind mole rat (the poorest high-frequency limit of any mammal) to 92 kHz for the wild house mouse, a range of 3.96 octaves (Heffner and Heffner, 1998). Indeed, only echolocating bats and cetacea are known to hear higher frequencies than rodents and including them in the comparison extends the high-frequency hearing limits of mammals to 150 kHz, only 0.71 octave higher (Bitter et al., 2001). Good high-frequency hearing is common in rodents, as it is in mammals as a whole, and the 20 rodent species for which behavioral data are available have a median upper limit of 52 kHz.

The variation in mammalian high-frequency hearing has been attributed to the selective pressures involved in sound localization (e.g., Heffner and Heffner, 1998; Masterton et al., 1969). Briefly, mammals with small heads and pinnae need to hear higher frequencies than larger mammals in order to use interaural intensity differences and pinna cues to localize sounds. That is, the interaural intensity-difference cue is effective only if an animal can hear frequencies that are high enough to be shadowed by its head thereby resulting in a difference in the intensity of a sound reaching the two ears. Similarly, pinna cues are available only if an animal hears sounds that are high enough to be modified by the pinna as a function of the angle of the sound source relative to the head. Just how high an animal needs to hear in order to use these two cues depends on the size of its head and pinnae; the smaller they are, the higher the animal must hear to use these two cues.

As illustrated in Fig. 3, the five rodents tested here conform to the relationship between head size and high-frequency hearing. This figure shows the relationship between 'functional' head size and high-frequency hearing, with functional head size defined as time required for sound to travel around the head from one ear to the
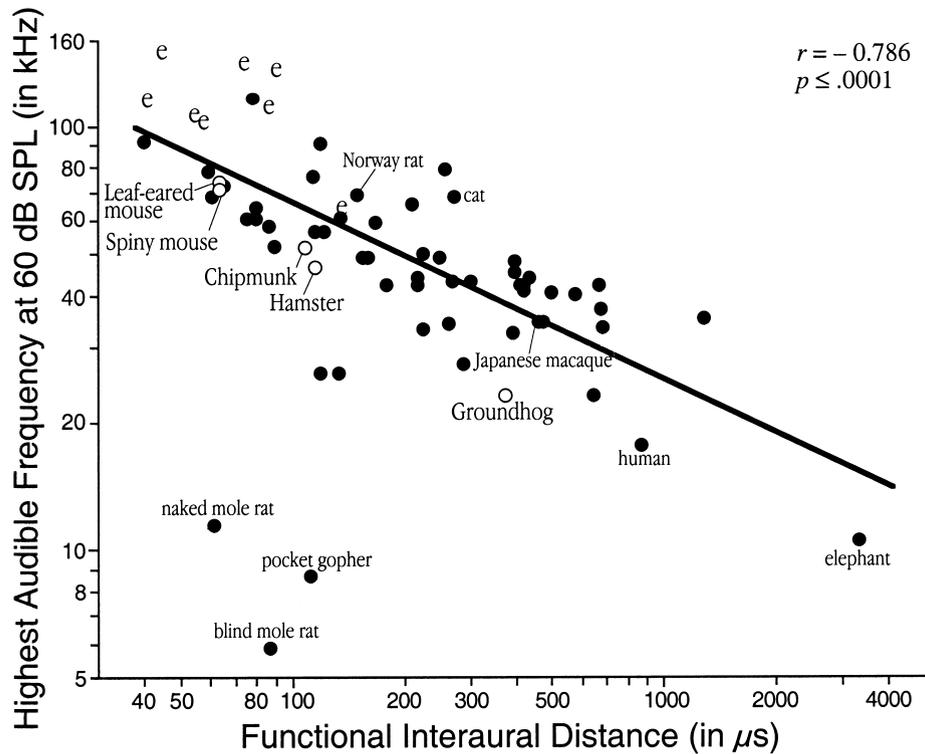
Fig. 3. High-frequency hearing limit (highest frequency audible at 60 dB SPL) varies with functional interaural distance (the number of μs required for a sound to travel from one auditory meatus to the other). Mammals with small interaural distances hear higher frequencies than larger mammals. Open circles indicate the five species in this study and are labeled. Animals that use echolocation (bats and cetacea) are indicated by the letter e. Additional species are labeled for reference. Note that the three subterranean species, blind mole rat, naked mole rat, and pocket gopher, were not included in the correlation (for references to individual species, see Koay et al., 1998).

other, a measure that is directly related to head size and indirectly related to pinna size. As can be seen, mammals with functionally small heads hear higher frequencies than those with large heads and, in general, larger pinnae (correlation coefficient, $r = -0.786$, $P < 0.0001$).

Although most rodents conform to the relationship between functional head size and high-frequency hearing, subterranean rodents are a notable exception (Fig. 3). Interestingly, the failure of the naked mole rat, pocket gopher, and blind mole rat to hear as high as predicted by their head size supports the idea that high-frequency hearing evolved in mammals for sound localization. This is because subterranean mammals, which live exclusively in burrows where directional responses to sound are limited, have also lost the ability to localize sound (e.g., Heffner and Heffner, 1990, 1992, 1993, 1998). The observation that mammals that do not localize sound lose the ability to hear high frequencies supports the theory that high-frequency hearing evolved in mammals for sound localization.

4.2. Secondary peaks of high-frequency sensitivity

Examination of the audiograms of the five rodents tested here reveals the existence of secondary peaks of sensitivity at frequencies well above the animals' frequencies of best hearing (e.g., at 50 kHz for the leaf-eared mouse and at 45 kHz for the spiny mouse in Fig. 2). Such secondary peaks have been noted in other species and their occurrence has been attributed by some to the specialization of the audiogram for ultrasonic communication (e.g., Brown, 1970; Floody, 1979).

Recent evidence, however, indicates that these peaks result from the directionality of the pinnae, which enables animals to localize sound in the vertical plane and to reduce front–back confusions (e.g., Butler, 1975, 1999; Heffner et al., 1996; Musicant and Butler, 1984; Roffler and Butler, 1968). Specifically, these secondary peaks of sensitivity have been shown in bats to vary with the elevation of the sound source (Koay et al., 1998; Wotton et al., 1995). Furthermore, the view that such peaks are due to the external ear and are not necessarily associated with communication is supported by the existence of a secondary peak of high-frequency sensitivity in the human audiogram at 13 kHz that is attributed to the acoustic characteristics of the auditory canal (Shaw, 1974). Thus, the existence of high-frequency peaks does not provide convincing evidence that the hearing of rodents was modified by selective pressure for intraspecific communication. Instead, the presence of ultrasonic vocalizations in rodents may represent the co-optation of high-frequency hearing, orig-

inally evolved for sound localization, for use in communication. Indeed, the frequency of a species' vocalizations seems to be determined by its audiogram, not the other way around, as naked mole rats, which lack high-frequency hearing because they do not need to localize sound, have developed an extensive repertoire of low-frequency communication calls (Heffner and Heffner, 1993; Pepper et al., 1991).

4.3. Distribution of low-frequency hearing limits

The variation in mammalian low-frequency hearing is even greater than that for high-frequency hearing. Among rodents, the 60-dB low-frequency hearing limit extends from 28 Hz (black-tailed prairie dog) to 2.3 kHz (spiny mouse and wild house mouse), a range of 6.36 octaves. For mammals as a whole, low-frequency hearing limits extend from 17 Hz (Indian elephant) to 10.3 kHz (little brown bat), a range of 9.24 octaves that is almost twice the 4.67-octave range in high-frequency hearing (Heffner and Heffner, 1998).

In attempting to explain the variation in low-frequency hearing, it has been noted that high- and low-frequency hearing are correlated such that animals with good high-frequency hearing tend to have poor low-frequency hearing, and vice versa (Heffner and Masterton, 1980; Koay et al., 1998). However, before addressing this relationship, it should be noted that mammals appear to fall into two groups based on whether they have good or poor low-frequency hearing, a dichotomy that is especially well illustrated by the five rodents tested here (Fig. 4).

4.3.1. Dichotomy in the distribution of low-frequency hearing limits

For some time we have noticed a gap in the distri-

Fig. 5. (A) Bimodal distribution of mammalian low-frequency hearing limits (lowest frequency audible at 60 dB SPL). Note that only audiograms conducted in air are represented. Histogram bin widths are 2/3 octave. (B) Distribution of mammalian high-frequency hearing limits (highest frequency audible at 60 dB SPL). The distribution appears to be unimodal with slight skew towards the low-frequencies due primarily to the subterranean animals which have relinquished high-frequency hearing (cf. Fig. 3). Histogram bin widths are 1/3 octave.

bution of low-frequency hearing limits in the region from 125 to 500 Hz and conservatively assumed it was due to sampling error that would disappear as the audiograms of additional species became available. However, as more audiograms were added to the sample, the gap persisted, and the distribution took on a distinctly bimodal appearance. Fig. 5A shows the distribution of 60-dB low-frequency limits for mammals (only audiograms conducted in air are shown because of the difficulty in equating air and water thresholds). Of the 58 species for which low-frequency limits are available, 38 have extended low-frequency hearing with 60-dB hearing limits below 125 Hz (Fig. 6). Another 19 species have restricted low-frequency hearing with 60-dB limits above 500 Hz. Only one species falls within the two-octave gap from 125 to 500 Hz the pocket gopher (*Geomys bursarius*), an animal whose
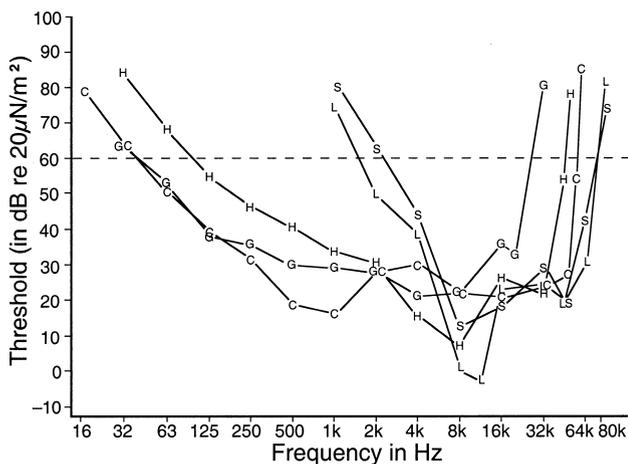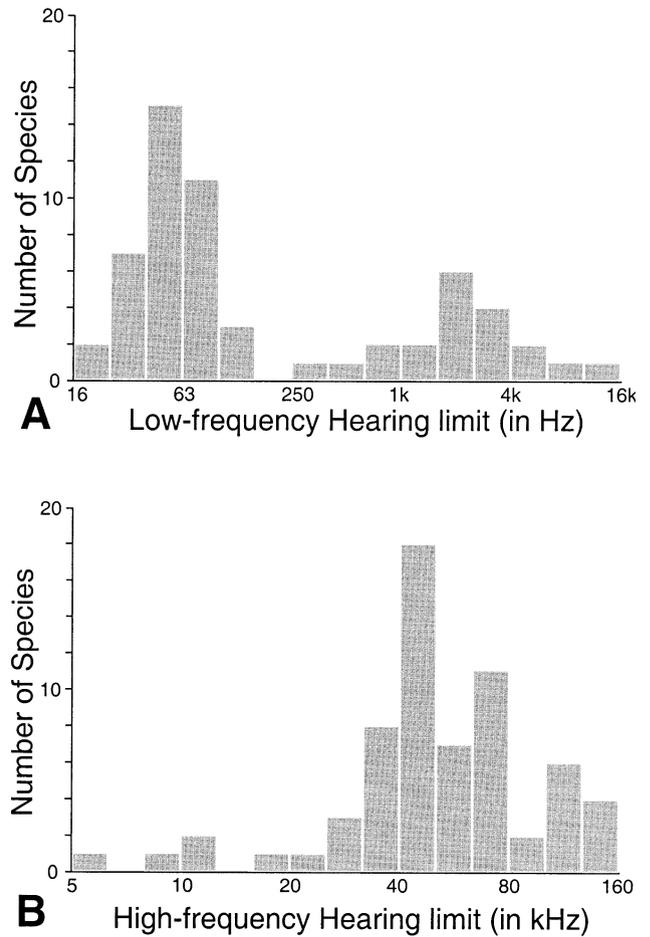

Fig. 4. Audiograms of the five rodents in this study. Note the dichotomy in low-frequency hearing. C, chipmunk; G, groundhog; H, hamster; L, Darwin's leaf-eared mouse; S, spiny mouse.
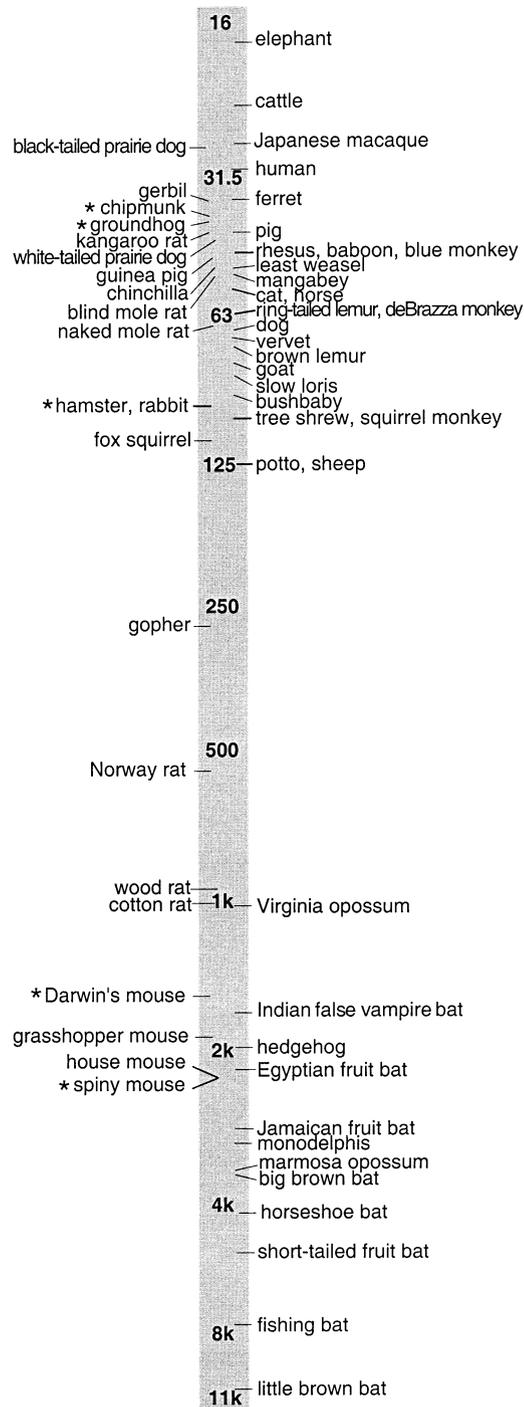
Mammalian Low-frequency Hearing

Fig. 6. Distribution of mammalian low-frequency hearing limits (lowest frequency audible at 60 dB SPL) with individual species indicated. Note that rodents, shown on the left, fall into both the extended and restricted low-frequency hearing groups (for references to individual audiograms, see Koay et al., 1998).

hearing is adapted to a subterranean environment (Heffner and Heffner, 1990). In contrast to the bimodal distribution of low-frequency limits, no similar dichotomy is apparent in the distribution of high-frequency

hearing limits (Fig. 5B). Thus, it appears that mammals can be divided into two groups based on their low-frequency hearing limits.

It should be noted that, for purposes of comparison, we have defined the low-frequency hearing limit as the lowest frequency audible at 60-dB SPL, although animals can actually hear lower frequencies at higher intensities. For example, using an 80-dB definition lowers the low-frequency limit for the laboratory rat from 540 to 290 Hz (Heffner et al., 1994) and for the chipmunk from 39 Hz to 14 Hz. The 60-dB definition was chosen because few animals have been tested beyond this limit and the lowest frequency audible at any intensity is usually not known. However, the 60-dB limit is not an unreasonable definition of useful hearing because the sounds an animal must hear to survive (i.e., sounds produced by other animals) tend not to be very loud. Nevertheless, the exact location of the gap between the two distributions depends on the definition of hearing limits. Interestingly, using a higher intensity to define hearing limits would increase the size of the gap. This is because the two groups differ in the steepness of the low-frequency slopes of their audiograms with the restricted low-frequency animals having steeper slopes than the extended low-frequency animals (a difference that can be seen in Fig. 4). This difference is reliable as demonstrated by a statistical comparison of the slopes of the audiograms, as defined by the difference (in octaves) between the lowest frequency audible at 30 dB and at lowest audible at 60 dB ($n = 58$, $P = 0.0001$, Mann–Whitney U). Thus, using a higher intensity to define the hearing limits would increase the size of the gap between the two groups while shifting it to slightly lower frequencies.

4.3.2. Potential explanations of the dichotomy in low-frequency hearing

One possible explanation for the dichotomy in low-frequency hearing is that the two groups differ along some dimension such as body size, phyletic lineage, or lifestyle. However, there is no obvious feature that distinguishes the two groups (Fig. 6). Although the animals in the group with restricted low-frequency hearing tend to be small (with the exception of the opossum), the group with extended low-frequency hearing also contains small animals (e.g., gerbil, mole rats, least weasel). In addition, although the species belonging to a particular Order tend to fall into one group or the other, rodents are found in both, thus making a phylogenetic division difficult. Nor is the dichotomy based on trophic level as predators and prey can be found in both groups. Similarly, the two groups do not divide along other lines such as type of habitat or activity cycle (e.g., nocturnal vs. diurnal). Thus, at this time we are unable to account for the dichotomy in low-

frequency hearing in terms of morphology, phylogeny, or ecology.

Another possibility is that the two groups differ in the mechanisms they use to perceive the pitch of low-frequency sounds. Briefly, there are two different neural mechanisms that may underlie pitch (e.g., Moore, 1993; Wever, 1949). In one, frequency is encoded by temporal mechanisms that are based on phase-locking. Here nerve firing tends to occur at a particular phase of the stimulating waveform, and the intervals between successive neural impulses are thus a multiple of the tone period (1/frequency). However, temporal coding is limited to low frequencies because phase locking declines as frequency increases (e.g., Rose et al., 1967). In the second, higher frequencies are encoded by a spatial or place mechanism in which tones of different frequencies excite hair cells and fibers at different locations along the basilar membrane. However, the actual frequency ranges over which either the temporal or the place mechanisms are dominant for the perception of pitch have not been agreed upon in theory nor determined in practice. Some observations suggest that the upper limit of the temporal mechanism for the perception of pitch is 4–5 kHz (e.g., Moore, 1993). However, as described below, there is also reason to believe that the upper limit of the temporal mechanism for pitch perception may be much lower.

4.3.2.1. Upper limit in the use of temporal information for pitch perception. The predominant view, summarized by Moore (1993, 1997), is that the upper limit of temporal coding for the perception of pitch is about 5 kHz. Evidence for this limit includes the following observations: (1) the upper limit of neural phase locking in the squirrel monkey auditory nerve is 4–5 kHz (Rose et al., 1967); (2) human frequency difference limens for tone bursts increase above 5 kHz, an observation consistent with the belief that place coding of frequency is less precise than temporal coding (e.g., Møller, 2000); (3) humans have no clear sense of melody in tones above 5 kHz; and (4) the residue pitch or missing fundamental resulting from combination tones is only observed when the combination tones are below about 5 kHz.

Central to this view is the assumption that the upper limit of phase locking in the human auditory nerve is the same as in the squirrel monkey. Although initially a reasonable assumption, it is now apparent that the upper limit of phase locking varies between species. For example, phase locking in the guinea pig begins to decline at about 600 Hz and is no longer detectable above 3.5 kHz, which is almost one octave lower than in the squirrel monkey (Palmer and Russell, 1986). Moreover, it is difficult to determine the highest frequency for which neural phase locking is actually used: Is it the highest frequency at which phase locking

can be detected or the frequency at which it begins to decline?

The lack of a firm value for the upper limit of phase locking in humans weakens the psychophysical evidence regarding the upper limit of temporal coding. The observation that human frequency difference limens increase above 5 kHz and that humans have no clear sense of melody above 5 kHz may be due to a lack of selective pressure to maintain these abilities above 5 kHz rather than to any inherent limitation of the place mechanism. Similarly, it is possible to explain the residue pitch in terms of a temporal or a place mechanism – it is the correspondence of the upper limit of this phenomenon with the upper limit of phase locking in the squirrel monkey auditory nerve that makes a temporal explanation attractive (Moore, 1997). In short, we do not know if the human auditory nerve phase locks to 5 kHz and therefore cannot be confident that the temporal coding of frequency extends to 5 kHz.

On the other hand, there are at least two observations suggesting a more restricted upper limit for the role of temporal mechanisms in pitch. The first has to do with the perception of the pitch of click trains constructed so that they can potentially be matched in pitch either on the basis of pulse rate, which is a temporal basis, or on the basis of fundamental frequency, which is interpreted as a spatial or place basis. For click trains composed of all positive or all negative clicks, pulse rate and repetition rate are identical. However, pulse rate and repetition rate differ when patterns of alternating positive and negative clicks are used. For example, a train of alternating positive and negative clicks has a pulse rate twice its repetition rate. When asked to match the pitch of two click trains of less than 100 pulses per second (pps), one with uniform-polarity clicks and the other with a pattern of positive and negative clicks, subjects match them by setting the trains to equal pulse rates, a temporal basis, regardless of differences in fundamental frequency (Flanagan and Guttman, 1960). However, at pulse rates of 200 pps or more, subjects adjust click trains by equating their fundamental frequencies, regardless of differing pulse rates, which was interpreted as evidence for place coding of frequency. This result suggests that the upper limit of the temporal mechanism for pitch perception may be between 100 and 200 Hz. Consistent with this result is the physiological finding that there are two forms of click train encoding in auditory cortex, one for click trains below 100−200 pps, which is independent of click polarity, the other for higher click train rates, which is dependent on click polarity (Steinschneider et al., 1998)

A second line of evidence comes from psychophysical studies of cochlear implant patients. These studies indicate that pitch changes with the frequency of stimuli

only up to about 300 Hz (e.g., Shannon, 1983). Taken together, the observations of Flanagan and Guttman and those of Shannon suggest an upper limit of the temporal mechanism for pitch perception of around 200–300 Hz. Because this upper limit corresponds to the gap in mammalian low-frequency limits, it suggests the possibility that the animals in the group with restricted low-frequency hearing may not use temporal coding for pitch perception.

4.3.2.2. Some mammals do not use temporal coding for pitch perception. Some mammals do not use temporal coding for pitch perception because they do not hear low enough for phase locking to occur. For example, the low-frequency hearing limit of the little brown bat (10.3 kHz) is too high for phase locking, and therefore temporal encoding, to occur (Fig. 6). The same conclusion may hold for other mammals that do not hear low frequencies, such as the big brown bat and marmosa opossum, which do not hear below 4 kHz. Thus, the question arises as to which other mammals might not use temporal encoding for pitch perception.

The correspondence of the gap in mammalian low-frequency hearing limits with the evidence for a 200–300-Hz upper limit for the temporal mechanism for pitch perception suggests the possibility that the two phenomena may be related. Specifically, whereas mammals with extended low-frequency hearing are probably using both the place and temporal mechanism for pitch perception, those with restricted low-frequency hearing may be using only the place mechanism.

It should be noted that neural phase locking may still occur in animals in the restricted low-frequency hearing group because it is used in sound localization to extract the binaural phase-difference cue. Thus, it is possible that the upper limit of phase locking in some animals is determined by its use for sound localization rather than by its use for pitch perception. Sound localization studies have indicated that the upper limit of the use of binaural phase difference in mammals varies with the size of an animal's head with small animals using it at higher frequencies than large animals (Brown, 1994) – the current upper limits extend from 500 Hz for cattle to 6.3 kHz for the Jamaican fruit bat, although some very small mammals, such as the big brown bat, are unable to use the binaural phase cue at all (Heffner et al., 1999, 2000).

Because some animals do not use phase locking for sound localization and others may not use it for pitch perception, the following combinations may occur (candidate species are listed in parentheses): (1) Animals that use phase locking in both pitch perception and sound localization (humans, cats, and chinchillas). (2) Animals that use phase locking in sound localization but not in pitch perception (laboratory rat, Egyptian and Jamaican fruit bats). (3) Animals that use phase

locking in pitch perception but not for sound localization, a situation that may be found in subterranean mammals that have good low-frequency hearing, but have lost the ability to localize brief sounds (gophers and mole rats). (4) Animals that do not use phase locking in either pitch perception or sound localization (big brown bat).

If the restricted and extended low-frequency animals differ in terms of the mechanisms used to encode frequency, then they might also be expected to show other differences in auditory processing, particularly in the cochlea. Indeed, frequency maps of the cochlea, which show the projection of frequency along the cochlear partition, indicate that mammals fall into different groups as defined by the normalized slope of the relationship (i.e., by the coefficient of the exponential term when cochlear distance is expressed as a proportion or percentage of total partition length; Greenwood, 1996). In one such group, which includes the Norway rat and the marsupial, *Monodelphis domestica*, octaves subtend a larger percentage of the cochlear length than they do in a second group, which includes human, cat, guinea pig, chinchilla, monkey, and gerbil (Greenwood, 1996; Müller, 1996). As can be seen in Fig. 6, the animals in the first group have restricted low-frequency hearing while those in the second group all have extended low-frequency hearing. Thus, whether or not an animal uses temporal coding for pitch may be reflected in its cochlear frequency map. However, whether an animal uses temporal and/or place coding for pitch perception must ultimately be determined behaviorally.

4.4. Relation between high- and low-frequency hearing

In attempting to explain the variation in low-frequency hearing, previous studies identified two potential explanatory factors: functional head size and high-frequency hearing limit (Heffner and Heffner, 1985; Heffner and Masterton, 1980). These studies found that although both factors are significantly correlated with low-frequency hearing limit, high-frequency hearing is directly correlated with low-frequency hearing while functional head size is indirectly correlated with low-frequency hearing through its correlation with high-frequency hearing. Thus, animals with good high-frequency hearing generally have poor low-frequency hearing. With the addition of the five rodents in this report, as well as the division of mammals into two groups based on low-frequency hearing, it is useful to reexamine this relationship.

The relationship between high- and low-frequency hearing in mammals was examined separately for animals with extended and restricted low-frequency hearing, defined by whether an animal's 60-dB low-frequency limit was below 250 Hz. Functional head size

was defined as the shortest distance around the head from one auditory meatus to the other. Aquatic audiograms were excluded because of the difficulty in equating underwater thresholds with those obtained in air. Subterranean mammals were also excluded from the statistical analysis (but are depicted in the graphical presentation) because they have vestigial high-frequency hearing.

Among mammals with restricted low-frequency hearing, high- and low-frequency hearing are reliably correlated ($n = 18$, $r = 0.691$, $P = 0.0015$). The slope of the regression line is relatively steep with a tradeoff of 1.71 octaves of low-frequency hearing for each octave of high-frequency hearing gained or lost (Fig. 7). Partial correlation analysis indicates that this relationship remains significant when functional head size is held constant ($P = 0.022$). On the other hand, although head size is reliably correlated with low-frequency hearing ($r = -0.562$, $P = 0.015$), this correlation falls to chance when high-frequency hearing is held constant ($P = 0.246$).

For mammals with extended low-frequency hearing, high- and low-frequency hearing are less closely correlated, although the relationship is still strong ($n = 33$, $r = 0.567$, $P = 0.0006$). The slope of the regression line for this group is also less steep showing a tradeoff of only 0.72 octaves of low-frequency hearing for each

octave of high-frequency hearing gained or lost (Fig. 7). Partial correlation analysis indicates that this relationship remains significant when functional head size is held constant ($P = 0.0007$). On the other hand, functional head size is not reliably correlated with low-frequency hearing even without partialling out high-frequency hearing ($r = -0.293$, $P = 0.0873$).

These results indicate that high-frequency hearing is related to low-frequency hearing for both groups of animals. Functional head size, on the other hand, is indirectly related to low-frequency hearing through its correlation with high-frequency hearing (but only for the group with restricted low-frequency hearing). Thus, in attempting to explain the variation in low-frequency hearing, only high-frequency hearing need be considered as head size appears to play no direct role.

High-frequency hearing accounts for 46% and 30% of the variance in low-frequency hearing for the restricted and extended low-frequency hearing groups, respectively, indicating that it is a major factor influencing low-frequency hearing. In seeking reasons why high- and low-frequency hearing are related, it is necessary to consider both anatomical and functional factors.

4.4.1. Anatomical considerations in the relation between high- and low-frequency hearing

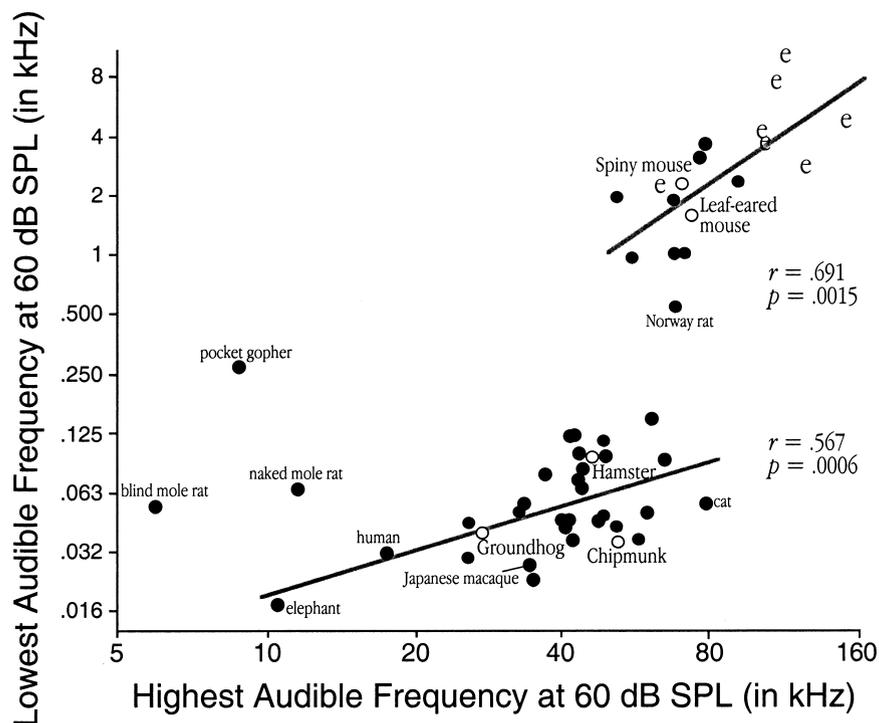One possible explanation of the relationship between

Fig. 7. Relation between the highest and lowest frequencies audible at 60 dB SPL for 51 species of mammals. Correlations are shown separately for animals with restricted and extended low-frequency hearing (upper and lower regression lines, respectively). Subterranean rodents (blind mole rat, naked mole rat, and pocket gopher) are depicted, but not included in the calculations. Open circles indicate the five species in this study. Echolocating bats indicated by the letter e.

high- and low-frequency hearing is that although the mammalian ear can be adapted to hearing very high or very low frequencies, no single ear can efficiently transduce and encode both. Such an incompatibility could arise in the middle ear if the mechanical configurations that are efficient at transmitting low frequencies are not effective at high frequencies (e.g., Fleischer, 1978; Nummela, 1999; Rosowski, 1992). Alternatively, there may be morphological constraints in the mammalian basilar membrane such that species cannot hear both high and low frequencies, at least not without loss of overall sensitivity (Hemila et al., 1995; Nummela, 1999; West, 1985).

Attractive as these hypotheses may be, the idea that mammals cannot hear well at both high and low frequencies is contradicted by the existence of species that do. Animals that hear in the top quartile for both high- and low-frequency hearing include the least weasel (50 Hz to 60 kHz), domestic cat, (55 Hz to 79 kHz), and bushbaby (92 Hz to 65 kHz). Thus, the implication that hearing range should be relatively constant across species is not supported. Moreover, contrary to expectations (Hemila et al., 1995; Nummela, 1999), broad hearing ranges are not achieved at the expense of sensitivity as hearing range and best sensitivity are not significantly correlated ($n = 55$, $r = -0.219$, $P = 0.1351$). Thus, the evidence so far indicates that the variation in high- and low-frequency hearing is not due to anatomical or physiological constraints in the mammalian ear, but is instead determined by what animals need to hear in order to survive, i.e., by selective pressure.

This is not to say that the anatomical characteristics of the ear have no effect on an animal's hearing. On the contrary, all of the animals with restricted low-frequency and good high-frequency hearing that have been examined (Virginia opossum, house mouse, Norway rat, horseshoe bat, and Egyptian fruit bat) have 'microtype' middle ears with low compliance and a relatively small incus making them best suited to transmit high frequencies (Fleischer, 1978; Rosowski, 1992). Similarly, all of the animals with extended low-frequency hearing that have been examined are known to have middle ears described as either freely mobile and compliant, making them well-suited to transmit low frequencies (guinea pig, chinchilla, kangaroo rat, human, macaques, gerbil, weasels, and chimpanzee) or as intermediate between the two types of ears (horse, cat, bushbaby, and tree shrew) (Fleischer, 1978; Rosowski, 1992). However, it is important to note that the structure of the ear is ultimately determined by what an animal needs to hear in order to survive. The idea that the hearing ability of an animal is determined by the size of its ear which, in turn, is determined by the size of its head is contradicted by the existence of small mammals with good low-frequency hearing (e.g., gerbil and least weasel). Furthermore, there is no obvious physical factor that prevents large animals from having ears suited for high-frequency hearing, as demonstrated by the domestic cat. It seems that animals that require good high- or low-frequency hearing evolve the type of ear capable of transducing the sounds they need in order to survive. To state that an animal hears low frequencies because it has an ear suitable for transmitting low frequencies addresses the question of how, but not why, it hears as it does.

4.4.2. Functional considerations in low-frequency hearing

The existence of animals with restricted low-frequency hearing suggests that they either have no need to hear low frequencies or that good low-frequency hearing might actually be detrimental. With regard to the first possibility, the fact that most vertebrates hear low frequencies demonstrates that it has advantages. Indeed, not only would low-frequency hearing be expected to aid the ability of an animal to detect many, if not most, sounds made by other animals, but low frequencies travel farther and could alert an animal to more distant danger. It is possible that very early mammals retained reptilian low-frequency hearing while adding the ability to hear high frequencies (Manley, 2000), which is the condition found so far in most extant mammals. Because low-frequency sensitivity is nearly universal among vertebrates, there is every reason to believe that it has strong adaptive value.

On the other hand, it is conceivable that good low-frequency hearing might be detrimental in situations where low-frequency sounds might mask or otherwise interfere with the analysis of high-frequency sounds. Indeed, it is well known that a sound has a greater masking effect on higher than lower frequencies (Wegel and Lane, 1924). Thus, animals in the restricted low-frequency group may be giving up 1.71 octaves of low-frequency hearing for each octave increase in high frequency to prevent low frequencies from masking the high frequencies they use to localize sound. Indeed, it has been noted that animals often localize high-pass noise more accurately than broadband noise (Heffner et al., 1995). Animals in the extended low-frequency group may additionally be affected by the high levels of ambient low-frequency noise that exist in the environment (Martin, 1984) and by a lack of biologically relevant sounds at very low frequencies. As a result, for each octave of high-frequency hearing which they relinquish because it is no longer required for sound localization, their low-frequency hearing is extended only 0.72 octaves into the low frequencies. Thus, the advantages of being able to detect low frequencies must be weighed against the

disadvantage that they may mask important higher frequency sounds.

References

Bitter, K.S., Heffner, R.S., Koay, G., Heffner, H.E., 2001. Behavioral audiogram of the short-tailed fruit bat, *Carollia perspicillata*. ARO Abstr. 24, 63–64.

Brown, A.M., 1970. Bimodal cochlear response curves in rodents. Nature 228, 576–577.

Brown, C.H., 1994. Sound localization. In: Fay, R.R., Popper, A.N. (Eds.), Comparative Hearing: Mammals. Springer, New York, pp. 57–96.

Butler, R.A., 1975. The influence of the external and middle ear on auditory discriminations. In: Keidel, W.D., Neff, W.D. (Eds.), Handbook of Physiology, Auditory System, Vol. V/2. Springer, New York, pp. 247–260.

Butler, R.A., 1999. The unfolding of an auditory illusion. Perspect. Biol. Med. 42, 157–173.

Flanagan, J.L., Guttman, N., 1960. On the pitch of periodic pulses. J. Acoust. Soc. Am. 32, 1308–1319.

Fleischer, G., 1978. Evolutionary principles of the mammalian middle ear. Adv. Anat. Embryol. Cell Biol. 55, 1–70.

Floody, O.R., 1979. Behavioral and physiological analyzes of ultrasound production by female hamsters (*Mesocricetus auratus*). Am. Zool. 19, 443–455.

Greenwood, D.D., 1996. Comparing octaves, frequency ranges, and cochlear-map curvature across species. Hear. Res. 94, 157–162.

Heffner, H.E., Heffner, R.S., 1995. Conditioned avoidance. In: Klump, G.M., Dooling, R.J., Fay, R.R., Stebbins, W.C. (Eds.), Methods in Comparative Psychoacoustics. Birkhaüser, Basel, pp. 73–87.

Heffner, H.E., Heffner, R.S., 1998. Hearing. In: Greenberg, G., Haraway, M.M. (Eds.), Comparative Psychology, A Handbook. Garland, New York, pp. 290–303.

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

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

Heffner, R.S., Heffner, H.E., 1985. Hearing in mammals: The least weasel. J. Mammal. 66, 745–755.

Heffner, R.S., Heffner, H.E., 1990. Vestigial hearing in a fossorial mammal, the pocket gopher (*Geomys bursarius*). Hear. Res. 46, 239–252.

Heffner, R.S., Heffner, H.E., 1992. Hearing and sound localization in blind mole rats, *Spalax ehrenbergi*. Hear. Res. 62, 206–216.

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

Heffner, R.S., Heffner, H.E., Koay, G., 1995. Sound localization in chinchillas. II: Front/back and vertical localization. Hear. Res. 88, 190–198.

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

Heffner, R.S., Koay, G., Heffner, H.E., 1999. Sound localization in an old-world fruit bat *Rousettus aegyptiacus*: Acuity, use of binaural cues, and relationship to vision. J. Comp. Psychol. 113, 297–306.

Heffner, R.S., Koay, G., Heffner, H.E., 2000. Sound localization in a new-world frugivorous bat, *Artibeus jamaicensis*: Acuity, use of binaural cues, and relationship to vision. J. Acoust. Soc. Am. 109, 412–421.

Hemila, S., Nummela, S., Reuter, T., 1995. What middle ear parameters tell about impedance matching and high frequency hearing. Hear. Res. 85, 31–44.

Koay, G., Heffner, R.S., Heffner, H.E., 1998. Hearing in a megachiropteran fruit bat *Rousettus aegyptiacus*. J. Comp. Psychol. 112, 371–382.

Manley, G.A., 2000. Cochlear mechanisms from a phylogenetic viewpoint. Proc. Natl. Acad. Sci. USA 97, 11736–11743.

Martin, G.R., 1984. An environmental limit on absolute auditory sensitivity in non-aquatic vertebrates. Behav. Process. 9, 205–221.

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

Møller, A.R., 2000. Hearing. Academic Press, New York.

Moore, B.C.J., 1993. Frequency analysis and pitch perception. In: Yost, W.A., Popper, A.N., Fay, R.R. (Eds.), Human Psychophysics. Springer, New York, pp. 56–115.

Moore, B.C.J., 1997. An Introduction to the Psychology of Hearing, 4th edn. Academic Press, London.

Müller, M., 1996. The cochlear place-frequency map of the adult and developing mongolian gerbil. Hear. Res. 94, 148–156.

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

Nummela, S., 1999. Scaling and modelling of the mammalian middle ear. Doctoral Dissertation presented to the Faculty of Science of the University of Helsinki, Helsinki.

Palmer, A.R., Russell, I.J., 1986. Phase-locking in the cochlear nerve of the guinea-pig and its relation to the receptor potential of inner hair-cells. Hear. Res. 24, 1–15.

Pepper, J.W., Braude, S.H., Lacey, E.A., Sherman, P.W., 1991. Vocalizations of the naked mole-rat. In: Sherman, P.W., Jarvis, J.U.M., Alexander, R.D. (Eds.), The Biology of the Naked Mole-Rat, Princeton University Press, Princeton, NJ, pp. 243–276.

Roffler, S.K., Butler, R.A., 1968. Factors that influence the localization of sound in the vertical plane. J. Acoust. Soc. Am. 43, 1255–1259.

Rose, J.E., Brugge, J.F., Anderson, D.J., Hind, J.E., 1967. Phase-locked response to low-frequency tones in single auditory nerve fibers of the squirrel monkey. J. Neurophysiol. 30, 769–793.

Rosowski, J.J., 1992. Hearing in transitional mammals: Predictions from the middle-ear anatomy and hearing capabilities of extant mammals. In: Popper, A.N., Fay, R.R., Webster, D.B. (Eds.), The Evolutionary Biology of Hearing. Springer, New York, pp. 615–631.

Shannon, R.V., 1983. Multichannel electrical stimulation of the auditory nerve in man. I. Basic psychophysics. Hear. Res. 11, 157–189.

Shaw, E.A.C., 1974. The external ear. In: Keidel, W.D., Neff, W.D. (Eds.), Handbook of Sensory Physiology, Vol. V(1). Springer, New York, pp. 450–490.

Steinschneider, M., Reser, D.H., Fishman, Y.I., Schroeder, C.E., Arezzo, J.C., 1998. Click train encoding in primary auditory cortex of the awake monkey: Evidence for two mechanisms subserving pitch perception. J. Acoust. Soc. Am. 104, 2935–2955.

Wegel, R.L., Lane, C.E., 1924. The auditory masking of one pure tone by another and its probable relation to the dynamics of the inner ear. Phys. Rev. 23, 266–285.

West, C.D., 1985. The relationship of the spiral turns of the cochlea and the length of the basilar membrane to the range of audible frequencies in ground dwelling mammals. J. Acoust. Soc. Am. 77, 1091–1101.

Wever, E.G., 1949. Theory of Hearing. Wiley, New York.

Wotton, J.M., Haresign, T., Simmons, J.A., 1995. Spatially dependent acoustic cues generated by the external ear of the big brown bat, *Eptesicus fuscus*. J. Acoust. Soc. Am. 98, 1423–1455.