Audiograms of ¢ve species of
hearing and

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Behavioral audiograms were determined for five species of rodents: gro
Darwin's leaf-eared mouse (*P   7   *), golden hamster (*M   ₋pınⱽ*

ceive a steady trickle of water (He¡ner and He¡ner, 1995). Pure tones were then presented at random intervals and followed at their o¡set 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. S⌐ 7

Eastern chipmunks (*T.* 7 7). 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× 25.4×30.5 cm) with corncob bedding and provided small wooden nest boxes (20×9×7.6 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, sun-£ower seeds, and mixed nuts with occasional supplements of fruits and vegetables.

Groundhogs, also known as marmots or woodchucks (*M.*). 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 (91×32×43 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.* 7). 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 (33×21.6×19 cm) with corncob bedding. They were given free access to rodent blocks and occasional pieces of apple.

Darwin's leaf-eared mice (*P.*). 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.*). 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. B 7

Testing was conducted in a carpeted, double-walled chamber (IAC model 1204; Industrial Acoustics Co., Bronx, NY, USA; 2.55×2.75×2.05 m). To reduce sound re£ections, 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 £oor to minimize sound-re£ecting surfaces in the vicinity of the animal. The groundhogs were tested in a cage (74×38.5×24 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 (35×21×24 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 when20 ured

that it did not interfere with the sound reaching the animal's ears. For the mice, chipmunks, and groundhogs, water was delivered to the spout from a constant-pressure water reservoir (Marriotte bottle) through an electrically operated water valve with the £ow 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 £ow 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 ¢x their heads in the sound ¢eld, allowing precise measurement of the intensity of the sound at their ears.

A contact circuit, connected between the water spout and cage £oor, 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 £oor, 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 o¡ .

2.3. A ⁷ ⁷

Sine waves from 16 to 80 000 Hz were generated by a tone generator (Hewlett Packard 209A or Krohn-Hite 2400) and the frequency veri¢ed 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 o¡ set. 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

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 ¢nal 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 classi¢ed 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:

Performance = Hit rate−(False alarm rate×Hit rate)

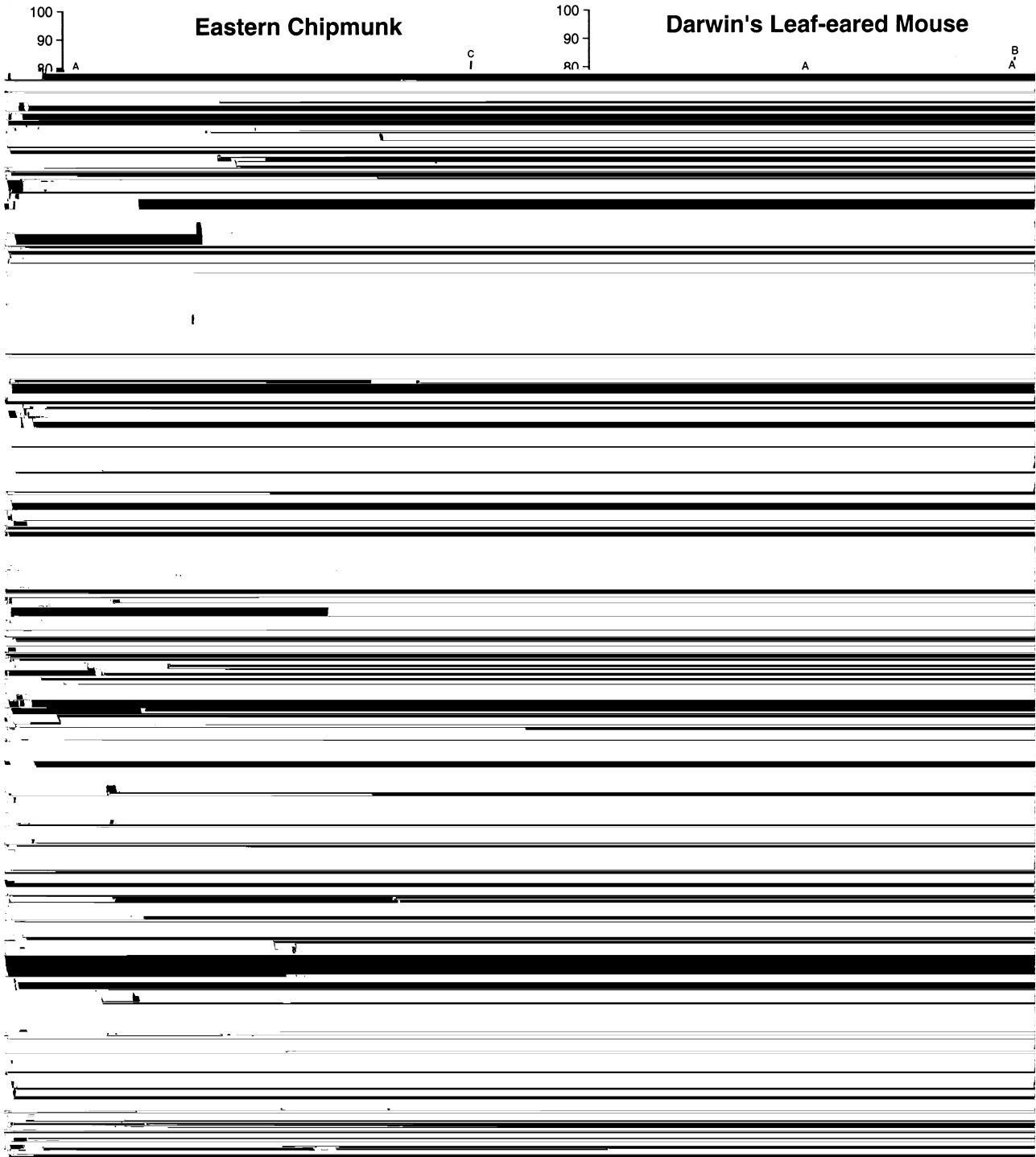This measure proportionately reduces the hit rate by the false alarm rate observed for a particular stimulus

Fig. 2. Audiograms of the ¢ve 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.

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-de¢ned 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.

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-de¢ned 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.

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. Di c i

The audiograms of these rodents and those of other mammals are discussed with respect to ¢ve 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 di¡erences in the mechanisms used in the perception of pitch, and (4) the variation in low-frequency hearing and its relation to high-frequency hearing sensitivity arence

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 coeſcient, = −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., He¡ner and He¡ner, 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. S ▸ - ⁊ ⁊

Examination of the audiograms of the ¢ve rodents tested here reveals the existence of secondary peaks of sensitivity at frequencies well above the animals' fre-

quencies 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; He¡ner et al., 1996; Musicant and Butler, 1984; Ro¥er and Butler, 1968). Speci¢cally, 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 modi¢ed by selective pressure for intraspeci¢c communication. Instead, the presence of ultrasonic vocalizations in rodents may rep-

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 (He¡ner and He¡ner, 1993; Pepper et al., 1991).

4.3. D ⁊ ⁊ - ⁊

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 (He¡ner and He¡ner, 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 (He¡ner 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 ¢ve rodents tested here (Fig. 4).

4.3.1. D ⁊ ⁊ ⁊ ⁊ - ⁊

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

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

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

Another possibility is that the two groups di¡er in the mechanisms they use to perceive the pitch of low-frequency sounds. Brie£y, there are two di¡erent 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 ¢ring 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 di¡erent frequencies excite hair cells and ¢bers at di¡erent 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. U   ⁊ ⁊   ⁊   ⁊
⁊   ⁊ . 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 di¡erence 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., MÖller, 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

was de¢ned as the shortest distance around the head

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 e⁄ciently transduce and encode both. Such an incompatibility could arise in the middle ear if the mechanical con¢gurations that are e⁄cient at transmitting low frequencies are not e¡ective 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 signi¢cantly correlated (= 55, = −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 e¡ect 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

disadvantage that they may mask important higher frequency sounds.

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