

The Evolution of Mammalian Sound Localization

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Mammals evolved better high-frequency hearing than non-mammals, and they use it for localizing sound. Does this mean they localize sound better than other vertebrates?

Introduction

The ability to localize sound is useful for survival because it allows an animal to determine the location of sound sources, which, in nature, are usually other animals. Indeed, the need to localize sound explains why terrestrial vertebrates have two ears, as differences in the time of arrival and the intensity of a sound at the two ears gives information about the direction of its source. However, unlike other terrestrial vertebrates (amphibians, reptiles, and birds), mammals have evolved the ability to hear high-frequency sounds. Specifically, amphibians and reptiles rarely hear above 5 kHz, and birds do not hear much above 10 kHz; however, almost all mammals hear far higher, with over half of mammals tested so far able to hear above 50 kHz. As we show, the primary source of selective pressure for the evolution of mammalian high-frequency hearing has come from the need to localize sound.

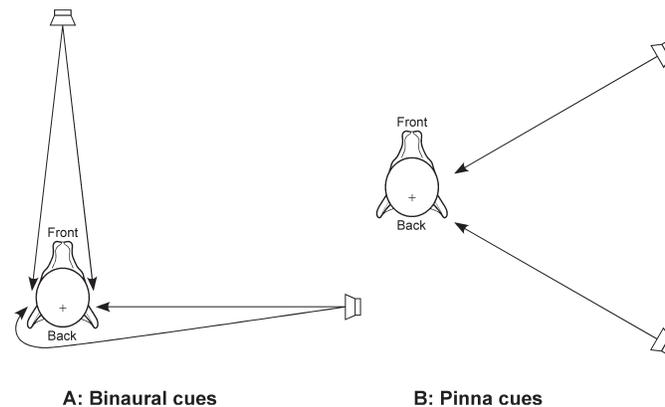


Figure 1. A: Differences in the time of arrival and intensity of a sound at the two ears are used to determine the azimuth of a sound source. However, these cues do not indicate the elevation of a sound source nor whether it is in front or behind the observer. B: The directionality of the pinnae to high frequency sounds enables an animal to determine if a sound source is in front or behind, as well as the elevation of the source.

There are three sound-localization cues available to mammals. The first is the binaural time-difference cue in which the auditory system compares the arrival time of a sound at the two ears to determine its azimuth (Figure 1A). This cue can be used to localize any low-frequency sound as well as high-frequency complex sounds such as clicks and noise.

The second is the binaural intensity-difference cue in which the difference in the intensity of a sound at the two ears is used to determine azimuth (Figure 1A). Because low-frequency sounds (long wavelengths) can bend around an animal's head with little or no attenuation, a mammal with a small head must hear frequencies that are high enough to be shadowed by its head to produce an intensity difference

between the ears. Thus, the smaller the animal, the higher it must hear in order to use the binaural intensity cue.

Finally, mammals evolved external ears, or pinnae, that alter the spectrum of a sound as a function of the location of the sound source (**Figure 1B**); monaural pinna cues enable an animal to avoid front-back confusions and localize sound in the vertical plane. Indeed, pinna cues also serve to localize sound in the horizontal plane and are especially important when a sound is audible in only one ear (Butler, 1999). For the pinnae to provide directional information, the sound must have a complex spectrum (such as clicks or noise), as opposed to pure tones, and it must contain frequencies high enough for its spectrum to be modified by the pinna. Thus, both the binaural intensity cue and monaural pinna cues require that animals be able to hear high frequencies.

The following is a description of what we know about mammalian sound localization and the role that high-frequency hearing plays in it. Among the questions we ask are: What is the evidence that mammals evolved high-frequency hearing for sound localization? Do mammals localize as accurately as the physical cues available to them allow or are other factors involved? Finally, do mammals have better sound-localization abilities than non-mammals?

High-Frequency Hearing in Mammals

By the late 19th century, it was known that mammals differed in their ability to hear high-frequency sounds and that some species could hear higher frequencies than humans. This was established by Francis Galton, who used a high-frequency whistle attached to his cane and operated by a rubber bulb to observe the unconditioned responses of animals to high-frequency sounds. Of the animals he observed, he found cats had the best high-frequency hearing, which he attributed to their need to hear the high-frequency sounds made by mice and other small prey (Galton, 1883). Thus, by this time, it was apparent that mammals varied in their ability to hear high frequencies, with the variation attributed to the individual needs of each species.

The study of mammalian hearing began to progress by the second half of the 20th century when reliable procedures for determining the sensory abilities of animals were developed (e.g., Stebbins, 1970). At first the results did not challenge the notion that the high-frequency hearing of animals was adapted to their individual needs. For example, the high-frequency hearing ability of bats was seen as an adaptation to their use of high-frequency echolocation signals, whereas

the good high-frequency hearing of mice was believed to be linked to their use of ultrasonic vocalizations, and the inability of humans to hear above 20 kHz was attributed to the importance of speech, which is primarily low frequency (Sales and Pye, 1974).

Systematic Variation in High-Frequency Hearing and Sound Localization

The discovery of the link between high-frequency hearing and sound localization was made in the 1960s when it was noticed that smaller mammals had better high-frequency hearing than larger ones (Masterton et al., 1969). Others, such as von Békésy and Rosenblith (1951), had already noticed the relation between size and high-frequency hearing, attributing it to an unspecified need for large mammals to hear low frequencies. However, noting that the magnitude of the binaural time-difference cue depends on the size of an animal's head, Masterton suggested that the smaller an animal's head, the smaller the maximum binaural time-difference would be and the more dependent the species would be on the binaural intensity-difference cue. Because small heads do not block low frequencies as effectively as they block higher frequencies, an animal must hear frequencies high enough to be attenuated by its head and pinnae in order to use the intensity-difference cue. Thus, it was proposed that the smaller a mammal's head, the higher it would have to hear to use the binaural intensity-difference cue.

To quantify the relationship between head size and high-frequency hearing, it was necessary to adopt a definition of those measures. This was done by defining head size, in units of time, as the maximum interaural time delay an animal might experience, which is the time it takes for sound to travel around the head from one ear to the other—referred to as *functional* head size. For terrestrial mammals, functional head size is determined by dividing the distance around the head (from the opening of one ear canal to the opening of the other) by the speed of sound in air. For marine mammals, functional head size is determined by dividing the distance between the middle ears (as measured through the head) by the speed of sound in water, as this is the path that water-borne sound takes when traveling from one ear to the other. High-frequency hearing ability is defined as the highest frequency audible at a particular level, typically, 60 dB sound pressure level (SPL).

The first statistical analysis of the variation in high-frequency hearing, which included body size as well as functional head

size as possible explanatory factors, was based on data from the 18 species of mammals whose hearing was known at that time (Masterton et al., 1969). The results showed that high-frequency hearing was reliably correlated not with body size, as heretofore expected, but with *functional* head size.

Over the years, the number of species whose high-frequency hearing is known has expanded by nearly four times to include mammals of extreme sizes and habitats, both wild and domestic, and at different trophic levels (Heffner et al., 2014). For the 69 species for which data are currently available, there remains a strong negative correlation between functional head size and the highest frequency audible at a level of 60 dB (with a correlation coefficient of $r = -0.79$). In other words, the smaller an animal's head size, the higher its upper frequency limit of hearing must be in order for its head to generate a useable binaural intensity difference (Figure 2).

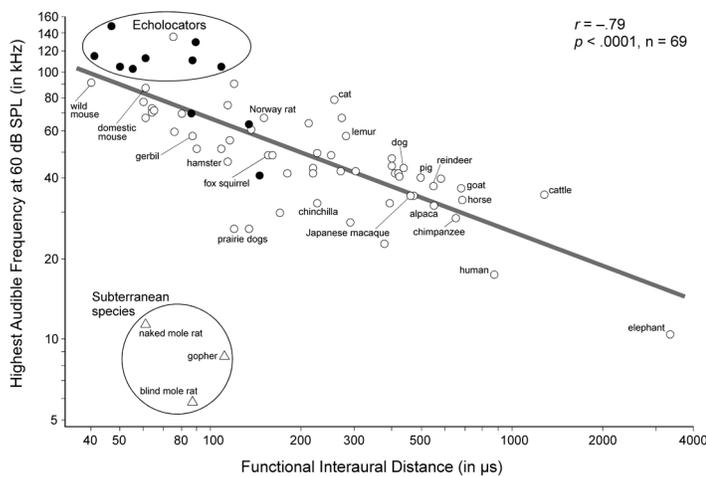


Figure 2. The smaller an animal's functional head size, the higher it must hear in order to use both the binaural intensity-difference cue and monaural pinna cues. The filled circles are bats. Note that bats that use laryngeal echolocation (labeled as "echolocators"), as well as the echolocating dolphin, hear slightly higher than predicted by their functional head size; the three non-echolocating bats fall among the other mammals. Subterranean rodents, which have relinquished the ability to localize brief sounds, do not hear high frequencies. Modified from Heffner et al. (2014).

Although the initial emphasis on explaining the variation in high-frequency hearing was that it was necessary for small animals to effectively use binaural intensity differences, it soon became apparent that it was also necessary for the external ear to generate monaural pinna locus cues, a point to which we will return shortly.

High-Frequency Hearing is a Species Characteristic

We want to emphasize that the relationship between high-frequency hearing and functional head size applies to species differences and not to variation in head size within a species. This was demonstrated in dogs, for which it was shown that the high-frequency hearing of individual dogs did not vary with their functional head size even though the head size of the largest dog tested, a St. Bernard, was twice as large as that of the smallest dog, a Chihuahua. Moreover, the size of the tympanic membranes of the dogs varied from 30 to 55.2 mm², yet their hearing was similar (Heffner, 1983). There are similar findings for humans (von Békésy and Rosenblith, 1951). Thus, although the size of the auditory apparatus is an important factor in determining the response properties of the ear, it is apparent that the audiogram does not passively follow the size of the middle ear.

Echolocating Bats

Although bats require good high-frequency hearing for passive sound localization, echolocating bats that emit tonal signals (laryngeal echolocators) all hear somewhat higher frequencies than similar-sized animals that do not echolocate. This suggests that selective pressure for echolocation has caused them to increase their high-frequency hearing beyond that required for passive sound localization by about half an octave, a conclusion supported by the observation that the three bats in Figure 2 that do not emit tonal calls (two non-echolocating bats and *Rousettus aegyptiacus*, which emits clicks) do not hear higher than predicted by the need to passively localize sound. Thus, the use of echolocation by bats, as well as by toothed whales, is an example of how, once high-frequency hearing evolved for passive sound localization, it was exploited for another function.

Humans

Humans have often been thought to differ from other mammals in that we are unable to hear "ultrasound," which is true by definition, as ultrasound is defined as any high-frequency sound beyond the human hearing range. However, given our large head size, the 60-dB upper limit of 17.6 kHz of young and healthy humans is not significantly different from that predicted by the regression line in Figure 2. Indeed, the observation that the Indian elephant (*Elephas maximus*) has an even lower upper limit of 10.5 kHz is further indication that our upper limit of hearing is not unique but is expected for a mammal with our large head size.

Noise Localization (Minimum Audible Angle)

Subterranean Rodents

Figure 2 shows that the blind mole rat (*Spalax ehrenbergi*), naked mole rat (*Heterocephalus glaber*), and pocket gopher (*Geomys bursarius*), which are subterranean rodents, lie far below the regression line, as they do not hear nearly as high as their small functional head sizes predict. Indeed their upper limits are within the range of those found in non-mammalian vertebrates such as birds. However, these findings do not weaken the theory that mammals evolved good high-frequency hearing for sound localization, but are the exceptions that prove the rule—not only do all three species lack good high-frequency hearing, they also lack the ability to localize brief sound (Heffner and Heffner, 1993). Thus it appears that subterranean animals adapted to the one-dimensional tunnels of an underground habitat have little use for sound localization and are therefore released from the selective pressure to hear high frequencies. In short, sound localization and high-frequency hearing go hand-in-hand in mammals. Mammals rely on high frequencies to localize sound and those that relinquish the ability to localize sound also give up their high frequency hearing.

Mammalian Sound-Localization Acuity

Given that mammals evolved high-frequency hearing for localizing sound, the question arises as to how well they use these cues. Put another way: Does each animal localize as accurately as permitted by the locus cues available to it?

Sound-localization acuity is commonly determined by training an animal to discriminate between the same sound emitted from loudspeakers on the animal's left versus right sides (e.g., Heffner et al., 2014). The sound is typically a 100-ms broadband noise burst that is too brief to be scanned or tracked by the animal. Such brevity is an important feature as we wish to know the ability of the auditory system to compute locus, not the ability of an animal to scan and track an ongoing sound to its source. An animal's "minimum audible angle" (MAA) is determined by centering the speakers on its midline and finding the smallest angle of separation it can discriminate 50% of the time.

It was originally assumed that all animals were under selective pressure to accurately localize sound, and an animal's acuity would be determined by the magnitude of the sound-localization cues generated by its head and pinnae. At first this seemed to be the case, as among the few mammals for which sound-localization acuity was known, acuity appeared to improve with functional head size. For example, the MAA for humans and elephants was 1-2°, for cats 5°, and

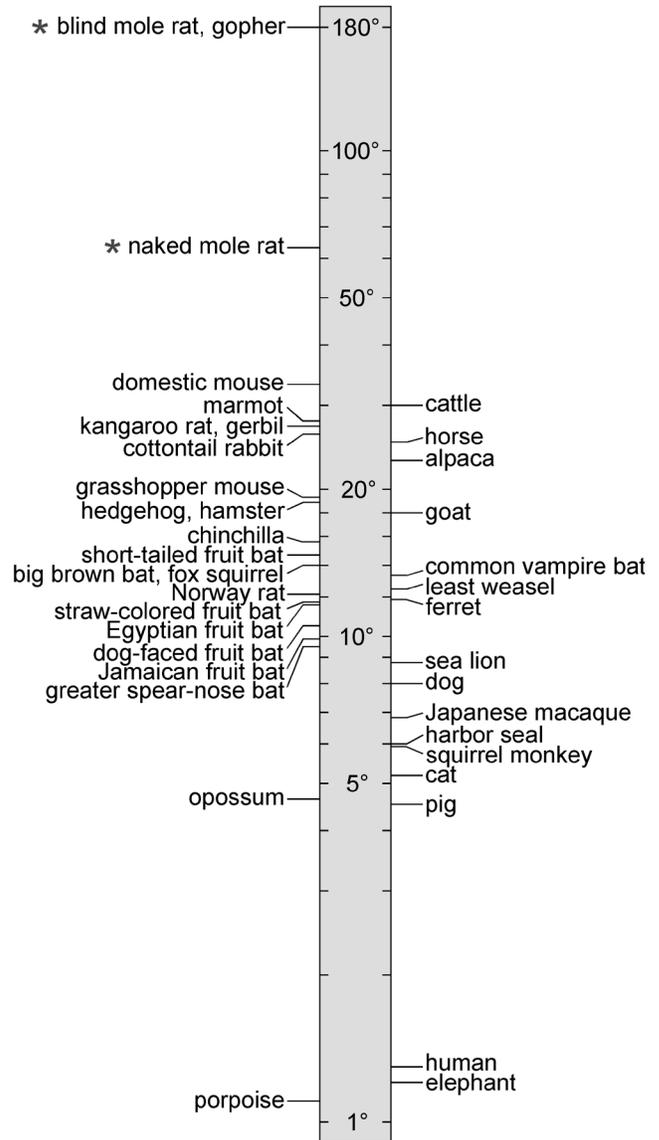


Figure 3. MAA of 39 species of mammals. With the exception of the subterranean rodents (asterisks), the animals were tested with a brief sound, either a click or 100-ms noise bursts. The subterranean rodents were unable to localize brief sounds and their thresholds were obtained with a 400 ms or longer duration noise burst. Modified from Heffner et al. (2014).

for Norway rats 12°. However, this changed when it was discovered that the MAA of horses and cattle were 25° and 30°, respectively, showing that having a large functional head size did not necessarily produce good sound-localization acuity. Overall, mammalian MAAs range from about 1° for humans and elephants to nearly 30° for cattle, 33° for mice, and 180° for subterranean species (Figure 3). Thus, the question arises: If a large head that generates large physical locus cues does not necessarily result in accurate sound-localization acuity, what drives the variation in localization thresholds?

Sound-Localization Acuity is Related to Vision

Accumulating data forced us to reject many possible explanations for the variation in sound-localization acuity, such as whether an animal was large or small, a predator or prey, diurnal or nocturnal, or had large or small binocular visual fields. We then discovered that sound-localization acuity was closely correlated with the *size of an animal's field of best vision*. Specifically, the narrower an animal's field of best vision, the better its sound-localization acuity.

This observation led to the proposal that the primary function of sound localization is to direct the eyes to the source of a sound (Heffner and Heffner, 1992). Thus, animals with narrow fields of best vision, such as humans and cats, require good sound-localization acuity to direct their best vision to scrutinize sound sources, whereas animals such as gerbils and cattle that have broad fields, known as *visual streaks*, do not require such acuity because most objects on the horizon are already within their field of best vision.

For comparative purposes, the width of an animal's field of best vision is estimated from microscopic analysis of its retina in which the density of retinal ganglion cells is mapped (or, in the case of primates that possess a fovea, the density of the receptors). The region of best acuity is then defined as the width of the horizontal visual field, in degrees, that subtends the portion of the retina containing ganglion cell densities greater than or equal to 75% of the maximum density. Examples of retinal maps are shown in **Figure 4**.

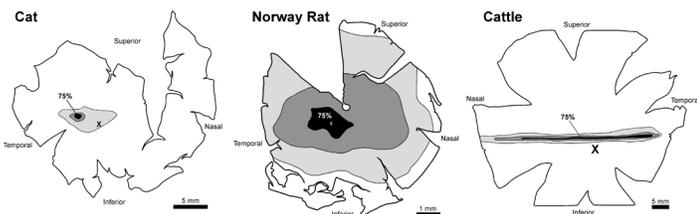


Figure 4. Retinal ganglion cell isodensity contours for the cat, Norway rat, and cattle. The region of best vision is defined as the 75% isodensity contour. Note the small area of best vision for the cat compared with the broad visual streak for cattle. The X indicates the location of the blind spot. Modified from Heffner and Heffner (1992).

The relationship between the width of the field of best vision and sound-localization acuity, shown in **Figure 5**, illustrates that mammals with narrow fields of best vision are more accurate localizers than mammals with broader fields ($r = 0.89$). Note that the definition of the field of best vi-

sion does not depend on absolute acuity, just the best acuity available. Indeed, correlational analysis indicates that, of the two factors, only the width of the field of best vision, and not absolute visual acuity, is related to sound-localization acuity (Heffner and Heffner, 1992). In short, it appears that the primary function of sound localization in mammals is to direct the field of an animal's best vision to the source of a sound for further analysis.

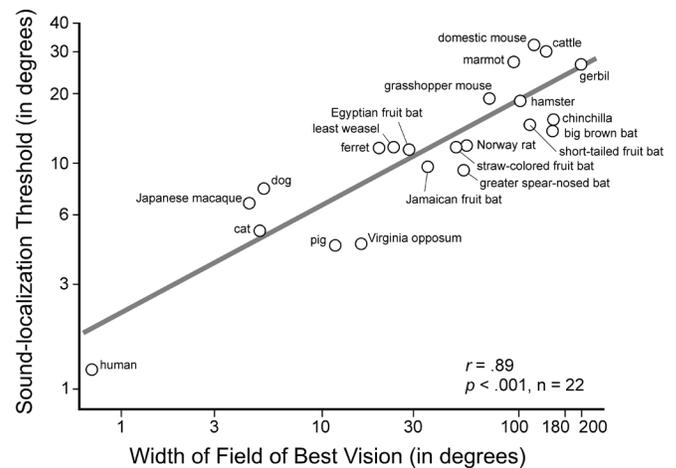


Figure 5. Relationship between the width of the field of best vision (75% isodensity contour) and sound-localization thresholds for 22 species of mammals. Species with narrow fields of best vision have smaller thresholds than those with larger fields of best vision. Modified from Heffner et al. (2001).

Some Mammals Do Not Use All Three Locus Cues

As previously noted, mammals have three sound-localization cues available to them: binaural time difference, binaural intensity difference, and monaural pinna cues. With careful testing, it is possible to demonstrate the ability of an animal to use each of these cues. Although initially surprising, results reveal that some species do not use all three cues.

Binaural Time and Intensity Difference Cues

The ability to use the binaural locus cues can be demonstrated by determining the ability of an animal to perform a left-right locus discrimination for *pure tones* presented from loudspeakers located in front of the animal at a fixed angle of separation, typically $\pm 30^\circ$. This is because low-frequency pure tones must be localized using the binaural time-difference cue, whereas high frequencies must be localized using the binaural intensity-difference cue.

Specifically, low-frequency pure tones that bend around the head with little or no attenuation can only be localized by comparing the time of arrival of a phase of each cycle of the tone at the two ears (the binaural phase-difference cue being a subset of the binaural time cue). However, the phase-difference cue becomes ambiguous for pure tones at high frequencies when successive cycles arrive too quickly for the nervous system to match the arrival of the same cycle at the two ears (Woodworth and Schlosberg, 1954). The exact “frequency of ambiguity” depends on an animal’s head size and the angle of the sound source relative to its midline—it is higher for smaller heads and sound sources closer to the midline.

Pure tones above the frequency of ambiguity, then, must be localized using the binaural intensity-difference cue (Figure 6). Thus, the ability of an animal to use the two binaural cues can be measured by determining the ability to localize pure tones above and below the frequency of ambiguity. Although many of the animals tested so far do use both the binaural time and intensity cues, there are some that have lost the ability to use one or the other cue.

Regarding the binaural time-difference cue, it is probably not surprising that some small animals, such as rats, mice, and some bats, have relinquished use of this cue and rely solely

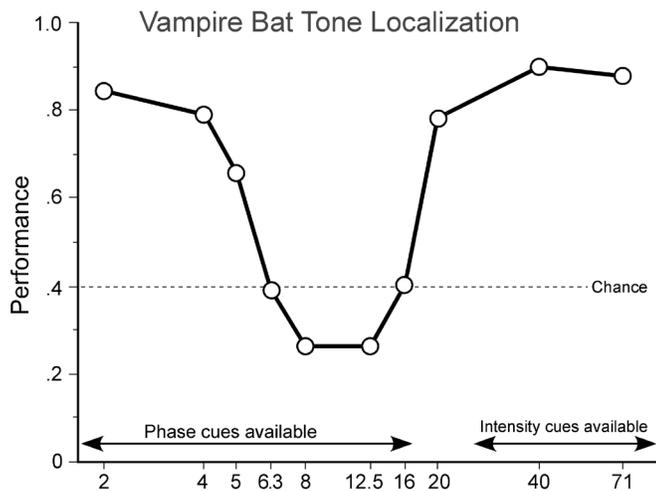


Figure 6. The ability of vampire bats to localize low- and high-frequency pure tones demonstrates their ability to use both the binaural phase and intensity difference cues. The dip in their performance in the midrange is because their auditory system was unable to use the binaural phase cue above 5 kHz, and the binaural intensity cue was not physically available until just above 16 kHz. Note that the bat does not use the binaural phase cue from 6.3 to 16 kHz even though it is physically available to them. Modified from Heffner et al. (2015).

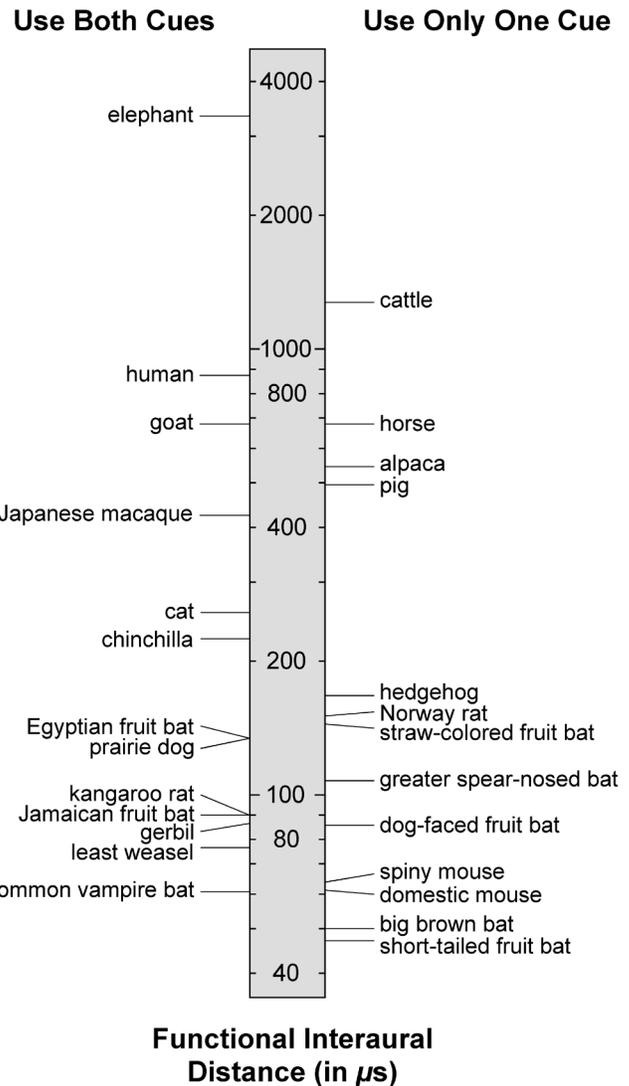


Figure 7. Many mammals use both binaural time and intensity difference cues (left side of figure). However, some use only one or the other binaural cue (right side of figure). Of the animals that use only one cue, those with functional interaural distances larger than 400 μs use only the binaural time cue; whereas those with interaural distances smaller than 200 μs use only the binaural intensity cue. Modified from Heffner et al. (2015).

on the binaural intensity-difference cue and pinna cues to adequately localize sound (Figure 7). However, there is no specific functional head size that separates those animals that use the binaural time cue from those that do not. For example, some species that use time cues, such as gerbils, are smaller than some that do not, such as Norway rats. Nor are animals that do not use the binaural time cue necessarily poorer sound-localizers than animals that use both binaural cues. For example, Norway rats with a MAA of about 12° degrees have better acuity than either the chinchilla (17°) or gerbil (27°), both of which use both binaural cues.

Evolution of Mammalian Sound Localization

On the other hand, some mammals cannot localize high-frequency tones, indicating that they do not use the binaural intensity-difference cue. As seen in **Figure 7**, the animals that do not use the intensity-difference cue are hoofed mammals, such as horses, cattle, pigs, and alpacas (*Vicugna pacos*). It should be noted that although some mammals cannot localize high-frequency pure tones, they can localize high frequencies that are amplitude modulated at a low frequency or that contain a band of high frequencies that produce a fluctuating envelope. This is because the envelope itself (rather than the carrier signal) provides a basis for a time comparison at the two ears. For example, alpacas could not localize a 4-kHz pure tone but could localize it well when it was modulated at 250 or 500 Hz. As a result, most natural sounds can be localized using the binaural time cue even if they contain only high frequencies because they naturally have an irregular envelope. So far, all mammals known to have relinquished the binaural intensity cue have large functional head sizes. Thus, with their large heads, some, but not all, large mammals have relinquished the binaural intensity cue, relying instead on the binaural time difference and monaural pinna cues to localize sound.

Pinna Cues

The ability to use pinna cues for locus is demonstrated by discriminating between two sound sources for which binaural cues are the same. This occurs for sources that are centered symmetrically around 90 degrees to one side, such as 60 and 120 degrees to the right, placing the speakers on what is known as the cone of confusion (**Figure 8**). In this case, the signal to be localized is a band of noise because locus information is derived from the way the pinna modifies the spectrum of high-frequency noise. **Figure 8** shows an alpaca that could perform a front-back locus discrimination but only if the sound contained high frequencies, in this case a 3-kHz high-pass noise. The fact that the animal could not perform the discrimination when a 2-kHz low-pass noise was presented demonstrates that pinna cues rely on the presence of high frequencies. Thus, although animals like alpacas may relinquish the binaural intensity-difference cue, they retain high-frequency hearing because it is required for using the pinna locus cues.

Why Do Mammals Use High-Frequency Locus Cues?

Did the evolution of high-frequency hearing and its use for binaural intensity and pinnae cues give mammals better localization ability than that of amphibians, reptiles, and birds?

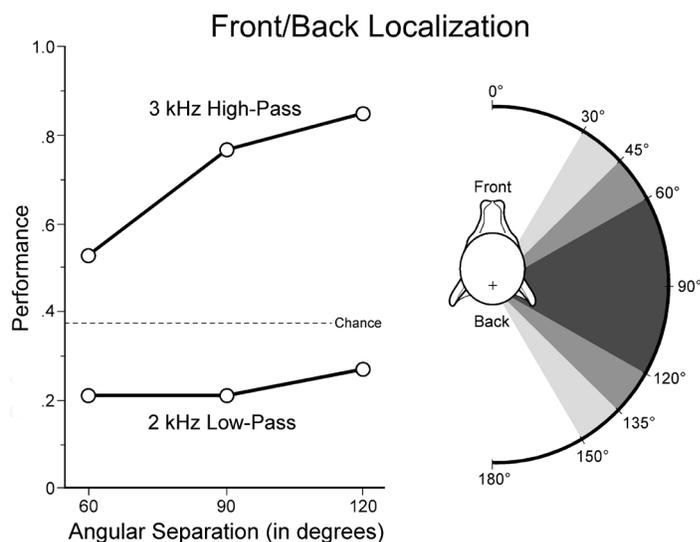


Figure 8. The pinna cues that enable mammals to discriminate sounds coming from the front versus those coming from the back require high frequencies. This is why alpacas can perform a front-back discrimination when a high-frequency sound (3 kHz high-pass) is presented but not when a low-frequency sound (2 kHz low-pass) is presented. From Heffner et al. (2014).

So far, no one has been able to train amphibians or reptiles to respond reliably to sound, and so we know little about their behavioral hearing abilities. Although birds readily learn to respond to sound, there is information on the ability of only seven species to localize brief sounds (Feinkohl and Klump, 2013). With the exception of owls, the MAA of birds ranges from 17° for starlings to 101° for zebra finches, suggesting that most mammals may exceed birds in left-right localization acuity.

The barn owl, on the other hand, appears to have exceptionally good sound-localization ability. However, the barn owl has been tested by training it to orient to the source of a sound and then determining its average error, resulting in a threshold of 3-5°. Just how that measure compares to MAA is not known, but it nevertheless appears that the barn owl's localization acuity may exceed that of most mammals. Interestingly, the barn owl possesses the equivalent of a mammalian external ear in the form of feathers around the opening to its ears and, although its ability to perform a front-back locus discrimination has not been tested, it is able to localize in the vertical plane, a discrimination for which mammals require pinna cues (Knudsen and Konishi, 1979).

The question of whether the evolution of high-frequency hearing in mammals resulted in better sound-localization abilities than non-mammals cannot be answered for the simple reason that sound-localization acuity is determined not by the available physical cues but by how accurate an animal needs to localize sound. As we have seen, mammalian

sound-localization acuity is driven by the need to direct the eyes to the source of a sound, not by the magnitude of physical cues. Although physical cues may set limits on acuity, we know of no clear example where this has occurred. However, we currently know little about the ability of birds to localize sound and almost nothing about the localization acuity of amphibians and reptiles. As with mammals, the ability of other terrestrial vertebrates may be strongly influenced by factors other than the magnitude of physical locus cues.

Finally, it is interesting to consider that the evolution of high-frequency locus cues in mammals might not have been driven by the need for more accurate localization but instead to compensate for the loss of an ability possessed by non-mammals. Specifically, the two ears of most non-mammalian vertebrates are interconnected, resulting in what is referred to as pressure-gradient receiver (Christensen-Dalsgaard, 2011). In amphibians and reptiles the connection is through the mouth; in the case of birds, the connection is through an interaural canal, which is a network of passage ways through the skull. As a result, sound reaching one ear can pass through to the other ear, an arrangement that appears to aid sound localization by enhancing the binaural time and intensity differences at low frequencies (Christensen-Dalsgaard, 2011). The ears of mammals, however, are acoustically isolated; why they gave up the interconnection is unknown, but one possibility is that it may have been to prevent breathing sounds from entering the ears and masking external sound.

Reptiles and amphibians breathe intermittently (Milsom, 1991), so such breathing noises would not be the disadvantage it is in mammals that breathe continuously. That continuous breathers need to isolate their ears from the throat is supported by the observation that birds, also continuous breathers, get around the problem of breathing sounds by connecting their ears through their interaural canal with the Eustachian tubes coming out in the roof of the mouth. By doing this, birds avoid the problem of breathing noise while retaining the directional advantages of acoustically connecting the two ears. Mammals, on the other hand, have isolated ears and thus may have evolved high-frequency hearing to compensate for the loss of coupled ears.

Acknowledgment

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Biosketches



Henry Heffner and Rickye Heffner are professors of Psychology at the University of Toledo. After receiving their doctoral degrees from Florida State University, they worked at the University of Birmingham (England) and Johns Hopkins University before moving to the University of Kansas in 1973, where they took over the animal laboratory at Parsons State Hospital and Training Center. Working at first on auditory cortical mechanisms and mental retardation, they began their comparative auditory research by studying the hearing and sound localization abilities of horses, cattle, and an elephant. In 1987, they moved their Laboratory of Comparative Hearing to the University of Toledo, where they have continued their comparative studies.

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Continued on page 35