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Hearing and sound localization in Cottontail rabbits, *Sylvilagus floridanus*

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Abstract

Cottontail rabbits represent the first wild species of the order of lagomorphs whose hearing abilities have been determined. Cottontails, *Sylvilagus floridanus*, evolved in the New World, but have spread worldwide. Their hearing was tested behaviorally using a conditioned-avoidance procedure. At a level of 60 dB SPL, their hearing ranged from 300 Hz to 32 kHz, a span of 7.5 octaves. Mammalian low-frequency hearing is bimodally distributed and Cottontail rabbits fall into the group that hears below 400 Hz. However, their 300-Hz limit puts them near the gap that separates the two populations. The minimum audible angle of cottontails is 27.6°, making them less acute than most other species of mammals. Their large sound-localization threshold is consistent with the observation that mammals with broad fields of best vision require less acuity to direct their eyes to the sources of sound.

Keywords Behavioral audiogram · Low-frequency hearing · Comparative hearing · Sound localization and vision · Animal psychophysics

Introduction

The Order Lagomorpha, with approximately 90 species, includes rabbits, hares, and pikas (Melo-Ferreira and Alves 2018). Currently, the only available audiogram for this Order is that of the domesticated Old-World rabbit, *Oryctolagus cuniculus*, a burrowing species (Heffner and Masterton 1980). To extend our survey of mammalian hearing to include a non-domesticated species in this group, we report here the audiogram of the Eastern cottontail rabbit (*Sylvilagus floridanus*).

The Cottontail rabbit is a member of a New-world genus native to much of North and Central America, including the northern parts of South America (Chapman et al. 1980). It is a smaller non-burrowing species, nesting in slight depressions, that can be compared to the larger domesticated representatives of Old-world burrowing rabbits (e.g., New Zealand White and Dutch Belted) that have served as models for mammalian sound localization (e.g., Blanks et al. 2007). Both the audiogram and noise-localization thresholds of three Eastern cottontails were determined for comparison with those of other mammals.

Methods

The rabbits were tested using a conditioned-avoidance procedure in which a thirsty animal was trained to maintain mouth contact with a water spout to receive a steady trickle of water. Warning sounds were presented intermittently, followed at their offset by a mild electric shock delivered via the spout. The animals learned to avoid the shock by breaking contact with the spout when they heard a warning sound.

The audiogram was determined for pure tones ranging from 125 Hz to 64 kHz. Sound-localization acuity (minimum audible angle) was determined for 100-ms broadband noise pulses centered left and right on the midline in the azimuthal plane.

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Subjects

Three Eastern cottontail rabbits, *S. floridanus* (two females A, B, and one male C), were wild trapped in Lucas County, Ohio, and maintained in the laboratory. They were approximately 6 months old and weighed 918–1099 g on ad libitum feed at the beginning of testing. They were housed in stainless steel cages ($61 \times 46 \times 70$ cm) and given free access to rabbit chow supplemented by occasional fruits and vegetables.

While on test, the animals received their water only in the test sessions and were weighed daily to monitor their deprivational state. During testing, they maintained at least 80% of their ad libitum weights and returned to those weights within a few days of ad libitum food and water.

Behavioral apparatus

All testing was carried out in a double-walled chamber (IAC model 1204, $2.55 \times 2.75 \times 2.05$ m). To reduce sound reflection, the floor was carpeted and the walls and ceiling were lined with egg crate foam. All acoustic and behavioral equipment was located adjacent to the chamber and the rabbits were observed over closed-circuit television.

The test cage measured $55 \times 31 \times 38$ cm and was constructed of 1-in (2.54-cm) welded wire mesh. The legs supporting the test cage were placed on 8-cm-thick foam pads as a precaution against substrate-borne vibrations. In the front of the cage, a water spout protruded through the floor to a comfortable drinking height. The spout consisted of 15-gauge stainless steel tubing with a 1.5×2.5 cm stainless steel oval welded to the tip serving as a lick surface. The tip of the spout protruded 5 cm above the cage floor, below the level of the animals' ears, thus minimizing obstructions between the ears and the loudspeakers. The water spout was connected via plastic tubing to a 50 mL syringe pump (Thompson et al. 1990) located outside the test chamber. The pump supplied a slow trickle of water as long as an animal maintained contact with the spout. The water delivery rate was adjusted, so that the animals could obtain their daily water in a single test session lasting 35–65 min. Requiring the animals to keep their mouths on the water spout served to keep their heads in a fixed position relative to the loudspeakers. A contact circuit, connected between the spout and cage floor, detected when a rabbit made contact with the spout and activated the syringe pump. In addition, a shock generator was connected between the spout and the cage floor to provide feedback and a mild cost for failing to respond to warning sounds. The shock (0.3 s) was adjusted for each rabbit to the lowest level that elicited a reliable avoidance response.

Finally, a 15-W light was mounted approximately 0.5 m below the cage and was turned on and off simultaneously with the shock to indicate to the animal when a shock had been delivered, and when it was safe to return to the spout at the end of successful detection trials.

Acoustical apparatus

Audiogram

Pure tones from 125 Hz to 64 kHz were produced using a signal generator (Krohn-Hite 2400 AM/FM) and were continuously verified by a frequency counter (Fluke 1900A). The signal was shaped by a rise/decay gate (Coulbourn S84-04) allowing 10 ms rise/decay times for all frequencies of 1 kHz and higher. Longer rise/decay times were used at lower frequencies to allow the signal to reach full voltage (and fall to zero voltage) over at least ten cycles. For the audiogram, pure tones were presented as four pulses of 400-ms duration with 100 ms between pulses. The intensity of the tones was adjusted in 5-dB steps using an attenuator (Hewlett Packard 350D), the linearity of which was calibrated throughout the voltage range used for the different intensities being tested. The electrical signal was then bandpass filtered (Krohn-Hite 3550; $\pm 1/3$ octave) to reduce any possible electrical noise and routed to an amplifier (Crown D75). Output from the amplifier to speaker was monitored for distortion and noise with an oscilloscope. Loudspeakers were placed at ear level 1 m in front of the animal's ears. A variety of loudspeakers, depending on the frequencies being tested, was used: 15-in (38-cm) woofer in a 0.45 m³ enclosure, piezoelectric tweeters (Motorola KSN 1005A), and ribbon tweeters (Foster E110T02). The woofer used to generate the lowest frequencies was placed on 8-cm-thick foam pads as a precaution against substrate-borne vibrations. Some frequencies were tested using more than one of the speakers.

The sound pressure level (SPL re 20 µN/m²) was measured daily using a Brüel and Kjaer (B&K) 1/4-in (0.64-cm) microphone, coupled with a preamplifier (B&K 2618), a microphone amplifier (B&K 2608), and spectrum analyzer (Zonic 3525). The measuring system was calibrated with a pistonphone (B&K 4230). Sound measurements were taken by placing the microphone in the position occupied by an animal's head when it was drinking and pointing the microphone directly toward the loudspeaker (0° incidence). Care was taken to produce a homogeneous sound field (± 1 dB) in the area occupied by the animal's head and ears. The tones produced by the loudspeakers during testing were examined for the presence of overtones or distortion by routing the output of the microphone amplifier directly to the spectrum analyzer (Zonic 3525). Background noise levels and spectra were also obtained in this manner. Analysis of the final test

signals indicated that any overtones were more than 10 dB below the animals' thresholds.

Sound localization

To determine minimum audible angle, a single 100-ms broadband noise burst (2–45 kHz) was emitted from one of ten piezoelectric tweeters (five pairs with closely matched spectra). Noise was generated (Grason–Stadler 1285, 100-kHz band), randomly attenuated through a 7-dB range (Coulbourn attenuator S85-08), and split into two channels via an equalizer (EQ3 Sound System). Both channels were then routed through rise-decay gates set on 0 ms rise-decay (Coulbourn S84-04), amplified (Crown D75), and routed to one of five pairs of speakers. The electrical signals to the speakers were monitored continuously on an oscilloscope outside the chamber. This arrangement allowed the rabbits to be tested on five different angles of separation during each session using broad-spectrum sounds with abrupt onsets and offsets. Matched speakers, together with spectra and intensity randomization on each trial, prevented the rabbits from cueing on acoustic features other than locus (as demonstrated by chance performance on small angles).

Behavioral procedure

Thirsty rabbits were trained to make continuous contact with the spout to obtain a steady trickle of water. Drinking from the spout oriented the rabbits to 0° azimuth.

For the audiogram, a train of four tone pulses was presented at random intervals (from 3.5 to 39 s after the previous trial) from a loudspeaker at 0° azimuth and at ear level. The last tone pulse was followed at its offset by a mild electric shock (300 ms maximum duration) delivered between the spout and the cage floor. The rabbits learned to avoid the shock by breaking contact with the spout whenever they heard a tone. The shock was adjusted for each individual to the lowest level that reliably produced an avoidance response. The mildness of the shock was confirmed by the readiness with which the animals returned to the spout after the shock had been delivered and the relatively low false-alarm rates.

Test sessions were divided into 2-s trials separated by 1.5-s intertrial intervals. Approximately 22% of the trials contained a pulsing tone (warning signal), whereas the remaining trials contained only silence (safe signal). The contact circuit detected whether a rabbit was in contact with the spout during the final 150 ms of every trial. If it 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 (warning signal) or as a false alarm if no sound was presented (safe signal).

Testing continued until a rabbit no longer responded to the warning signal above the level expected by chance, i.e., the hit rate was no longer significantly higher than the false-alarm rate ($p > 0.05$, binomial distribution). A typical test session for a trained animal consisted of approximately 35–75 warning trials and approximately four times as many safe (silent) trials during which a complete psychophysical curve could be generated.

The procedure for determining minimum audible angle (MAA) was similar. Speakers were paired and placed at five different angles of separation, with one pair used for each block of 6–8 warning trials and associated safe trials. Safe trials consisted of single 100-ms noise bursts emitted every 3.5 s from the right speaker of the pair; approximately 22% of trials were warning trials in which the noise burst was emitted from the left speaker and followed by avoidable shock. The speakers were arranged before each session, so that some angles were well above threshold and at least one angle was below threshold. Progressively smaller angles of separation were used until the rabbits could no longer discriminate between right versus left sound sources above chance.

Determining threshold

Hit rates and false-alarm rates were determined for each block of 6–8 warning trials and the approximately 30 associated safe trials for each stimulus intensity at each frequency (for the audiogram) or for each angle of separation (for minimum audible angle). The hit rate was then corrected for the corresponding false-alarm rate for each block of trials 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 observed under each stimulus condition (i.e., for each block of trials) and can range from Zero (no hits) to perfect performance (100% hit rate with no false alarms). Because false-alarm rates vary with the difficulty of the detection, this measure corrects the hit rate using the false-alarm rate specifically associated with that stimulus condition. Testing with this procedure has the advantage of providing not only a reward for hits (shock avoidance) and correct rejections (continued access to water), but also of imposing a cost for errors in the form of misses (shock) and false alarms (momentarily foregoing access to water). Because of the cost for misses, the animals cannot ignore the less salient signals and simply respond only to easily detectible signals without penalty. The procedure also has the advantage that the animals receive practice listening for signals near threshold and cannot use a strategy of missing a signal to bring about easier to detect signals on subsequent trials, as can occur in some tracking procedures.

For additional discussion of the method, see Heffner and Heffner (1995), Heffner et al. (2006), Koay et al. (1998).

Absolute threshold for tones was defined as the intensity at which the performance measure (Corrected Detection) equaled 0.50, usually obtained by interpolation. Chance performance is also noted and is defined as the score for which the hit rate and false-alarm rate cannot be reliably distinguished at a 0.05 level of confidence (binomial distribution). 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 and not improving. After the entire audiogram had been completed for an animal, each frequency was retested at least once to ensure threshold reliability.

Noise-localization threshold was defined as the angle at which the performance measure equaled 0.50. Testing was considered complete when scores at every angle stabilized and were no longer improving with practice (i.e., asymptotic performance). The average of the best half of scores at each angle was then used as the animal's final score for that particular angle.

Results

The rabbits adapted easily to the once-daily access to water. They drank 20–45 mL of water (35 mL average) in each session. Sessions lasted 35–65 min, so that thresholds could be obtained in every session. Early in training their body weights dropped to 83–88% of their incoming weights, and then stabilized at 83–98% once testing became routine for them. When returned to free water during breaks in testing,

their body weights increased to 111–119% of their incoming weights. This pattern is typical of animals on restricted access to water (Rowland 2007; Toth and Gardiner 2000).

Audiogram

The audiograms for the three Eastern cottontail rabbits are illustrated in Fig. 1. The rabbits showed good agreement, with the difference between individuals ranging between 1 dB (at 4 and 45 kHz) and 10 dB (at 250 Hz). Beginning at 125 Hz with an average threshold of 85 dB SPL, there was rapid improvement in sensitivity as frequency increased to a distinct best frequency at 4 kHz where their average sensitivity was −2.3 dB SPL. At higher frequencies, the rabbits remained sensitive up to 45 kHz beyond which there was a sharp decline in sensitivity (typical of high-frequency hearing) to 78 dB SPL at 64 kHz. The rabbits showed a relatively broad range of good sensitivity (thresholds of 20 dB SPL or less) from 1 to 32 kHz. The audible range at 60 dB SPL for Cottontail rabbits extends from 300 Hz to 56 kHz, slightly more than 7.5 octaves.

Noise-localization threshold (minimum audible angle)

The noise-localization performance of the Cottontail rabbits is illustrated in Fig. 2. All of the rabbits were able to perform above 90% corrected detection at the larger angles, but performance began to fall at 60° and declined rapidly to chance by 20°. The 50% localization threshold (minimum audible angle) averaged 27.6°.

Fig. 1 Audiograms of three Eastern cottontail rabbits (*Sylvilagus floridanus*). A, B, and C represent thresholds of individual rabbits with mean thresholds indicated by the solid line. The previously published audiogram for Domestic rabbits, *Oryctolagus cuniculus,* is shown for comparison (gray line, Heffner and Masterton 1980). The cottontails have good sensitivity over a relatively wide range and a single point of best sensitivity at 4 kHz. At a sound pressure level of 60 dB, their hearing range extends from 300 Hz to 56 kHz. Although the sensitivity of *O. cuniculus* extends further into the low frequencies, overall sensitivity for the two species is very similar
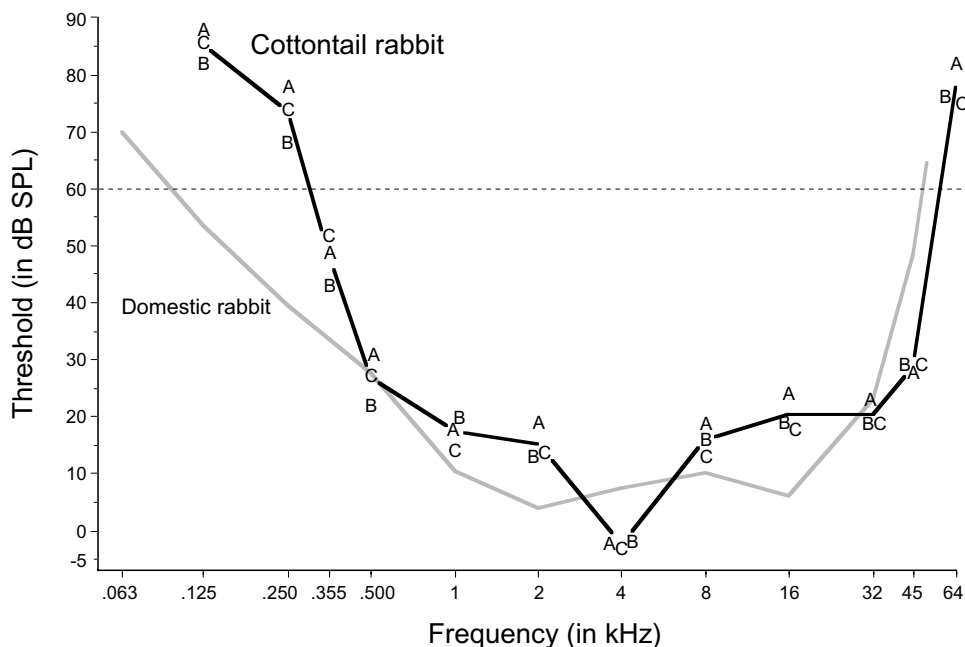
Fig. 2 Noise-localization performance of three Cottontail rabbits, *Sylvilagus floridanus*. Individual performances are indicated by A, B, and C. Note the good agreement between the three rabbits and good performance at large angles. The 50% corrected detection threshold was 27.6°. Performance fell to chance at 10° and 20°, indicating that the animals could not distinguish between the speakers based on locus and that there were no other detectable differences between the speakers
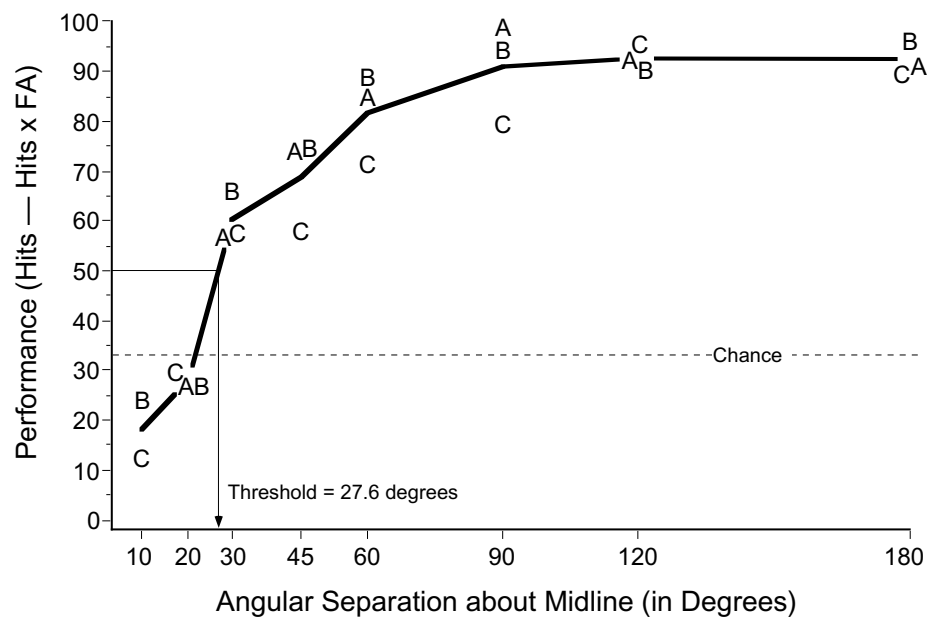
Discussion

Figure 1 compares the audiogram of the Cottontail rabbits to the only other Lagomorph whose hearing is known, *O. cuniculus* (Heffner and Masterton 1980). The two species are similar in their appearance and in much of their behavior. However, they have a long history of separate evolution in the Old and New Worlds. *O. cuniculus* evolved as a burrowing species and the domesticated strain is used for auditory studies, whereas *S. floridanus* does not burrow, but instead nests in grassy depressions (Chapman et al. 1980), and remains wild. The main difference between their hearing is the slightly better sensitivity of the Domestic rabbit at 250 Hz and below, which might be an adaptation to its burrowing lifestyle (cf., prairie dogs, Heffner et al. 1994). On the other hand, the hearing of the Cottontail rabbits extends slightly further into the high frequencies (56 kHz vs. 49 kHz at 60 dB SPL), which is consistent with its smaller functional interaural distance as discussed below. Although a few modern breeds of domestic rabbits have pendant ears ("lop ears"), those used in the audiogram study were New Zealand Whites with upright ears like the cottontails (Heffner and Masterton 1980), indicating that the position of their pinnae is not likely to account for the slight difference in hearing.

High-frequency hearing

Evidence has accumulated for 50 years that the main selective pressure for mammalian high-frequency hearing is the need to localize sound (Masterton et al. 1969; cf., Heffner and Heffner 2018). The basis for this idea is the relationship between functional interaural distance (an estimate of the availability of the binaural time-difference cue for sound localization) and the upper frequency limit of hearing in mammals. Functional interaural distance is a measure of the time required for a sound to travel from one ear to the other, either around the head (in air) or between the ears (in water), and is an estimate of the maximum interaural time cue available to an animal. It suggests that the smaller the binaural time difference available to a mammal, the higher frequencies it should hear as it becomes more reliant on the binaural intensity-difference cue. As shown in Fig. 3, both the New-world Cottontail rabbit reported here and the Old-world Domestic rabbit are consistent with this relationship and lie close to the regression line.

It has been erroneously stated that high-frequency hearing is correlated with the width of an animal's head and, therefore, cannot explain why cetaceans, with their physically large heads, have good high-frequency hearing (Manley 2010). However, aquatic mammals' heads are functionally smaller than they at first appear, because sound travels approximately three times faster in water and it travels through the head, from one bulla to the other, due to the impedance match between the head and surrounding water (Masterton et al. 1969; Nummela et al. 2007; Popov et al. 2016; Heffner and Heffner 2017). When the travel time of sound in water is taken into account, aquatic mammals do not deviate from the correlation, as shown in Fig. 3. With the addition of Cottontail rabbits, the initial set of 19 species has now grown to include 77 species (including additional aquatic and amphibious mammals as well as subterranean species), and the relationship showing that species with smaller functional interaural distances hear higher frequencies remains strong.

Although we argue that selective pressure for sound localization exerted a major force on high-frequency hearing in

Fig. 3 High-frequency hearing limit at 60 dB SPL varies with functional interaural distance. Species with small functional interaural distances hear higher than those with larger interaural distances. Aquatic and amphibious mammals (triangles) for whom sound travels underwater much faster than it does in air are consistent with this relationship. Echolocating mammals from any Order (black filled symbols); bats (squares); rabbits (stars); rodents (gray filled symbols). Subterranean rodents (diamonds) are not included in the regression analyses, but are illustrated to show that non-localizing species are not under selective pressure to hear high frequencies
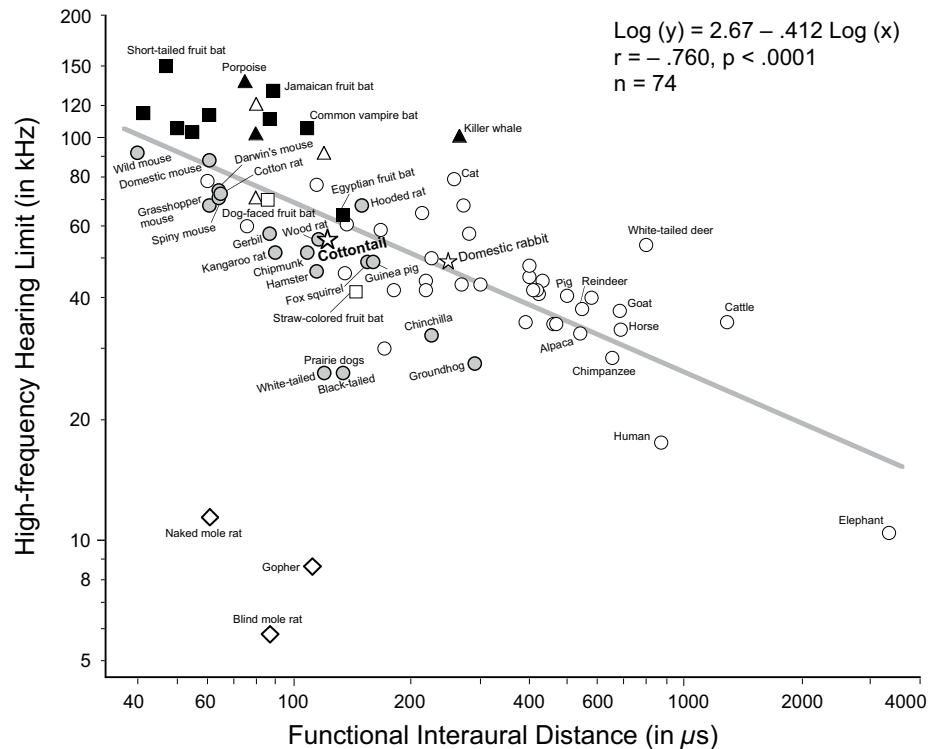
mammals, this does not exclude the influence of other factors. Indeed, given a correlation between high-frequency hearing and functional interaural distance of $r = -0.76$, it appears that although functional head size accounts for about 58% of the variance in high-frequency hearing, 42% remains unaccounted for. Some possible factors include communication that relies on high frequencies in some species (e.g., Noirot and Pye 1969; Ehret 2003). Another potential factor is the high-frequency pinna cues that prevent front–back confusions (e.g., Butler 1986; Heffner et al. 1995). The pinnae also serve as directional filters that allow animals to select signals containing high frequencies out of background noise. Since almost all sounds made by animals include high frequencies, the filtering function of pinnae no doubt contributes survival value to high-frequency hearing. Finally, even human speech includes high frequencies that enable us to isolate individual speakers in noisy environments (Monson et al. 2019)—possibly based on their location.

In addition, once mammals evolved high-frequency hearing, it could be exploited for other functions, such as for echolocation by many bats and cetaceans (indicated by black symbols in Fig. 3). Both aerial and aquatic echolocators have extended their high-frequency hearing compared to similar-sized non-echolocators (Heffner et al. 2013). The bats in Fig. 3 that do not echolocate (Dog-faced fruit bat; Straw-colored fruit bat) or that use tongue clicks instead of laryngeal calls (Egyptian fruit bat) also do not have extended high-frequency hearing, but instead lie very close to the regression line for all mammals.

If mammals evolved high-frequency hearing for sound localization, then we should expect that mammals that relinquished the ability to localize sound will have also lost their high-frequency hearing. Indeed, the three exclusively subterranean and non-localizing species that have been tested (Pocket gopher, Naked mole rat, and Blind mole rat) do not hear nearly as high as predicted by the regression line and appear as outliers in Fig. 3.

Early evolution of high-frequency hearing

Mammals evolved two ways to localize sound that are not commonly used by other vertebrates—specifically high-frequency hearing for binaural intensity-difference cues and external ears for pinnae cues. Among most non-mammalian terrestrial vertebrates (amphibians, reptiles, and birds), the two ears are interconnected internally, which increases the magnitude of the binaural time-difference cue, thus enhancing their ability to localize sound (e.g., Christensen-Dalsgard and Manley 2019). However, unlike other terrestrial vertebrates, mammalian ears are isolated from each other, raising the questions of why they lost the interconnection common to their ancestors and how they compensated for it. Current evidence indicates that the development of high-frequency hearing played a big role, and that involved a re-modeling of the middle ear.

Unlike other vertebrates, mammals developed specialized teeth and jaw movements to grind food before swallowing. Because such grinding is noisy, the jaw had to be uncoupled

from its tight connection to the skull to reduce noise transmitted to the ear via bone conduction (Mao et al. 2020). This involved changes in the jaw bones that led to some jaw bones evolving into the three-boned middle ear thereby breaking the direct connection between the jaw and the ear and reducing noise from chewing. The three-boned middle ear seems to have enabled more effective transduction of high frequencies that, in turn, provided the opportunity to take advantage of the directional filtering properties of the pinnae at high frequencies.

Virtually all modern mammals have pinnae, but they have only recently been documented in the fossil record of an early mammal, *Spinolestes xenarthrosus*, from about 125–127 million years ago (Ma) (Martin et al. 2015). Thus, pinnae were present before the rearrangement of the jaw bones to form the middle ear 123 Ma (Mao et al. 2020). We suggest that pinnae played a more important role than usually recognized in the early evolution of high-frequency hearing. If that is the case, some aspect of pinna size may prove to be a factor that accounts for some of the remaining variance in high-frequency hearing in mammals.
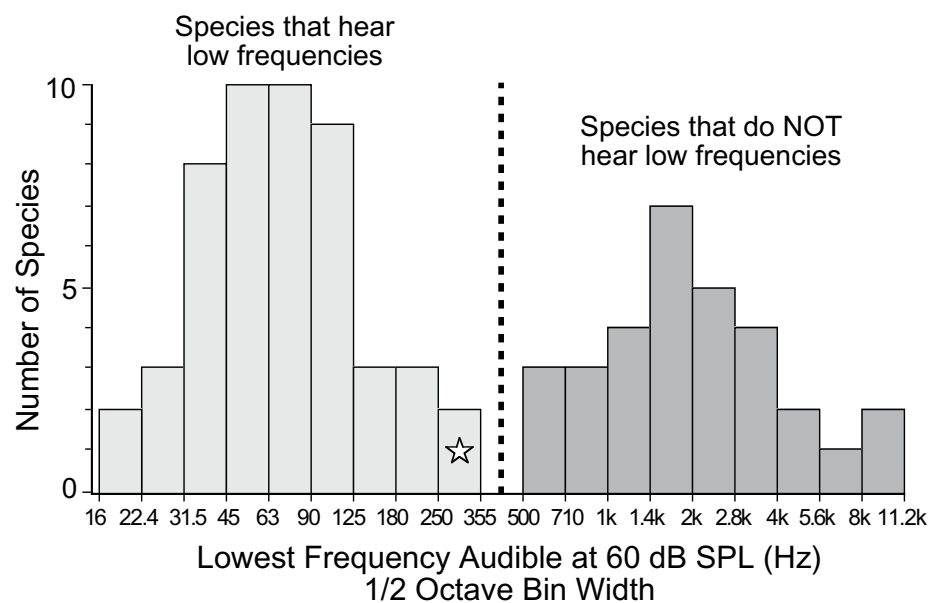
Low-frequency hearing

Low-frequency hearing limits in mammals encompass a range of 9.24 octaves, twice as broad as the 4.66-octave range of high-frequency hearing limits (5.9–150 kHz). More surprising is that, unlike high-frequency hearing, low-frequency hearing is not normally distributed, but instead is bimodally distributed (Fig. 4). Some mammals have good low-frequency hearing with the mode of that distribution encompassing low-frequency limits between about 45 Hz and 90 Hz. Other mammals have poor low-frequency hearing

with the mode of that distribution encompassing hearing limits that extend only as low as 1.4–2 kHz. This unexpected bimodal distribution of low-frequency hearing was reported nearly two decades ago (Heffner et al. 2001) and has not changed despite the addition of 24 species to the sample of behavioral audiograms. In the current sample, there remains a gap between these two distributions with no species yet tested having a low-frequency hearing limit between about 300 Hz and 520 Hz.

The Cottontail rabbit reported here, which has a low-frequency hearing limit of 300 Hz, lies closest to the gap, occupying the uppermost position in the group with good low-frequency hearing. Among the next nine species in the upper tail of the good-low-frequency group, seven are not typical surface dwellers: two are aquatic (Common bottle-nosed porpoise, Beluga whale), four are amphibious (Pacific walrus and Elephant seal both tested under water, Northern fur seal and Sea lion tested in air), and one is subterranean (Pocket gopher). At the high-frequency side of the gap are five species: two amphibious species (Elephant seal, Stellar sea lion tested under water), the Common vampire bat, the Hooded lab rat, and a primitive mammal, the Desert hedgehog. Altogether, this suggests that low-frequency hearing among terrestrial mammals is truly bimodally distributed with a clear gap between the two groups—a gap that is bordered by species that are either not typical within their order (e.g., subterranean rodents or the Common vampire bat with its unusually sensitive low-frequency hearing among bats), or species adapted for life in water. To date, there is no convincing explanation for this bimodal distribution of low-frequency hearing. Although morphological correlates are likely to emerge, an evolutionary explanation is also of interest.

Fig. 4 Distributions of lowest frequencies audible at 60 dB SPL. The 300-Hz low-frequency hearing limit of the Cottontail rabbit (star) places it at the upper end of the distribution of species that hear well at low frequencies. The dashed vertical line at 400 Hz represents an approximate border between the two distributions. Among species in the lower group, low-frequency hearing is not correlated with high-frequency hearing, but among those in the upper group, high-frequency hearing accounts for about 36% of the variance in low-frequency hearing (see text)

It is well known that some desert rodents (e.g., Gerbils and Kangaroo rats) and chinchillas have unusually large bullae thought to make their good low-frequency hearing possible. However, large bullae are not essential, because many rodents in the squirrel family, as well as least weasels, are equally small and have similar low-frequency hearing without enlarged bullae (Heffner and Heffner 1985b; Heffner et al. 2001). Such comparisons suggest that there must be more than one morphological adaptation to accommodate low-frequency hearing.

It seems unlikely that the length of the basilar membrane is a constraint on low-frequency hearing, because there are many species that hear both very low and high. For example: Domestic cats at a level of 60 dB hear from 0.055 to 79 kHz (Heffner and Heffner 1985a); Chipmunks hear 0.039–52 kHz (Heffner et al. 2001); Gerbils hear 0.036 Hz–58 kHz (Ryan 1976); Least weasels hear 0.050–60 kHz (Heffner and Heffner 1985b). Because many species that hear below about 400 Hz also hear well at high frequencies, low-frequency hearing is not reliably correlated with high-frequency hearing ($r = 0.154$, $p = 0.360$). However, among species that do *not* hear low frequencies well (species on the right side of Fig. 4), there is a moderate correlation ($r = 0.605$, $p = 0.0017$) accounting for about 36% of the variance in high-frequency hearing *within that group*. Thus, it seems that a substantial portion of mammals that hear in air have been able to extend their low-frequency hearing below 400 Hz without comparable sacrifice of high-frequency sensitivity. It is as if some mammals have a second means of transducing sound that permits them to extend their hearing range below 400 Hz. It has been proposed that such a mechanism might be the temporal code for frequency in the cochlea (Heffner et al. 2001). There have been relatively few comparative studies of the actual frequencies over which the temporal and place mechanisms operate to enlighten this question (e.g., Walker et al. 2011; for a review, see Vater and Kossl 2011; Heil and Peterson 2017; Verschooten et al. 2019); almost none of these comparative studies were carried out on species with poor low-frequency hearing. Yet, evidence continues to accumulate, showing that cochlear mechanisms in the lower-frequency apical region are different from those in the rest of the cochlea, but that such discontinuities are hard to find in species that do not hear low frequencies (Greenwood 1996; Sasmal and Grosh, 2019). We may eventually discover the mechanisms underlying the bimodal distribution of low-frequency sensitivity, but the selective pressures that led to this difference remain unexplored.

Sound localization

Cottontail rabbits, with their mean minimum audible angle of 27.6°, are relatively poor localizers. Only Kangaroo rats, Gerbils, Domestic mice, Cattle, and the subterranean species

have worse localization acuity (Fig. 5). However, their acuity is consistent with their visual features, namely nearly complete panoramic visual fields and a visual streak (unpublished observation). Although many species, most notably primates, have their highest acuity (most densely packed ganglion cells) in a circular area called a fovea or area centralis, some species, like rabbits, have their best acuity spread in a narrow horizontal line across the retina, called a visual streak, giving them good acuity that spans the horizon. We reported many years ago (Heffner and Heffner 1992) that sound-localization acuity
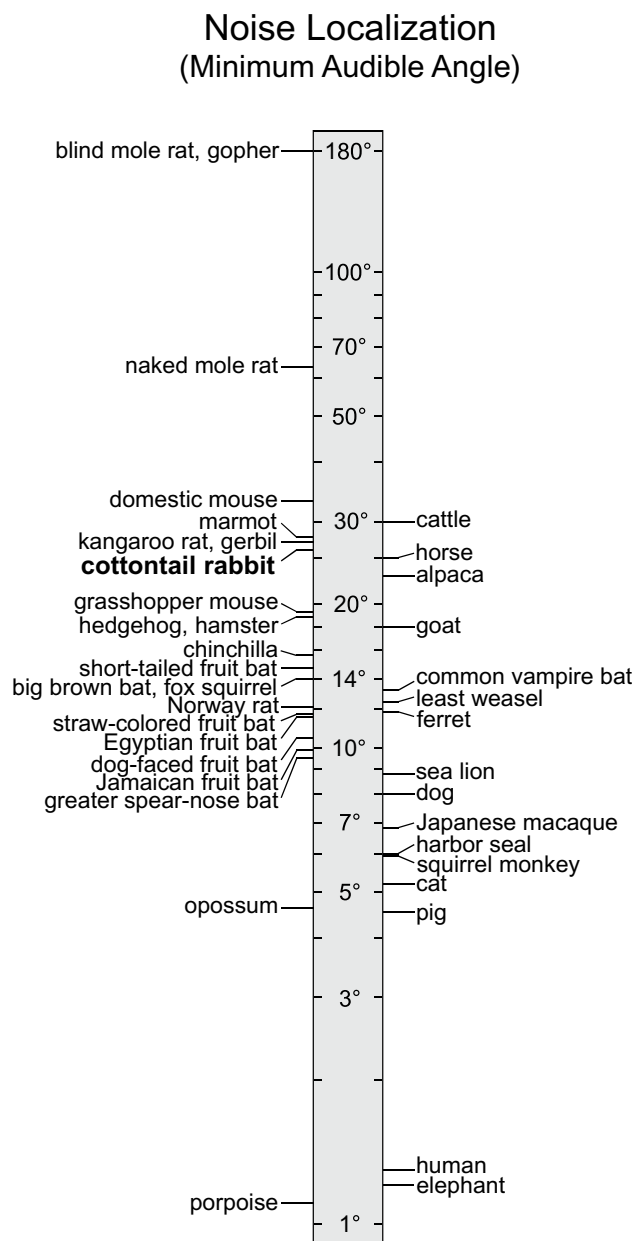
Fig. 5 Distribution of sound localization thresholds for brief noise bursts or clicks among mammals. Note log scale. Cottontail rabbits are among the poorer localizers with their average threshold of 27.6°

(MAA) is not reliably related to the magnitude of the binaural locus cues (as estimated by functional interaural distance) as we once expected. To revisit the question of whether some other factor, such as simple visual acuity or the magnitude of the binaural locus cues, also contributes to the variation in localization acuity, a multiple regression analysis was performed. When the effects of all three factors are considered, neither visual acuity ($p = 0.92$) nor functional interaural distance ($p = 0.66$) improves our ability to predict sound-localization acuity beyond that provided by a measure of the field of best vision ($p < 0.0001$). In short, localization acuity remains most closely predicted by its role in directing visual orientation and scrutiny of sound sources.

In summary

Cottontail rabbits conform to the pattern established by the majority of mammals. Their high-frequency hearing is closely predicted by their functional interaural distance. Their low-frequency hearing falls within the group that hears well below 400 Hz. Their sound localization, although poor, is expected of an animal with a broad field of best vision (visual streak). Although unremarkable in their hearing, Cottontail rabbits broaden, beyond a single domesticated species, our sample of mammalian Orders whose hearing has been examined. Having a good sample of what is typical helps us to appreciate the unusual when it occurs.

Compliance with ethical standards

Code availability Not applicable.

Conflict of interest There was none provided for conflicts of interest.

Ethics approval University of Toledo Animal Care and Use Committee.

Informed consent Not applicable.

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