

Primate Hearing From a Mammalian Perspective

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ABSTRACT

This review discusses hearing performance in primates and selective pressures that may influence it. The hearing sensitivity and sound-localization abilities of primates, as indicated by behavioral tests, are reviewed and compared to hearing and sound localization among mammals in general. Primates fit the mammalian pattern with small species hearing higher frequencies than larger species in order to use spectral/intensity cues for sound localization. In this broader comparative context, the restricted high-frequency hearing of humans is not unusual. All of the primates tested so far are able to hear frequencies below 125 Hz, placing them among the majority of mammals. Sound-localization acuity has been determined for only three primates, and here also they have relatively good localization acuity (with a minimum audible angle roughly similar to other mammals such as cats, pigs, and opossums). This is in keeping with the pattern among mammals in general, in which species with narrow fields of best vision, such as a fovea, are better localizers than those with broad fields of best vision. Multiple lines of evidence support the view that sound localization is the selective pressure on smaller primates and on other mammals with short interaural distances for hearing high frequencies. © 2004 Wiley-Liss, Inc.

Key words: audiogram; primates; mammals; audition

This is a review of the hearing of primates and the selective pressures involved in the evolution of mammalian hearing. Only behavioral tests of hearing are considered because it is the behavior of whole animals, not the mechanisms that might underlie it, that is subject to selective pressures. The responses of individual neurons and small groups of neurons may be relevant to how primates and other animals hear as they do, but not why. Similarly, morphological differences in the middle and inner ear are only alluded to as they provide mechanisms to support hearing; a good review of this topic can be found in Nummela (1995). Different mechanisms may be used to achieve similar abilities and do little to explain the origin of different hearing abilities in different species.

The earliest comparative studies of hearing were conducted by Francis Galton in the late 1800s. By observing the natural responses of different species to unexpected high-pitched whistles, Galton discovered that cats can hear higher than humans and that humans lose their high-frequency hearing as they get older. However, he also thought that small dogs could hear high frequencies but that big dogs could not. We now know that large and small dogs all hear high frequencies (Heffner HE, 1983), but that big dogs do not necessarily respond to them, perhaps because high-pitched sounds are not as likely to

signal danger to a large animal as are low-pitched sounds. Think of grass rustling as a mouse scurries through it compared to the thud of a branch broken by a buffalo. So, for the purposes of comparing hearing abilities across species, data were only considered if they were based on hearing tests that followed behavioral principles in which adequate rewards and punishments ensured that the animals detected and discriminated sounds to their best abilities.

Nearly all of the sounds in nature are made by animals, either by vocalizing or, more often, by moving through their environment. Accordingly, it follows that our ears serve as animal detectors and a description of the sounds

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that we can detect (our audiogram) is the most basic description of our auditory abilities. Once an animal has been detected, we can derive its location from the sounds it generates. Indeed, mammals reflexively orient toward an unexpected sound, and sound localization acuity is another important descriptor of our hearing ability. Finally, having detected and located an animal in our vicinity, it is useful to know something about it and its intentions (is it potential food, mate, or predator?); if it is vocalizing, what do the calls mean? Such identification and interpretation refers to the ability to respond based not on the sound's physical features but on the biological features of the sound's source. These questions are more complex and require not only the ability to detect differences in frequency, intensity, and tempo, but also the cognitive ability to associate them with environmental events and contingencies. Although these cognitive abilities appear well developed in primates, the focus of this review is on the basic sensory abilities of sound detection and localization as less is known about the abilities of animals to identify sound. We will discuss the features that seem to influence these abilities among mammals in general and show how primates fit into this mammalian pattern.

MATERIALS AND METHODS

The data included in this review come only from tests in which animals were motivated to respond even to low-intensity sounds. Unconditioned responses, like those observed by Galton, habituate rapidly because animals quickly learn to ignore sounds in their environment that do not signal important events. Similarly, motivation to avoid errors has been integrated into the hearing tests included here. Otherwise, sounds that are soft but still audible may simply be ignored because of the effort required to maintain vigilance. Good tests also make it in the animal's best interest to avoid responding when there is no sound. These false positive responses can render meaningless the true detection responses if they are numerous. Thus, the data included for this discussion have fulfilled fairly rigorous requirements and the procedures have proved to produce reliable estimates of hearing whenever the same species or individuals have been retested (Heffner and Heffner, 1988; Koay et al., 2002). Finally, whenever possible, we have selected studies in which signals were presented from a loudspeaker rather than headphones. This allows the sound gathering properties of the pinnae to contribute to the audiogram as they do in the natural environment.

The audiogram is the most basic measure of hearing. It is a graph of detection thresholds as a function of pure-tone frequency (Fig. 1). The audiogram line represents a series of thresholds; a threshold is defined as the least intense sound that can be detected 50% of the time (after correction for spurious responses, or false alarms). Thresholds are expressed here and throughout this review in dB SPL re 20 microNewtons per square meter. Frequencies and intensities above the line can be detected and those below the line cannot. (To be entirely accurate, we must note that intensities just below the audiogram line would occasionally be detected, while those just above it would occasionally be missed.) It is important to remember that these thresholds are generated by experienced listeners with no distractions or background noise. The 60 dB level is marked because it is a common measure of

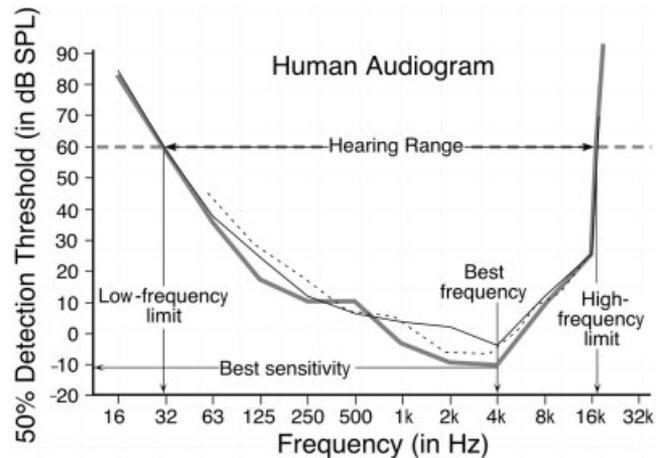


Fig. 1. Average audiogram of seven humans tested in a soundproof chamber with sounds presented from a loudspeaker, the same conditions used for testing animals (bold gray line) (Jackson et al., 1999). For comparison, standard audiograms from Davis (1960) (thin line) and Sivian and White (1933) (dashed line) are also shown. The important descriptors of auditory sensitivity used for comparing species are indicated. Sixty dB SPL (indicated by the horizontal dashed line) is a comfortably loud sound typical of normal conversation and is a common criterion for useful hearing. As can be seen, there is little variation in upper and lower hearing limits.

useful hearing. We often compare species based on the lowest frequency they can detect at a level of 60 dB (low-frequency hearing limit) and the highest frequency they can detect at a level of 60 dB (high-frequency hearing limit). The difference in octaves between the upper- and lower-frequency limits defines the hearing range. There is a practical reason for not choosing a higher definition of hearing limits such as 70 or 80 dB. When determining threshold, sounds at least 15–20 dB above threshold must be initially presented to a subject in order for it to know what to listen for. To define an 80 dB threshold, we must also present intensities near 100 dB, and these are very difficult to produce without distortion (which could be detected in lieu of the pure tone).

Two further parameters that can be used for comparing species are evident in Figure 1: the frequency of best hearing and the best sensitivity of which a species is capable (4 kHz at –10 dB in this audiogram). Both of these values are estimates that are limited by the number of frequencies that were actually tested. For example, had the human thresholds been determined at intermediate frequencies (e.g., 3.2 or 4.1 kHz), the average threshold might have been even lower.

The human audiogram illustrates another limitation of selecting a frequency of best hearing, namely, some species hear a broad range of frequencies, with sensitivity at no single frequency being clearly superior. In this example, there is only 1 dB difference between the sensitivity at 2 kHz and that at 4 kHz, well within the range of individual variation.

RESULTS AND DISCUSSION

Before discussing patterns that occur when comparing the hearing abilities of primates, we should describe the audiograms that are currently known. Because so many

TABLE 1. Hearing limits for 19 species of primates*

Species	High-frequency limit (kHz)	Low-frequency limit (kHz)	Best frequency (kHz)	Best sensitivity (dB)	Hearing range (octaves)
<i>Lemur catta</i>	58	0.067 ²	8	3	9.76
<i>Eulemur fulvus</i> ¹	43	0.072	8	-1	9.22
<i>Nycticebus coucang</i>	44	0.083	16	9	9.05
<i>Perodicticus potto</i>	42	0.125	16	1	8.39
<i>Galago senegalensis</i>	65	0.092 ²	32	3	9.46
<i>Callithrix jacchus</i> ⁴	30		7	-9	
<i>Saimiri sciureus</i>	43	0.100	8	4.5	8.75
<i>Aotus trivirgatus</i>	49.5		10	-8	
<i>Erythrocebus patas</i> ³	30.5 ³	0.245 ³	8 ³	14 ³	6.96 ³
<i>Macaca fascicularis</i>	42		1	1	
<i>Macaca fuscata</i>	34.5	0.028	1	5	10.29
<i>Macaca mulatta</i>	42		8	4	
<i>Macaca nemestrina</i>	34.5		1.8	5	
<i>Cercopithecus aethiops</i>	45	0.069	1.4	-4	9.35
<i>Cercopithecus mitis</i>	48 ²	0.046 ²	1.4	4	10.03
<i>Cercopithecus neglectus</i>	43	0.063	5.7	2	9.38
<i>Papio cynocephalus</i>	40	0.045 ²	8	0	9.80
<i>Pan troglodytes</i>	28.5		8	3	
<i>Homo sapiens</i>	17.6	0.031	4	-10	9.15

*For references, see Figures 2, 3, 6, and 7.

¹Personal communication (D. Sutherland and R.B. Masterton).

²Extrapolated value based on a threshold of 50 dB or higher.

³Tested using headphones.

⁴Published under the name *Hapale jacchus*.

primates have been tested, they are divided into related groups for convenience of illustration. A list of the primate species covered in this review can be found in Table 1.

Strepsirrhine Primates

Figure 2 illustrates the audiograms for four primitive primates whose audiograms have been determined. The human audiogram has also been included for comparison. Although not a primate, we have also included a tree shrew, *Tupaia glis*, because it has been considered to represent an intermediate form between insectivores and strepsirrhines and because it has a similar habitat and lifestyle. All of the species represented here have hearing that becomes gradually more sensitive as frequency increases above their low-frequency hearing limit (slowly falling curve from 125 Hz to 8 kHz), and all show a rapid decrease in sensitivity (sharply rising curve above 32 kHz) as their high-frequency limit is approached. Indeed, the shapes of the audiograms are remarkably similar; their main difference is where they lie along the frequency axis. All of the strepsirrhines and the tree shrew hear higher frequencies than humans do, and none hear as low. This difference in high- and low-frequency hearing is not peculiar to strepsirrhines, but is nearly universal among small mammals, as discussed below.

Old World and New World Monkeys

Figure 3 illustrates audiograms for Old World monkeys. In addition to the yellow baboon and the patas monkey, there are average audiograms for three members of the genus *Cercopithecus* (DeBrazza's monkey, blue monkey, and vervet) and for four macaques (rhesus, Japanese, pig-tailed, and cynomolgus). We have treated the genera *Cercopithecus* and *Macaca* as single cases because the species are so closely related; however, the individual

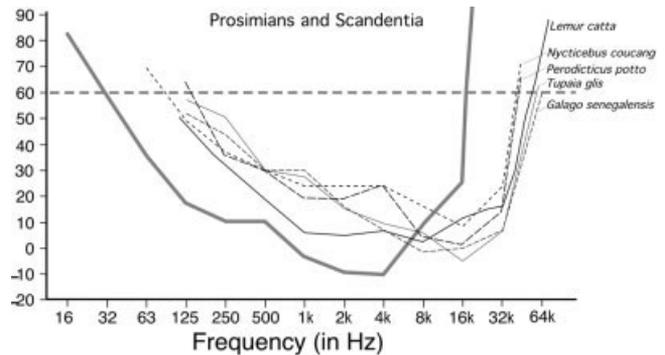


Fig. 2. Average audiograms for the ring-tailed lemur (*Lemur catta*) (Gillette et al., 1973), lesser bushbaby (*Galago senegalensis*) (Heffner HE et al., 1969b), potto (*Perodicticus potto*) (Heffner and Masterton, 1970), slow loris (*Nycticebus coucang*) (Heffner and Masterton, 1970), and tree shrew (*Tupaia glis*) (Heffner HE et al., 1969a). The human audiogram represented by the gray line is included for comparison.

species are illustrated in the scatter plots. Although most of the audiograms are complete, testing was not carried out at frequencies low enough for a low-frequency hearing limit to be established for the baboon. The shape of the audiograms is typical, with more gradual changes in sensitivity at lower frequencies than at higher frequencies. Eight of the species have good overall sensitivity with thresholds below 10 dB SPL over several octaves, and their low-frequency sensitivity is similar to that of humans. All hear approximately an octave higher than humans do. Only the patas monkey seems unusual with poor sensitivity overall (no thresholds below 10 dB) and much poorer hearing at low frequencies, with no responses obtained below 125 Hz. Although this is possibly a true

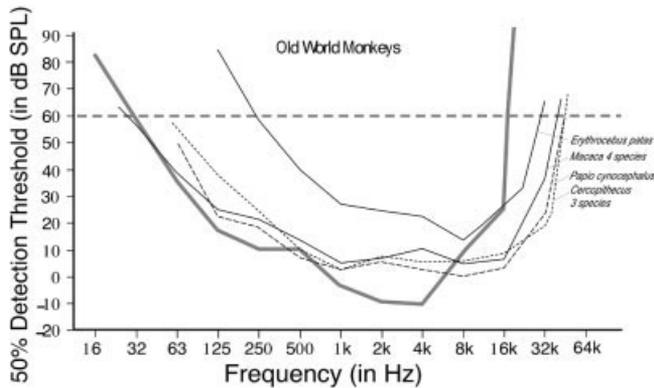


Fig. 3. Average audiograms for the patas monkey (*Erythrocebus patas*) (Smith et al., 1987), yellow baboon (*Papio cynocephalus*) (Hienz et al., 1982), four macaques [*Macaca fascicularis* (Stebbins et al., 1966); *M. fuscata* (Jackson et al., 1999); *M. mulatta* average from Pfingst et al. (1975, 1978), Lonsbury-Martin and Martin (1981), and Bennett et al. (1983); *M. nemestrina* (Stebbins et al., 1966)], and three Cercopithecus [*Cercopithecus aethiops* (Owren et al., 1988), *C. mitis* (Brown and Waser, 1984), *C. neglectus* (Owren et al., 1988)]. The human audiogram represented by the gray line is included for comparison.

representation of the hearing for that species, the patas monkeys were tested using headphones, and it can be difficult to calibrate the intensity of auditory signals with headphones, especially at low frequencies, and headphones eliminate the contribution of the sound-gathering function of the pinnae. Accordingly, data from this species are not included in the comparative analyses presented below.

Audiograms for three species of New World monkeys (squirrel monkey, owl monkey, and marmoset) are illustrated in Figure 4. As with the strepsirrhines, the entire audiogram is shifted along the frequency axis toward higher frequencies compared to humans. Although the typical shape is present with its slope shallower at low frequencies than at high frequencies, one additional feature appears in the midrange of frequencies. Whereas the other species illustrated so far had relatively little variation in sensitivity in the midrange where hearing is best, these species have a slight W-shape to their audiograms with good hearing near 2 kHz and 8 kHz, but less sensitivity around 4 kHz. This is often characterized as two peaks of sensitivity, with various functions attributed to the upper peak such as communication (often specified as mother-infant communication) or echolocation in the case of bats (Long and Schnitzler, 1975; Bohn et al., 2001; Sterbing, 2002). However, the shape can also be characterized as a region of reduced sensitivity (here around 4 kHz) in an otherwise smooth audiogram. Such a region of reduced sensitivity has been attributed to the pinnae, which are directional, amplifying some frequencies and attenuating others, depending on the direction of the sound source and orientation of the pinnae (Rice et al., 1992). Such filtering provides directional cues for localization in elevation and front/back discriminations. Whenever the filtering properties of the pinnae have been examined, they have been found to be quite directional in the region of these peaks and dips in the audiogram, lending support to the hypothesis that these differences in sensi-

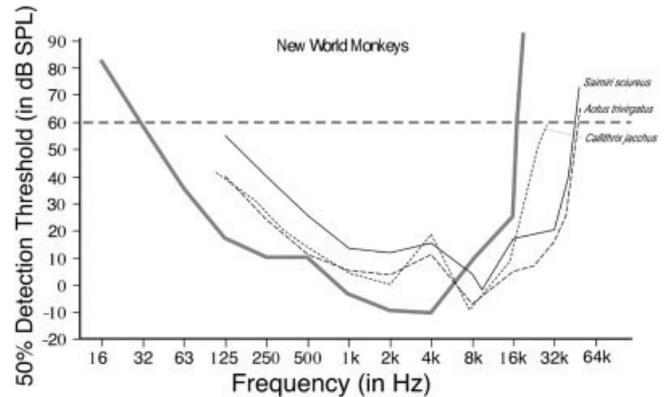


Fig. 4. Average audiograms for a squirrel monkey (*Saimiri sciureus*) (Beecher, 1974; Green, 1975), owl monkey (*Aotus trivirgatus*) (Beecher, 1974), and marmoset (*Callithrix jacchus*) (Seiden, 1958). The human audiogram represented by the gray line is included for comparison.

tivity are related to the pinnae and sound localization (Koay et al., 1998, 2003). The importance of high frequencies for sound localization does not rule out the possibility that mothers and infants take advantage of their ability to hear high frequencies and use them to communicate over short distances, since high frequencies are less likely to propagate over longer distances to be heard by predators. This shape is very common among mammals and is not peculiar to New World primates; in addition to the examples noted above, it is found among marsupials, rodents, carnivores, and hoofed mammals (Heffner and Heffner, 1983, 1985a; Heffner and Heffner, 1985; Frost and Masterton, 1994; Heffner et al., 1994; Heffner et al., 2001b).

Hominoidea

Only one species of ape has been tested for auditory sensitivity, a chimpanzee (*Pan troglodytes*). It is illustrated in Figure 5, along with the audiogram for humans. As with the other primates, its high-frequency hearing is more sensitive and its low-frequency hearing is less sensitive compared to that of humans. Because both of the determinations that contributed to the average for chimpanzees were made using sounds presented via headphones, the low-frequency hearing may not be comparable to tests presenting sounds via loudspeakers due to difficulties in calibrating headphones at low frequencies.

As shown in Figures 2, 3, 4, and 5 and in Table 1, primates vary in their ability to detect sound. As depicted in Table 1, their high-frequency hearing limits range from 17.6 kHz for humans to 65 kHz for the lesser bushbaby, a difference of 1.88 octaves. Low-frequency hearing limits range from 28 Hz for Japanese macaques to 125 Hz for the potto. The best frequency of hearing ranges from 1.4 kHz for the blue monkey and vervet to 32 kHz for the lesser bushbaby. The best sensitivity ranges from -10 for our sample of humans to 14 dB for the patas monkey (although this could be an underestimate). The question we must address is whether this variation is unusual and whether the differences among primates are peculiar to primates or are part of the larger pattern of variation observed among mammals as a whole.

One observation is quickly made from the audiograms of primates: when moving from strepsirrhines to New World

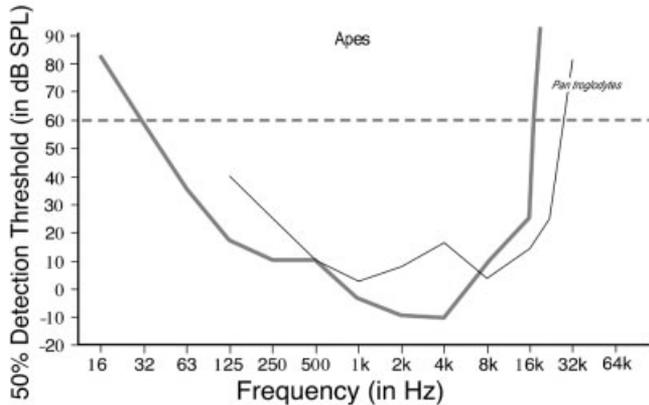


Fig. 5. Average audiogram for the chimpanzee (*Pan troglodytes*) [3 individuals (Elder, 1934); 2 individuals (Kojima, 1990)]. The human audiogram represented by the gray line is included for comparison.

monkeys, Old World monkeys, apes, then humans, high-frequency hearing decreases and, instead, the hearing range extends further into the low frequencies. Although it was once tempting to consider this an evolutionary progression eventually culminating in hearing specialized for human speech, a broader comparison among all mammals shows us that this is not so. For example, even though the audiogram of the chimpanzee is incomplete, it is clear that its hearing is similar to that of humans. Likewise, elephants hear slightly lower frequencies than humans do and not as high. Despite relatively good low-frequency hearing and poor high-frequency hearing, neither of these species has speech (Heffner and Heffner, 1982). Instead, high-frequency hearing varies because high frequencies are more useful to small species than to large species for sound localization. Low-frequency hearing seems to vary with high-frequency hearing, but the relationship is complex. These points are discussed in detail below.

High-Frequency Hearing

High-frequency hearing limits in mammals span a range of 4.7 octaves (Fig. 6B), and we have known for more than 35 years that this variation in high-frequency hearing is systematic (Masterton et al., 1969). Mammals with small heads (or, more precisely, short travel times for sound as it travels from one ear to the other) hear higher frequencies than mammals with large heads. The explanation for this relationship does not lie in the physical scaling of the auditory bulla and cochlea, with smaller middle and inner ears being associated with better high-frequency hearing and larger ears being associated with better low-frequency hearing. Indeed, since the auditory apparatus is so small, even small mammals (such as gerbils and kangaroo rats and their relatives) can have a middle ear large enough to transduce low frequencies, with each bulla of some species being as large as the brain case (Webster and Webster, 1975). Yet a large bulla is not essential for hearing low frequencies as illustrated by the least weasel (Heffner and Heffner, 1985a). On the other hand, large animals can have a small ear regardless of the size of their skull if there is selective pressure to do so. Scaling arguments such as these address the mechanisms

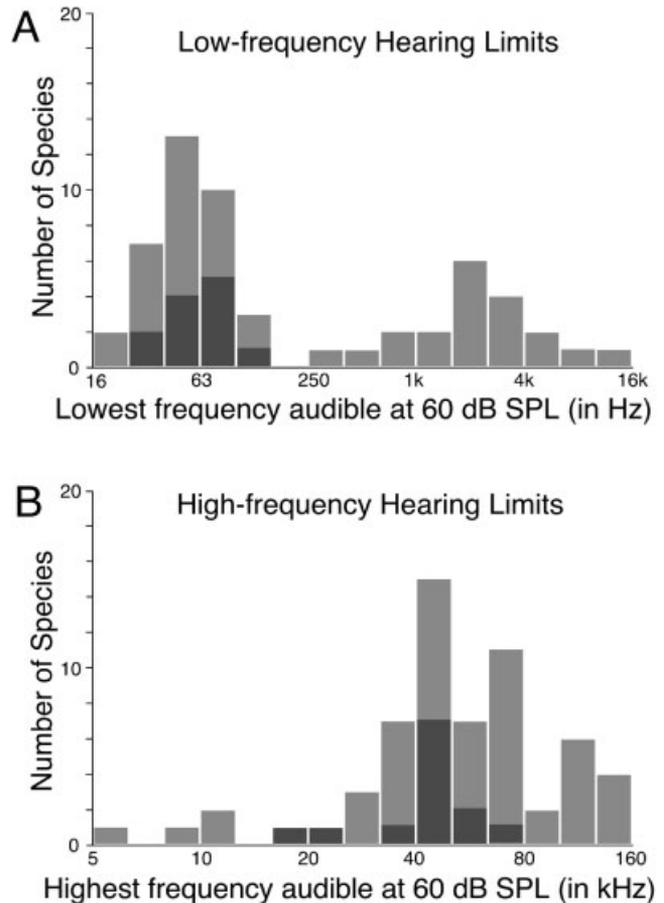


Fig. 6. Distribution of low-frequency hearing limits (A) and high-frequency hearing limits (B) among mammals. Low-frequency hearing is bimodally distributed with species in the left cluster hearing low frequencies (below 250 Hz) and those in the right cluster unable to do so; high-frequency hearing is distributed approximately normally. Darker shading indicates primates. Bin widths for the low-frequency limits are 2/3 octave, but bin widths for the high-frequency limits are 1/3 octave to accommodate the different ranges covered (9.24 octaves for the range of low-frequency limits and 4.7 octaves for the range of high-frequency limits). Because high-frequency hearing limits have been determined for more species than low-frequency hearing limits, the number of species in the two distributions is not equal. In both distributions, the three *Cercopithecus* species all fall into a single bin and are counted as a single case; the four *Macaca* fall into two adjacent bins and are counted as one case in each.

underlying the variation in high-frequency hearing, but it is also important to examine the selective pressures that shape the hearing of mammals. In the case of high-frequency hearing, the explanation for the close correlation with head size (more specifically, interaural distance, as will be shown below) is that being able to detect high frequencies allows mammals to localize sound using pinna cues and spectral differences between the ears (Heffner and Heffner, 1992a).

There are three basic cues to sound locus in the horizontal plane, two of which require comparing the sounds at the two ears: the difference in the time of arrival at the two ears, and the difference in the frequency-intensity

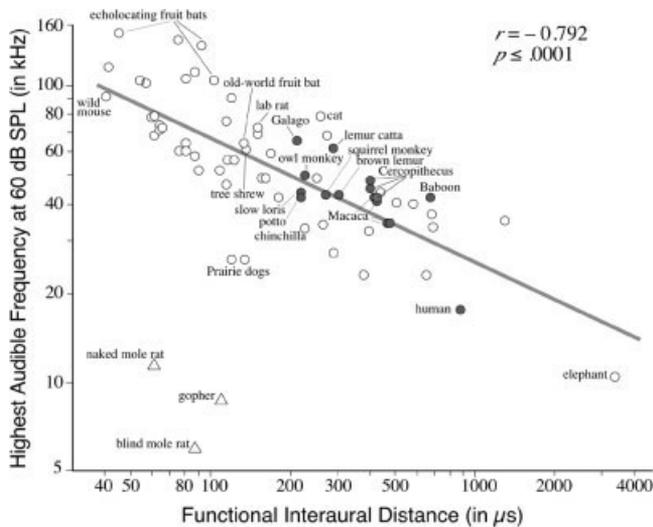


Fig. 7. Relationship between maximum functional interaural distance (as measured by the time in microseconds required for a sound in air or water to travel from one auditory meatus to the other) and high-frequency hearing limit (the highest frequency audible at 60 dB SPL). Primates are indicated by filled circles and are named, along with some other familiar species for comparison. The statistical analysis and regression line do not include the three subterranean species, indicated by triangles, for reasons described in the text. The regression line in this and subsequent figures was determined by minimizing the sum of squared residuals (Data Desk 6.0, Data Descriptions).

spectrum of a sound at the two ears. The magnitude of both of these differences depends on how far apart the ears are. These cues can be exceedingly small in species with close-set ears. For example, the greatest time delay possible for a domestic mouse is 61 μ sec, and for little brown bats and wild mice it is 40 μ sec. Since the smallest time delay thought to be resolvable is about 9 μ sec (Klump and Eady, 1956), these small interaural distances provide little working range to distinguish the locations of sounds between 90° to the right or left (maximum interaural time difference) and sound sources located at the midline (zero time difference). Thus, small mammals are forced to rely on spectral-intensity differences at the two ears or on cues provided by the directional properties of the pinnae at high frequencies, the third cue for localizing sound. However, these cues are also minimal unless an animal can hear frequencies high enough (i.e., wavelengths short enough) to be shadowed by its small head and pinnae. The higher the frequencies that are audible, the greater these spectral cues will be. For this reason, small species are under greater selective pressure to hear high frequencies for use in sound localization than are large species.

The binaural cues are used for localizing sound sources in the horizontal plane, but animals also localize sounds in elevation and distinguish between front and back sounds. For these tasks in which binaural cues contribute little or not at all, the filtering characteristics of the pinnae provide locus cues (as well as helping the animal to pick out sounds from a noisy background) (Heffner et al., 1995). The pinnae act as directional filters that modify the spectrum of a sound reaching the tympanic membrane depending on the orientation of the pinnae to the sound.

High-frequency hearing is essential for using pinna cues to localize sound. Low frequencies are not attenuated by the pinnae and are not reflected by the small contours of the concha and tragus. There are no standardized measures on which we can compare species based on pinna characteristics, but the general rule is that smaller pinnae only affect higher frequencies [compare Heffner et al. (1996)]. Thus, binaural cues and pinna cues both require higher frequencies in smaller species.

The relationship between interaural distance in microseconds (i.e., functional head size) and high-frequency hearing limit is illustrated in Figure 7. The relationship was first reported in 1969 based on a sample of only 18 species heavily weighted with primates, including humans (Masterton et al., 1969). But the relationship has not weakened as the number of species with behaviorally determined audiograms has more than tripled and its representation of lifestyles and mammalian orders has greatly improved. As can be seen, mammals with small heads or close-set ears are able to hear higher frequencies than species with larger interaural distances ($r = -0.792$; $P \leq 0.0001$). Undoubtedly, some of the variance not accounted for (beyond measurement error) is due to the imperfect correspondence between head size and pinna size, shape, and location, since some small species have large pinnae and vice versa.

Primates support the correlation and, being medium-sized mammals, lie along the middle of the regression line. None of the primates, including humans, deviates significantly from the regression line. It is tempting to speculate that humans do not hear as high as most other mammals because we are specialized for speech, and for a long time that possibility remained untested because humans were not only the only mammals that used speech, but were also the largest mammal whose hearing had been tested. With the establishment of even more restricted high-frequency hearing in elephants (Heffner and Heffner, 1982) and later in underground mammals (Heffner and Heffner, 1993), it became much harder to argue that poor high-frequency hearing was a specialization for speech. A simpler explanation is that, in the absence of selective pressure to hear high frequencies for sound localization, larger mammals such as humans and elephants have not retained that capacity.

There are two lines of evidence supporting the contention that the basis for the correlation between functional interaural distance and high-frequency hearing lies in the importance of high frequencies for sound localization in small mammals. First, removal of frequencies above 10 kHz (frequencies that distinguish the hearing of nearly all mammals from that of nonmammals) degrades the ability of small mammals to localize sound, particularly those that cannot make use of interaural time differences (Heffner et al., 2001a). For localization in elevation or far from the midline (including front/back discriminations), removal of high frequencies is devastating (Musicant and Butler, 1984; Heffner et al., 1995). Thus, there is firm evidence that high frequencies are used for sound localization and that small mammals with small pinnae rely on higher frequencies than large animals (Heffner HE and Heffner, 2003).

A second line of evidence supporting sound localization as the selective pressure underlying the possession of good high-frequency hearing is the absence of high-frequency hearing in mammals that do not localize

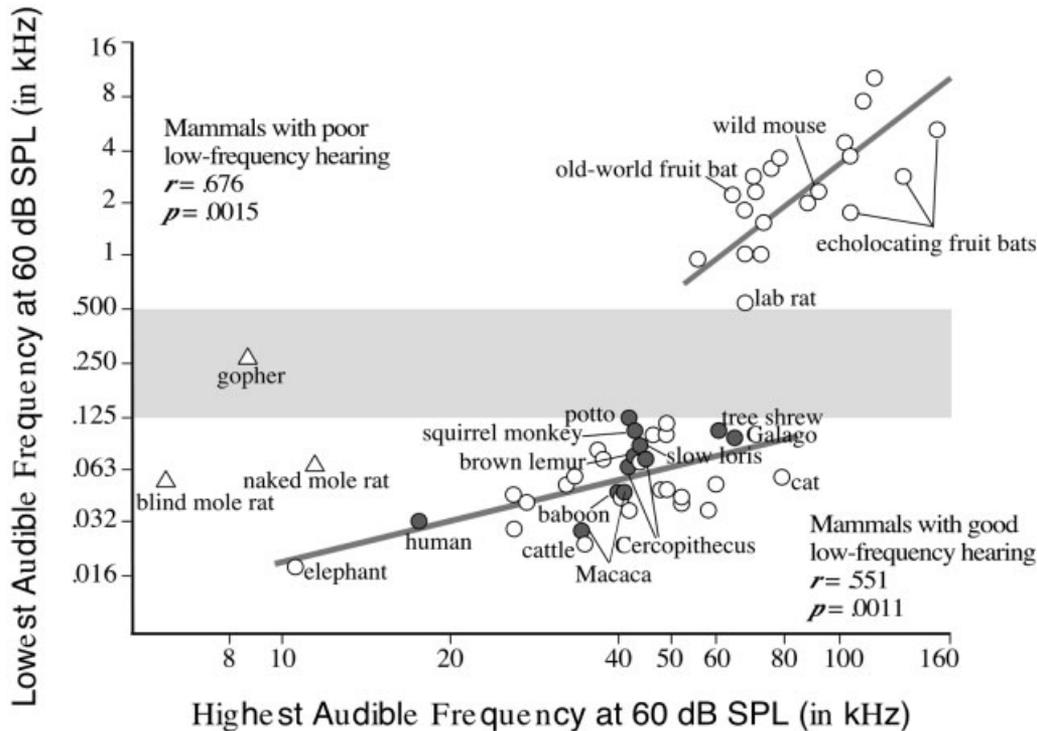


Fig. 8. Relation between the highest and lowest frequencies detected at 60 dB. The gray shading indicates the gap in the distribution of low-frequency hearing limits; species with restricted low-frequency hearing lie above the shading and species with extended low-frequency hearing lie below it. Primates are represented by filled circles. Subterranean species represented by open triangles are not included in the statistical analysis.

sound. Subterranean mammals live their entire lives underground in long narrow tunnels in which sounds are either in front or in the rear and their directional responses to those sounds are similarly restricted. We can describe them as living in a one-dimensional world that has released them from selective pressure to localize sounds, either horizontally or vertically. Three such species have been tested for both auditory sensitivity and sound localization and they are represented by the triangles in Figure 7. All three species are incapable of localizing brief sounds (although they can home in on long-duration sounds from widely spaced sources), and, with 60 dB high-frequency limits between 5.6 and 11.5 kHz, they hear no higher than most nonmammals. It seems that without selective pressure for sound localization, there is also no selective pressure to hear high frequencies. It is perhaps worth noting that both black-tailed and white-tailed prairie dogs, species that spend much time underground and that rarely stray far from the safety of a tunnel entrance, are similarly deviant (Fig. 7), although not to the extreme of the exclusively underground mammals (Heffner et al., 1994).

The three subterranean species also illustrate that scaling of ear and head do not dictate high-frequency hearing abilities. Small mammals with small skulls do not automatically possess middle and inner ears that transduce high frequencies. Finally, the three subterranean species provide additional examples in which an absence of good high-frequency hearing, even when accompanied by moderate sensitivity to low frequencies, is not associated with speech.

So far, we have dealt with species averages and comparisons between species. Nevertheless, it is reasonable to ask, given the argument above, whether high-frequency hearing varies according to interaural distance within species. There is little evidence on this question, but the evidence that exists indicates that high-frequency hearing limit is a species character. High-frequency hearing in humans varies very little among healthy individuals and a correspondence with head size has not been found even when sought (R.B. Masterton, personal communication). Domestic dogs have functional head sizes that vary by a factor of two (Chihuahua to St. Bernard). However, when these and other breeds were tested, their high-frequency hearing varied only from 41 to 47 kHz; indeed, members of the smallest and the largest breeds both had the best high-frequency hearing (Heffner HE, 1983). Thus, the limited evidence available argues that high-frequency hearing ability is a species character and not an individual character. The study of different breeds of dogs also concluded that the upper limit of hearing for the species is very near the value predicted by the interaural distance of the smaller breeds—it is as if the species hears high enough for its smallest members to localize sound. It is also worth noting that not only did interaural distances range over a factor of two, but the area of the tympanic membrane also varied by a factor of two. Thus, although this physical character of the middle ear of dogs scaled with body weight, it had no detectable influence on hearing in this sample. Again, despite their undoubted influence, physical mechanisms are not automatic determinants of hearing abilities.

Low-Frequency Hearing

Low-frequency hearing varies among mammals over an even wider range than high-frequency hearing. The low-frequency hearing limits of mammals extend over a range of 9.24 octaves. This broad range of low-frequency hearing abilities would not be expected from a study of primates alone, for their low-frequency hearing limits range over only 3.1 octaves from the 27 Hz of Japanese macaques to the 125 Hz of the potto. Figure 6A illustrates the distribution of low-frequency hearing limits among mammals and Figure 6B shows the distribution of high-frequency hearing limits for comparison. The distribution of primates is shown in darker gray.

In addition to the much greater variation in low-frequency hearing, Figure 6A illustrates another finding that is even more unexpected: low-frequency hearing (unlike other auditory parameters) is bimodally distributed among mammals (Heffner et al., 2001b). Most mammals are able to hear below about 125 Hz (as are most species in all other classes of vertebrates), whereas some have poor low-frequency hearing. So far, all primates fall into the group of mammals with comparatively good low-frequency hearing. The dichotomy of low-frequency hearing limits is so distinct that there is an apparent gap in the distribution for land mammals extending from approximately 125 to 520 Hz. Only two low-frequency limits for air-conducted sound fall within this range: the semiaquatic fur seal whose auditory apparatus is a compromise between air and underwater hearing (Babushina et al., 1991), and the pocket gopher, a subterranean mammals with poor sensitivity throughout its hearing range. The exact shape of the distribution of low-frequency hearing may change as the sample size increases, but since mammals of all sizes, from small bats to elephants, and a wide range of lifestyles are now included, it seems unlikely that the overall bimodal shape of the distribution will change.

There is yet no satisfactory explanation for the variation in low-frequency hearing or its unusual distribution. The potential explanations, though, are of two types. One type looks to evolutionary explanations and seeks distinctions in selective pressure that might affect low-frequency hearing. The other type examines auditory mechanisms looking for differences in the ear apparatus itself or in the auditory nervous system.

Search for selective pressures on low-frequency hearing. There are no readily apparent features that distinguish the two groups [for a complete list of the species in each group, see Heffner et al. (2001b)]. The species with restricted low-frequency hearing tend to be small (mice, bats, small marsupials) but not exclusively so because the Virginia opossum is included. Conversely, most of the species with better low-frequency hearing are large, but several are not (gerbils, kangaroo rats, least weasel, tree shrew), demonstrating that it is quite possible for small mammals to have good low-frequency hearing. In addition, although all of the species in most orders fall into one group or the other, Rodentia is relatively evenly divided between the two groups (although the division is not along taxonomic lines within Rodentia). Predators and prey are in both groups, as are nocturnal and diurnal species, and those inhabiting open areas and dense forests. Our only conclusion is that the eventual explanation

for the dichotomy in mammalian low-frequency hearing is likely to be subtle.

Implications of bimodal distribution of low-frequency hearing for pitch encoding. Species that hear low frequencies may use a different code for pitch than species that do not hear low frequencies (although this gives no evolutionary or ecological insight as to why these species differ). Pitch is encoded by two different mechanisms in mammals. One mechanism encodes pitch temporally with neurons firing in synchrony with the acoustic signal (i.e., phase locking). However, such temporal coding is limited to low frequencies, probably to frequencies below 0.3 kHz (Flanagan and Guttman, 1960; Shannon, 1983). The other mechanism for encoding pitch works at higher frequencies and encodes them spatially. Tones of different frequencies excite hair cells and their innervating axons at different locations along the basilar membrane. The actual frequency limits of these mechanisms have been determined for very few species and are likely to vary somewhat and probably overlap [for a discussion of the operating range of the two mechanisms and an evaluation of the evidence, see Heffner et al. (2001b)].

Even though evidence regarding the exact use of the two mechanisms for pitch perception in different species is meager, we do know enough to propose that species will differ in their use of the two mechanisms. If the temporal code for pitch is confined to frequencies below about 300 Hz, then its limit corresponds to the gap in mammalian low-frequency hearing limits. This in turn suggests that none of the animals with restricted low-frequency hearing (i.e., those in the right cluster in Fig. 6A) use the temporal code for pitch perception, but rely instead on a spatial code along the basilar membrane. The species with relatively good low-frequency hearing (which may be the basal, or plesiomorphic, condition for mammals since their reptilian ancestors almost certainly heard low frequencies) are able to use both the spatial and the temporal code for pitch. Even if the correspondence between the mechanisms of pitch perception and the ability to hear low frequencies proves to be perfect, it will still not explain why some species forego low-frequency hearing and the temporal code for pitch. It does not appear to be a change inherited from a common ancestor or an adaptation to any selective pressure yet proposed.

Explanations based on physical limitations. A simpler mechanistic explanation has also been explored to explain the variation in low-frequency hearing: basilar membranes may be subject to limitations of how many frequencies can be represented. In other words, if an animal hears very low frequencies, it may have to forego hearing at very high frequencies and vice versa. Similarly, the middle ear apparatus for conducting sound might restrict the frequency range of hearing because of physical limitations on the efficiency of sound conduction (Fleischer, 1978; Rosowski, 1992; Nummela, 1999). Indeed, there is a reliable relationship between high- and low-frequency hearing limits among mammals, illustrated in Figure 8.

Among primates and other species that hear below 125 Hz, the relationship is reliable ($r = 0.55$; $P = 0.0011$), but the slope of the regression line is shallow. For every octave of high-frequency hearing gained, only 0.72 octave of low-frequency hearing is lost. Species in this group force us to

Sound-Localization Thresholds Among Mammals (Minimum Audible Angle in degrees)

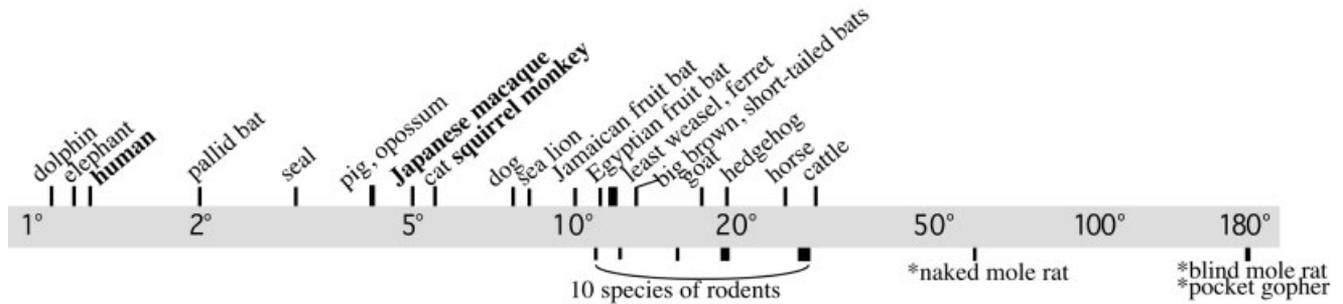


Fig. 9. Sound-localization thresholds for 35 mammals. Thresholds were determined for left-right discriminations around midline and represent the smallest angle of speaker separation for which left and right speakers could still be distinguished (also known as minimum audible angle). The signals were broadband clicks or brief noise bursts, but were brief enough to prevent tracking in on the intensity of the sound. It should be noted that these thresholds probably represent the best sound localization acuity for the species listed because they use maximally localizable signals (broadband rather than pure tones); the sound sources are located in front of the animal where binaural differences change more rapidly with each degree of locus change; and binaural cues as well as pinna cues are effective (as opposed to elevation or front/back localization) (Heffner et al., 1995). The subterranean mammals cannot localize brief sound and their thresholds are based on long-duration or repeated signals and so are not comparable to the other thresholds illustrated. Note the log scale.

recognize that it is quite possible to accommodate a very wide range of frequencies with a single ear. Neither the basilar membrane nor the physical apparatus for conducting sound necessarily restricts the range of frequencies that can be transduced and encoded. Cats are particularly good examples with their ability to hear 10.5 octaves (55 Hz to 79 kHz at a level of 60 dB) while retaining sensitivity that is among the best known (Heffner and Heffner, 1985b). The many primates that hear more than nine octaves (Table 1) also illustrates the readiness with which both low and high frequencies can be transduced by a single ear.

Among mammals that do not hear below 250 Hz, the correlation between low- and high-frequency hearing limits is strong ($r = 0.68$; $P = 0.0015$) and the slope of the regression line is steeper, indicating that, on average, for every octave of high-frequency hearing gained, 1.7 octaves of low-frequency hearing are lost. This suggests two possibilities. High-frequency hearing may be unusually advantageous in this group (as it probably is for bats) (Heffner et al., 2003) and justifies foregoing the ability to hear low frequencies. Alternatively, we could interpret this steep regression line as indicating that for some species, there is selective pressure to avoid hearing low frequencies because low frequencies interfere in some way with the ability to extract information from high frequencies. As yet, there is no basis for deciding between either of these alternatives. However, we believe it is important to consider the latter possibility because we know that it is quite possible to sustain good low-frequency hearing even in the presence of good high-frequency hearing, suggesting that low-frequency hearing is not governed by passive mechanics but rather by selective pressures, not all of which are currently recognized.

Sound Localization

Because sound localization is a very useful function of hearing and because it seems to be a basis for strong

selective pressure on the audiogram, it is of interest to ask whether there is variation in sound localization and what factors might underlie that variation. Figure 9 illustrates the behaviorally determined sound-localization thresholds, or minimum audible angles, for mammals. It shows that mammals do indeed vary in their localization acuity for signals that are too brief to be scanned or tracked. Thresholds range from the 1° thresholds of humans and elephants to thresholds greater than 25° for cattle and some rodents. Only three primates have been assessed, and they have relatively good acuity.

As with low-frequency hearing, no simple lifestyle or ecological factor readily appears to account for the wide variation in sound localization. Both good and poor acuity can be found in nocturnal and diurnal species and in species occupying either open or cluttered environments. Likewise, trophic level is not a satisfactory explanation (Heffner and Heffner, 1992b), although it appears to be correlated with relevant visual explanatory factors as described below.

Because the magnitude of the physical cues for locus (interaural time and spectral differences) is larger for species with large heads and widely spaced ears, it would seem reasonable to expect that the variation in sound localization acuity could be accounted for by differences in interaural distance. However, the magnitude of physical cues does not determine the sensory capacities of animals. If strong selective pressure exists, evolutionary processes usually overcome obstacles imposed by physics. If, on the other hand, selective pressure is absent, the availability of cues will not result in their use. Just as most mammals do not see ultraviolet light despite its presence, mammals with large heads will not be good localizers if good acuity does not improve their fitness.

If we consider the functioning and adaptive behavior of an animal as a whole rather than concentrating on individual sensory systems in isolation, we immediately realize that the most immediate response to a brief unex-

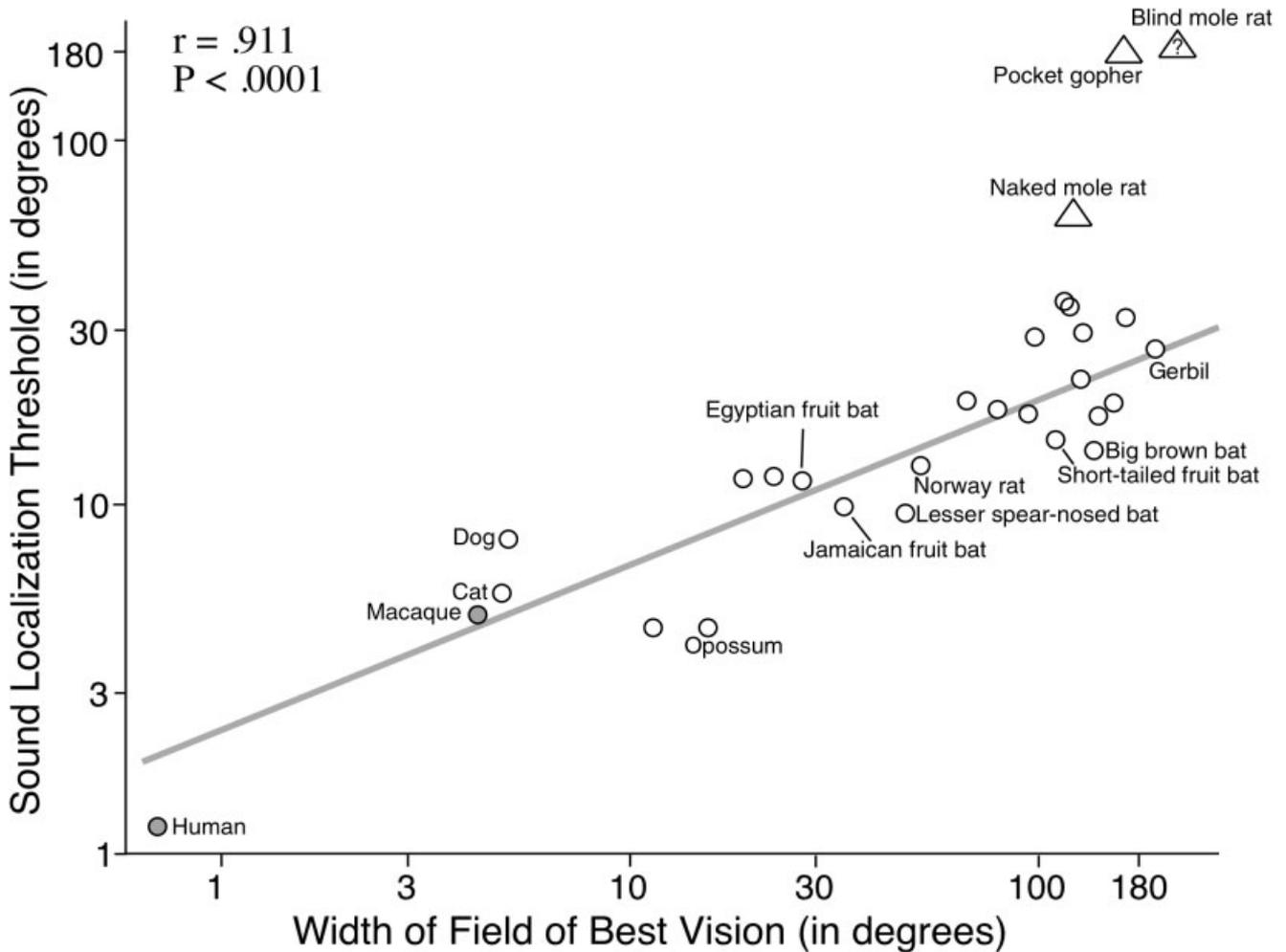


Fig. 10. Relation between the width of the field of best vision and sound-localization thresholds for 29 species of mammals. Species with narrow fields of best vision are far more acute localizers of sound than species with broad fields of best vision.

pected sound is an orienting reflex. Attention turns toward the sound source and this involves turning the head, eyes, and ears for identification or scrutiny. The visual orienting reflex to a sound is fast and accurate and is one of many indicators of how closely coordinated are the auditory and visual systems in the brain (Stein and Meredith, 1993). If we consider that an important function of hearing is to tell the eyes where to look, then some aspect of vision could conceivably affect the value of good acuity for sound localization. We have examined several visual parameters, including visual acuity, the size of the binocular and panoramic visual fields, and the width of the field of best vision. The width of the field of best vision is the only factor so far found to account for the variation in sound localization among mammals (Fig. 10). It is based on the notion that when the eyes orient toward a sound source, it is the region of best vision that is oriented. If that field of best vision is very broad, like a broad searchlight, then the ears need not be very precise in the directions they provide. In an animal like a horse or rabbit with a broad visual streak, much of the entire panorama is within their field of best vision and very little acuity would

seem to be required in order to bring a sound source within their best field of view. Humans and many other primates, on the other hand, have their best vision concentrated in a very narrow field served by a fovea only 1–2° wide, requiring considerable precision from the auditory system in order to direct the fovea to a sound source.

The width of the field of best vision can be relatively easily determined by mapping the density of retinal ganglion cells (or in the case of species with foveas, the receptors) and determining the horizontal width of the region with a density of cells at least 75% of maximum (Heffner and Heffner, 1992b). We have done this for many of the species whose sound localization acuity has been determined, and the width of the field of best vision accounts for approximately 84% of the variance in sound localization acuity. Humans and macaques are the only two primates for whom complete data are available and they fit the pattern established among the broader sample of mammals. The good localization acuity of humans and macaques is expected given their visual adaptation that concentrates their best vision in a narrow fovea. Although we

do not have a measure of the width of the field of best vision of squirrel monkeys, we know their fovea is less distinct, consistent with their slightly larger sound-localization threshold (Stone and Johnston, 1981). Localization acuity is not known for any of the strepsirrhines, but it is likely that species such as the Philippine tarsier, galago, and mouse lemur will have progressively poorer sound-localization acuity, ranging from approximately 9 to 12°, based on the width of their fields of best vision (Stone and Johnston, 1981; Tetreault et al., 2004). The dwarf lemur may have much poorer localization acuity as it is reported to have very little variation of acuity across its retina (Tetreault et al., 2004).

No other visual parameter examined, including the size of the visual fields and the absolute visual acuity, can account for as much of the variance in sound localization as does the width of the best visual field. Further, when the width of the field of best vision is mathematically removed as a factor using partial correlations or multiple analysis of variance, other visual parameters are no longer reliably related to sound localization (Heffner and Heffner, 1992b). Similarly, predators tend to be better localizers than prey species, but they also tend to have more frontally placed eyes and narrower fields of best vision. When all of the factors are considered together, it is the width of the field of best vision that accounts for most of the variance.

We have gained further confidence that a major selective pressure driving sound-localization acuity is its use for directing vision by examining unusual cases. First, subterranean species are consistent with this hypothesis. They live exclusively in dark burrows where the visual orienting reflex would seem to have no use and where other directional responses are limited. One of the species, the blind mole rat, has become so specialized that its vestigial eyes are buried in muscle. All three of the species examined are incapable of localizing brief sounds.

Echolocating bats are another group that might be expected to have a different relationship between sound localization and vision because their vision is very poor and they “see” using echolocation. However, many bats do use their eyes for orienting to obstacles in their environment and even detecting and approaching food (Koay et al., 1998; Heffner et al., 1999), and, like other animals, they are alerted to activity in their environment by sounds. Thus, even though the visual acuity of echolocating bats is poor (Pettigrew et al., 1988), they can see. When the passive sound-localization acuity of bats is plotted as a function of the width of their field of best vision, they, too, conform to the pattern set by nonecholocating mammals. Thus, the guidance of the eyes by the ears is a function that remains useful in a wide variety of mammalian lifestyles.

In summary, it seems that basic hearing abilities are not unusual among primates. They fit the mammalian pattern with small species hearing frequencies high enough for their small heads and pinnae to produce spectral/intensity cues for sound localization. The restricted high-frequency hearing of humans is expected as an adaptation for sound localization; it is not likely to be a specialization for speech as there are other mammals with similarly restricted high-frequency hearing unaccompanied by speech. Low-frequency hearing is relatively good among all of the primates tested so far placing them among the majority of mammals. Finally, the acuity of

sound localization is known for only three primates; the two whose width of best vision is also known are relatively good localizers. This finding is in keeping with the pattern among mammals in general, in which species with narrow fields of best vision, such as a fovea only 1–2° wide, are better localizers than those with broad fields of best vision. We believe this is because orienting the eyes for visual scrutiny requires more precise directional information when the field of best vision is very narrow.

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