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The Evolution of Mammalian Hearing

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Abstract. In amphibians, reptiles and birds, the ears are internally coupled either through the mouth or through an interaural canal, an arrangement that makes the ears directional and enhances sound-localization cues. In the evolution of mammals, however, the two ears became isolated. Having lost the directionality of coupled ears, mammals evolved both the ability to hear sounds well above 10 kHz and external ears. This allowed them to use two high-frequency cues for localizing: the difference in the intensity of a sound at the two ears, and the directionality induced by the pinnae (another mammalian invention). Because the magnitude of the high-frequency locus cues depends on the size of the head and pinnae relative to the wavelength of the sound, smaller mammals hear higher frequencies than larger mammals in order to use these cues. Localization *acuity*, however, is related *not* to the magnitude of the locus cues available to an animal, but to the accuracy needed to direct the eyes to a sound source. The result is that mammals with relatively narrow fields of best vision (e.g., humans and cats) require more accurate localization acuity to direct their gaze than do animals with broad fields of best vision (e.g., gerbils and cattle). So why did mammals give up the directional advantage of coupled ears? We suggest that mammals, because they breathe continuously, needed to isolate their ears from their mouth to prevent breathing sounds from masking external sounds. Amphibians and reptiles do not require such isolation because they are intermittent breathers. Birds, which, like mammals, are continuous breathers, isolated their ears from their mouth by evolving a canal that connects their ears through the skull, allowing them to retain the advantages of coupled ears.

INTRODUCTION

There were three major anatomical developments in the evolution of the mammalian ear. One was the evolution of the three-boned middle ear. The second was the development of external ears (pinnae). The third, less recognized, was the acoustic isolation of the two ears.

In non-mammalian tetrapods (amphibians, reptiles, and birds), sound not only reaches the external surface of the tympanic membrane, but then passes through the head to the internal surface of the opposite tympanic membrane. In amphibians and most reptiles, sound travels between the ears through the mouth (buccal cavity); in birds and crocodylians, it travels through an interaural canal. This arrangement makes the ear act as a pressure-difference receiver, enhancing the directionality of sound^{1,2}. But the ears of mammals are isolated from each other, which may have forced mammals to develop other mechanisms for localizing sound. This, in turn led to the development of two additional anatomical structures. We propose the following scenario.

First, along with the isolation of the two ears, mammals evolved the three-boned middle ear enabling them to hear higher frequencies than non-mammalian tetrapods, that is, above 10 kHz. Although it is often stated that the development of high-frequency hearing allowed early mammals to communicate at frequencies inaudible to non-mammalian predators and to detect the high frequencies produced by insect prey³, evidence indicates that high-frequency hearing is primarily driven by the need to localize sound.

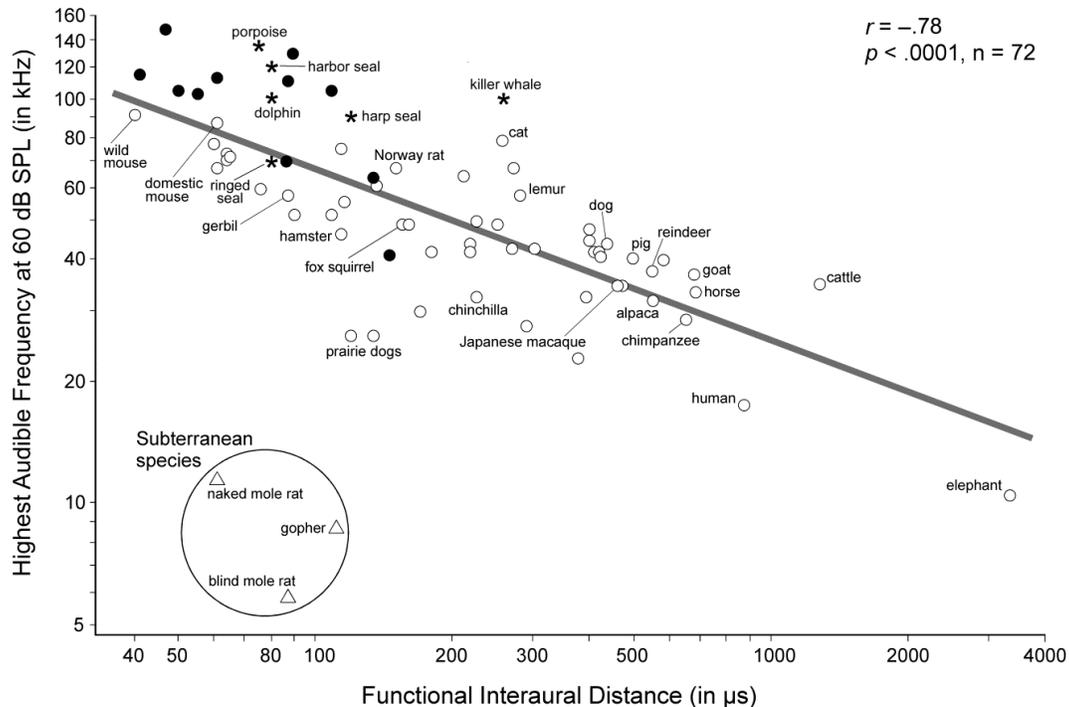


FIGURE 1. The smaller an animal’s functional head size, the higher it must hear in order to use pinnae cues and/or the binaural intensity-difference locus cue. The stars represent cetaceans and pinnipeds whose hearing was determined underwater. The filled circles are bats; the eight bats shown here that use laryngeal echolocation hear slightly higher than predicted by their functional head size⁴. The triangles are subterranean rodents that have relinquished the ability to localize brief sounds and therefore do not hear high frequencies. (Modified from Heffner and Heffner, 2016⁵ [copyright AIP]. For references to individual audiograms see Koay et al., 1998⁶ and Heffner et al., 2014⁷; for the killer whale, see Branstetter et al., 2017⁸.)

Second, along with high-frequency hearing, early mammals were characterized by external ears, pinnae⁹, that alter the high-frequency spectrum of a sound as a function of the location of the sound source. The frequency-dependent cues produced by the pinnae are useful in reducing front-back confusions as well as in localizing sound in the vertical and azimuthal planes¹⁰.

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 small mammals had better high-frequency hearing than larger mammals¹¹. A detailed analysis revealed that high-frequency hearing was not related to the size of an animal, but to the magnitude of the binaural locus cues available to it: the difference in the time of arrival of a sound at the two ears (binaural time cue) and the difference in the intensity of a sound at the two ears (binaural intensity cue). In other words, the smaller an animal’s head, the smaller the availability of the binaural time cue and the higher the frequencies it would have to hear for its head to form a sound shadow and generate an interaural intensity difference. Later research demonstrated the importance of high-frequency hearing for the use of pinna cues and it became apparent that the smaller a mammal’s head and pinnae, the higher it needed to hear to use pinna cues as well as the binaural intensity cue⁵.

The relationship between high-frequency hearing and magnitude of locus cues is shown in Fig. 1 where high-frequency hearing is defined as the highest frequency audible at 60 dB sound pressure level (SPL). The availability of locus cues to a species is indicated by the “functional” interaural distance. For terrestrial mammals, functional interaural distance is determined by dividing the distance around the head from the opening of one ear canal to the other by the speed of sound in air. For marine mammals, it is determined by dividing the distance between the bullae, 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. As shown in Fig. 1, the correlation between functional interaural distance and high-frequency hearing is $r = -.78$.

There are several points to consider regarding Fig.1. First, the relationship is not simply between head size and high-frequency hearing, but between the maximum difference in the time of arrival of a sound at the two ears. Although marine mammals have *physically* large heads, they have relatively small *functional* interaural distances because the speed of sound traveling through their heads is much faster than the speed of sound in air, a point that was made when this relationship was first described (Masterton et al., 1969). However, overlooking this fact has caused some researchers^{8,12} to conclude that cetaceans are an exception to this relationship, when in fact they are not.

Second, high-frequency limit of hearing does not vary within a species. For example, although the functional interaural distance of dogs varies by a factor of two, and their tympanic membranes vary from 30-55 mm², all dogs have the same high-frequency hearing limit (a similar situation exists for humans). Thus, the audiogram does not passively vary with the size of the middle ear^{5,13}.

Third, humans are often thought to differ from other mammals in that we are unable to hear “ultrasound”, which is true by definition because ultrasound is any high-frequency sound inaudible to humans. However, given our relatively large head size, our 60-dB high-frequency hearing limit is not significantly different from that predicted by the regression line in Fig.1. Indeed, the Indian elephant, with its larger head, has an even lower upper limit of 10.5 kHz.

Fourth, although the high-frequency hearing limits of bats are close to those predicted by the regression line in Fig. 1, echolocating bats that emit laryngeal echolocation calls hear somewhat higher than similar-sized animals that do not echolocate. In contrast, non-echolocating bats (and fruit bats that use tongue clicks) do not hear higher than predicted⁴. Thus, the use of echolocation by bats, as well as by toothed whales (e.g., dolphins, killer whales), is an example of how, after mammals evolved high-frequency hearing, it was exploited for another function.

Fifth, that mammals require high frequencies for sound localization is demonstrated by the observation that progressively filtering high frequencies out of a broadband sound degrades an animal’s ability to localize sound. This is particularly apparent when localizing in the vertical plane or making front-back discriminations for which binaural cues are unavailable. Because the pinnae cannot modify long wavelengths, removing high frequencies eliminates pinna cues¹⁴. Indeed, although humans need to hear only up to 4 kHz to understand speech, our 60-dB high-frequency hearing limit is 17.6 kHz because our pinnae require frequencies above 6 kHz to be provide directional cues¹⁰. Filtering out high frequencies also degrades the ability to use the binaural intensity cue to make left-right locus discriminations as demonstrated by testing animals, such as mice, that do not use the binaural time cue to localize in the azimuthal plane¹⁵.

Finally, the most powerful evidence that high-frequency hearing is determined by the need to localize sound, and not by other factors such as body weight or size of the middle ear, is the failure of small subterranean mammals to hear high frequencies. Subterranean animals live entirely in underground tunnels and do not localize sound. The absence of sound localization removes the selective pressure for high-frequency hearing⁵. As a result, despite having functional interaural distances similar to other small rodents that hear high frequencies, such as hamsters (46.5 kHz), gerbils (58 kHz), and domestic mice (85.5 kHz), the pocket gopher, blind mole rat and naked mole rat have comparable hearing limits of 8.7 kHz, 5.9 kHz, and 11.5 kHz, respectively. In other words, mammals that have relinquished the ability to localize sound have no better high-frequency hearing than birds despite having a mammalian cochlea and three-boned middle ear.

The Function of the Ears is to Direct the Eyes to Sound Sources

It is common to think that animals would be under selective evolutionary pressure to localize sound as accurately as the physical cues available to them permit, but this is not necessarily the case.

The sound-localization acuity of different species can be compared by determining their minimum audible angle (MAA)—the smallest angle they can discriminate between two loudspeakers centered on 0° azimuth. At first, we expected that animals with large heads, and concomitant wide-set ears, would have better sound-localization acuity than animals with small heads and close-set ears (which generate smaller binaural locus cues). However, we were forced to re-examine our ideas about the variation in sound-localization acuity when we discovered that horses and cattle had poorer sound-localization acuity than rats.

We considered several possible explanations for the variation in sound-localization acuity: Whether an animal was large or small, a predator or prey, diurnal or nocturnal, or had large or small binocular visual fields. What we concluded was that sound-localization acuity was closely correlated with the size of an animal’s field of best vision¹⁶. Specifically, the narrower an animal’s field of best vision, the better its sound-localization acuity.

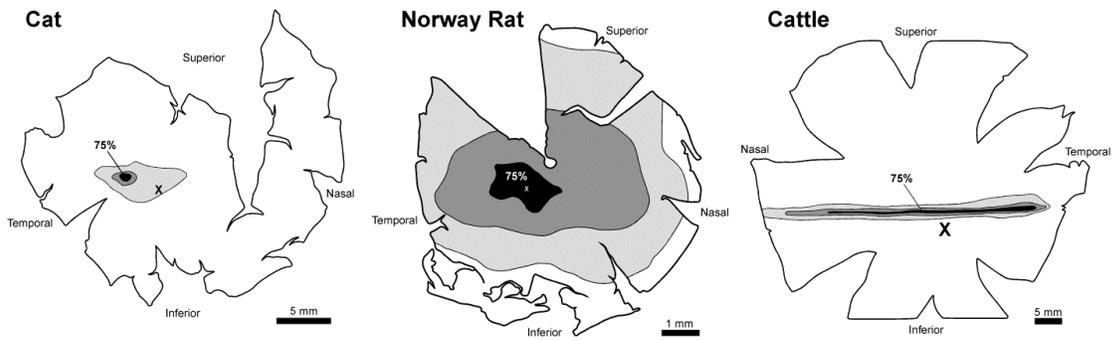


FIGURE 2. Retinal ganglion cell isodensity contours for the cat, Norway rat, and cattle. The region of best vision is defined as the 75% isodensity contour. Note small area of best vision for the cat compared with the broad visual streak for cattle. The X indicates the location of the blind spot. (From Heffner and Heffner, 2016⁵ [copyright AIP].)

The width of the field of an animal's best vision can be estimated by mapping the density of retinal ganglion cells (or, in the case of primates that possess a fovea, the density of the receptors). For comparative purposes, we defined the region of best acuity as the width (in degrees) of the horizontal visual field 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 Fig. 2. The relationship between the width of the field of best vision and sound-localization acuity is shown in Fig. 3. As can be seen, mammals with narrow fields of best vision are more accurate localizers than mammals with broader fields; indeed, the correlation is quite high, $r = 0.89$. This relationship, along with the observation that mammals adapted to living exclusively in the dark have lost the ability to localize sound (subterranean rodents) supports the idea that the primary purpose of mammalian sound localization is to direct the eyes to the source of a sound. Thus, any species that loses vision seems also to lose its ability to localize sound.

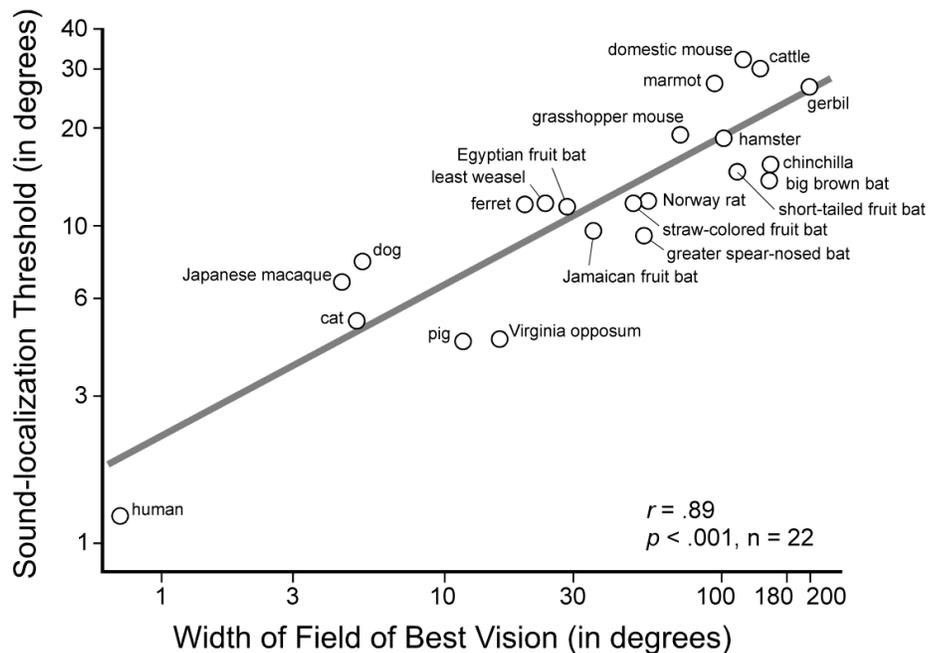


FIGURE 3. Relationship between the width of the field of best vision (75% isodensity contour) and sound-localization thresholds for 22 species of mammals. Species with narrow fields of best vision have smaller thresholds than those with larger fields of best vision. Note that bats fit the relationship. (From Heffner and Heffner, 2016⁵ [copyright AIP].)

Some Mammals Do Not Use All Available Locus Cues

As previously noted, mammals have three potential sound-localization cues: binaural time differences, binaural intensity differences, and pinna cues. Some mammals use all three cues and early in the history of the discipline this was assumed to be universal. However, there are other mammals that use only one or the other of the binaural cues, and the subterranean rodents, being unable to localize sound, apparently don't use any of the cues.

The ability to use the two binaural locus cues can be demonstrated by determining the ability of an animal to localize pure tones. In this test, the animals are trained to localize tones presented from loudspeakers located in front of them at a fixed angle of separation, typically $\pm 30^\circ$. Because low-frequency pure tones can bend around an animal's head with little or no attenuation, they must be localized with the binaural time cue (referred to in the case of pure tones as the binaural phase cue). At higher frequencies, pure tones cannot be localized using the phase cue because successive cycles arrive too quickly for the nervous system to match the arrival of the *same* cycle at the two ears, at which point the phase cue becomes ambiguous and tones must be localized using the binaural intensity-difference cue.

The ability of an animal to use pinna cues can be demonstrated by determining its ability to perform a front-back discrimination using noise bursts with speakers symmetrically centered on the interaural line so that there are no binaural time or intensity differences between the front and back locations. Animals that use pinna cues are able to localize high-frequency noise, but not low-frequency noise, because the pinnae are directional only at high frequencies.

The left side of Fig. 4 shows the species that use both binaural cues; the right side shows those that use only one of the binaural cues. Species are listed in the order of their functional interaural distance. Note that those animals that do not use the binaural time-difference cue are small animals, such as rats, mice, and some bats; they rely solely on the binaural intensity-difference cue and pinna cues to localize sound. However, there is no specific functional head size that separates those animals that use the binaural time cue from those that do not. In Fig. 4, there are six species that use the binaural time cue that are smaller than some that do not. 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, which do not use the binaural time cue, have a threshold of 12° degrees, whereas chinchillas and gerbils, which use both binaural cues, have thresholds of 17° and 27° , respectively.

Further towards the top of Fig. 4 are horses, alpacas, and pigs that have large functional interaural distances and have lost the ability to use the binaural intensity-difference cue; they rely solely on the binaural time and pinna cues to localize. Again, there is no specific interaural distance at which an animal relinquishes the binaural intensity cue as other large mammals, such as humans and elephants use both binaural cues.

With regard to pinnae locus cues, it is interesting to note that even if a species does not use the binaural intensity-difference cue, it continues to hear the high frequencies needed for using the pinnae to localize sound. Indeed, the only mammals that have relinquished pinna locus cues are marine mammals that lack pinnae, such as true seals, although they still use the binaural intensity-difference cue¹⁷, and subterranean rodents, which lack pinnae and do not localize sound.

Upper Limit of the Binaural Phase Cue

As previously noted, the ability of a species to use the binaural phase cue can be demonstrated by determining its ability to localize pure tones that are too low in frequency to be localized using the binaural intensity cue. This has led to the discovery that mammals vary in the highest frequency at which they can use the binaural phase cue. In humans, the upper frequency limit for binaural phase is around 1.3 kHz. In other mammals, it ranges from about 1.0 kHz (alpaca) to 6.3 kHz (Jamaican fruit bat)^{7,18}. Because the phase cue depends on synchronous neural firing, this suggests that the phase-locking ability of the auditory system varies between species. This variation has not been extensively studied and may yet yield insight into the factors that determine the upper limit of binaural phase.

The Mammalian Ear

By evolving isolated ears, mammals relinquished the directionality of the pressure-difference receiver, setting them on a different evolutionary trajectory. This resulted in the evolution of external ears and the ability to hear above 10 kHz, which was necessary to generate pinna cues, but also enhanced the binaural intensity-difference cue.

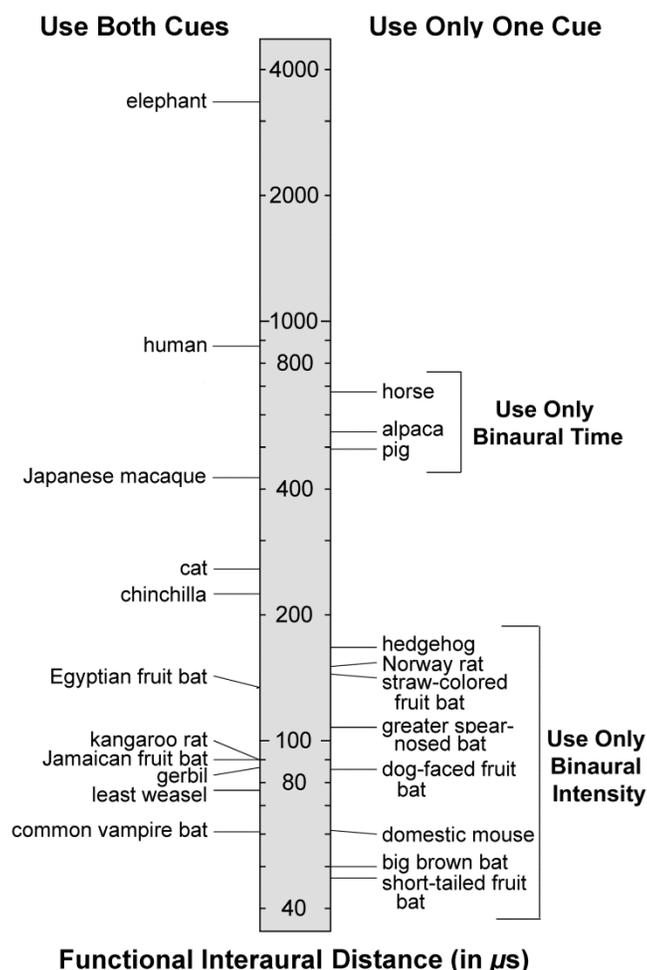


FIGURE 4. Many mammals use both binaural time and intensity difference cues (on the left). However, some use only one or the other cue (on right). Of the mammals that use only one cue, those with functional interaural distances larger than 400 μs use only the binaural time cue whereas those with interaural distances smaller than 200 μs use only binaural intensity cue. However, in both cases, there are similar-sized species that retain use of both cues (Modified from Heffner and Heffner, 2016⁵ [copyright AIP]).

The question is whether these changes gave mammals better sound-localization acuity than amphibians, reptiles, and birds, or whether it was just to compensate for the loss of the pressure-difference receiver mechanism.

So far, no one has been able to train amphibians or reptiles to respond reliably to sound so we know little about their behavioral hearing abilities. Although birds easily learn to respond to sound, minimum audible angles have been determined for only six species. A seventh species, the barn owl, has been tested by training it to orient to the source of a sound, which shows it to have a threshold of 3-5°. Just how that threshold compares to minimum audible angle is not known, but it indicates that accurate sound localization does not necessarily require hearing frequencies well above 10 kHz.

Finally, we turn to the evolutionary question and ask why the two ears of mammals became isolated. One possibility is that because mammals are continuous breathers, they isolated their ears from their mouth cavity to prevent breathing sounds from masking external sound. This interpretation is supported by the observation that birds, which are also continuous breathers, isolated their ears from their mouths by using an interaural canal through their skull. However, this idea doesn't explain the presence of the crocodilian interaural canal as they breathe intermittently and thus can easily cease breathing for long periods if necessary to prevent breathing sounds from interfering with the perception of external sounds.

SUMMARY

The development of reliable techniques for measuring the auditory abilities of animals has led, over the last 50 years, to a better understanding of the evolution of mammalian hearing.

The evolution of mammalian hearing was accompanied by three anatomical changes: The isolation of the two ears from each other, the development of the three-boned middle ear, and the appearance of the external ear (pinna). We suggest that these developments are related. The three-boned middle ear enables mammals to hear frequencies well above the 10-kHz upper limit of non-mammalian tetrapods, which enables them to use the binaural intensity difference and pinna cues. Moreover, the smaller an animal's interaural distance, the higher it hears in order to generate binaural intensity and pinna locus cues. The use of high frequencies for sound localization may have evolved as a consequence of losing the advantage of interconnected ears that serve as pressure-difference receivers that enhance the directionality of sound.

The sound-localization ability of mammals varies, not as a function of the availability of the physical cues, but based on the selective advantage to an animal to survive and reproduce. Localization acuity, the minimum audible angle, is highly correlated with the width of the field of an animal's best vision, suggesting that the function of sound localization is to direct the eyes to the source of a sound. The use of the locus cues also varies—some large animals do not use the binaural intensity difference cue, some small animals do not use the binaural time difference cue, animals that lack external ears do not use pinnae cues, and subterranean rodents foregoing all locus cues and hence localization itself.

One result of this research is to suggest other questions that might fruitfully be answered. One is whether the mammalian ear is somehow superior to that of non-mammalian tetrapods, especially birds. A second is whether there is an explanation for the variation in mammalian low-frequency hearing ability, which varies more than their high-frequency hearing. A third is whether the variation in the upper limit of the ability to use binaural phase difference cue, which ranges from 1 kHz to 6.3 kHz, is reflected by species differences in the upper limit of phase locking in the auditory system. Finally, there is the question of why mammals evolved isolated ears.

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