

High-Frequency Hearing

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Glossary:

Azimuth – direction along the horizon relative to a listener

Δt – difference in the time of arrival of a sound at the two ears

Δf_i – difference in the frequency-intensity spectra of a sound at the two ears

Functional head size – the time it takes for sound to travel around the head from one ear to the

Octave – an interval between two frequencies that have a 2 to 1 ratio (.25 kHz to .5 kHz and 50 kHz to 100 kHz are both intervals of one octave)

Subterranean animals – animals that live their entire lives below ground

Synopsis:

The nearly universal ability of mammals to hear frequencies above 10 kHz is a distinctly mammalian trait among vertebrates. The primary source of selective pressure for mammalian high-frequency hearing appears to be its role in localizing sound through use of the binaural spectral-difference cue, pinna cues, or both.

Introduction

The first systematic study of high-frequency hearing was conducted by Francis Galton in the second half of the 19th century. Using a high-frequency whistle attached to his cane and operated by a rubber bulb, Galton observed the unconditioned responses of animals, including those of the London Zoological Gardens, to high-frequency sounds. His observations, which he briefly summarized in his book, “Inquiries in Human Faculty and Its Development” (1883), indicate that he found significant species differences in the ability to hear high frequencies or, as he referred to them, “shrill sounds”. Of the animals he observed, he found cats to have the best high-frequency hearing, an

ability he attributed to their need to hear the high-frequency sounds made by mice and the other small animals they catch. He also found small dogs to have good high-frequency hearing, although he believed that large dogs did not, as he was never able to get them to respond to his whistle. Thus, by the late 19th century, it was apparent that mammals vary in their ability to hear high-frequency sounds.

The purpose of this chapter is to explain both why mammals have good high frequency hearing and why they differ in this ability. The explanation we offer does not address how mammals hear high frequencies, but why they do—mammals evolved high-frequency hearing for the purpose of localizing sound. Thus, the following is a description of the evolutionary pressures that have led to high-frequency hearing in mammals, rather than the mechanisms that underlie this ability.

Before beginning, some preliminary information will be useful. First, most non-mammalian vertebrates do not hear significantly above 10 kHz: birds have an upper limit of 8-12 kHz, (Dooling, R. J. *et al.*, 2000) while reptiles, amphibians, and most fish do not hear above 5 kHz (Heffner, H. E. and Heffner, R. S., 1998; for an example of fish that hear high frequencies, see Mann, D.A. *et al.*, 2001). Thus, the almost universal ability of mammals to hear frequencies above 10 kHz is a distinctly mammalian trait among vertebrates. Second, the term “ultrasonic” refers to frequencies above the nominal upper limit of humans, which is 20 kHz, and is therefore an anthropocentric term. A more appropriate perspective would be gained if we focus on the distinction between mammals and other vertebrates and consider any hearing above 10 kHz to be noteworthy. Finally, it should be noted that sound is perceived on a log scale, which in music is stated in octaves. Thus, although the difference between an upper limit of 50 and 100 kHz may seem greater than that between 5 and 10 kHz, both are differences of just one octave.

High-frequency Hearing and Sound Localization

Although it was known that some mammals had better high-frequency hearing than others, it was not until 1967 that the discovery of systematic variation in mammalian high-frequency hearing was made by the late R. Bruce Masterton. In the course of determining the hearing abilities of several species of mammals, in preparation for a study of auditory cortex, he noticed that smaller mammals had better high-frequency hearing than larger ones. Because he was studying sound localization at the time, he realized that this observation had implications for the use of the binaural locus cues: the difference in the time of arrival of a sound at the two ears (which he referred to as Δt), and the difference in the frequency-intensity spectra of the sound reaching the two ears (Δfi). Noting that the magnitude of the binaural time-difference cue depends on the size of an animal's head, he suggested that the

smaller an animal's head, the more dependent it would be on the binaural spectral-difference cue (Masterton *et al.*, 1969). However, to use the binaural spectral-difference cue, animals must hear frequencies high enough to be attenuated by their head and pinnae (thus generating intensity differences between the two ears) because small heads do not block low frequencies as effectively as they block higher frequencies. Therefore, the smaller an animal's functional head size (defined as the time it takes for sound to travel around the head from one ear to the other), the higher it must hear to use the binaural spectral-difference cue for sound localization.

The relation between functional head size and high-frequency hearing has remained robust since its discovery ($r = -0.79$, $p < 0.0001$) and has been shown to hold for over 60 species ranging in size from mice and bats to humans and elephants (Fig. 1). However, two points should be noted about this relationship. First, as can be seen in Figure 1, it does not apply to

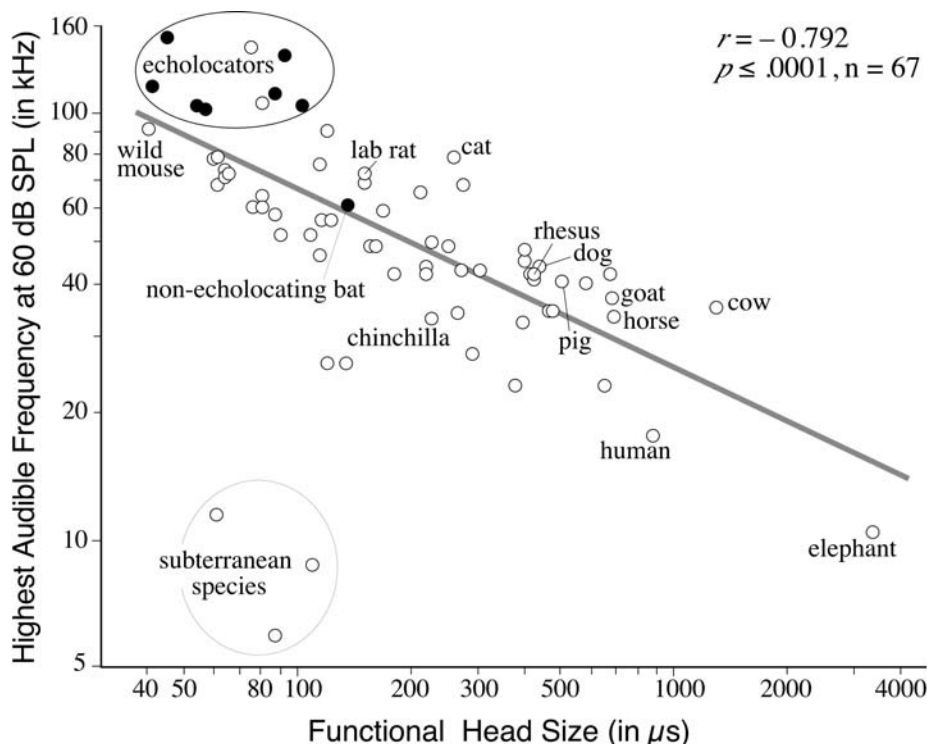


Figure 1. Relation between functional head size and high-frequency hearing (highest frequency audible at 60 dB sound pressure level) for mammals. This relationship is explained by the need of small mammals need to hear higher frequencies than larger mammals in order to use the binaural spectral-difference cue and/or pinna cues to localize sound. Note that the subterranean species (naked mole rat, blind mole rat, and gopher), which do not localize sound, have lost the ability to hear high frequencies. Echolocating bats hear slightly higher than predicted based on their functional head size. Filled circles indicate bats, open circles indicate all other mammals. (The open circles among the echolocators are two species of cetacea.) For references to individual audiograms, see Koay, G. *et al.*, 1998a, and Heffner, R. S. *et al.*, 2003; For tables of the absolute thresholds of mammals, go to the website at <http://psychology.utoledo.edu/lch>

subterranean mammals; they are an exception that we shall later see proves the rule. Second, the relationship applies only to comparisons between species, not within species. For example, although dogs differ in head size by a factor of two (from Chihuahuas to St. Bernards), what little individual variation they show in high-frequency hearing is not related to their functional head size (Heffner, H. E., 1983). Thus, Galton (1883) was wrong on one point—large dogs do have good high-frequency hearing. The failure of large dogs to respond to Galton's whistle both demonstrates the weakness of using unconditioned responses for testing sensitivity and also suggests that large dogs may be unconcerned by objects that make only high-frequency sounds because such objects (usually other animals) are generally small.

Binaural Spectral-difference Cue

The importance of high-frequency hearing for localizing sound in the horizontal (azimuthal) plane can be demonstrated by determining the ability of an animal to localize a broadband signal (i.e., noise) from which high frequencies are removed. Filtering out high frequencies has been shown to degrade azimuthal localization in monkeys, humans, chinchillas, and mice (Brown, C. H. *et al.*, 1982; Butler, R. A., 1986; Heffner, R. S. *et al.*, 1996, 2001a). Because the binaural time-difference cue is available in the low-frequency component of the signal, a decline in performance may be attributed to the absence of high frequencies necessary for using the binaural spectral-difference cue (assuming the use of pinna cues has been ruled out).

Although there is little doubt that the use of binaural spectral-differences requires mammals to hear high frequencies, it is only part of the reason that mammals evolved high-frequency hearing. This point was dramatically demonstrated by the discovery that some mammals lack the ability to use the binaural spectral-difference cue but still hear high frequencies. Briefly, the ability to use the two binaural cues can be assessed by determining the ability of an animal to localize pure tones. Use of the binaural time-difference cue is indicated by the ability to localize low-frequency tones that pass around the head with little or no intensity difference between the ears. The ability to localize tones that are too high in frequency to permit the use of the

binaural time cue indicates that an animal can use the binaural spectral-difference cue (e.g., Heffner, R. S. *et al.*, 2001b; Heffner, H. E. and Heffner, R. S., 2003). The results of this test indicate that most mammals use both binaural cues (as, for example, do humans, monkeys, and cats). Yet, some species do not use binaural time differences (such as hedgehogs, mice, laboratory rats, and some bats), and others are either partially or completely unable to use binaural spectral differences (Heffner, H. E. and Heffner, R. S., 2003). Specifically, Indian elephants and domestic goats are unable to localize pure tones in the upper end of their hearing range indicating that they do not use the spectral information in their highest audible frequencies to localize sound (Heffner, H. E. and Heffner, R. S., 2003; Heffner, R. S. and Heffner, H. E., 1982). Domestic pigs, horses, and cattle are more extreme in that they cannot localize high-frequency tones at all, leading to the conclusion that they have completely relinquished the ability to use the binaural spectral-difference cue (Heffner, H. E. and Heffner, R. S., 2003; Heffner, R. S. and Heffner, H. E., 1986, 1989). To explain the existence of good high-frequency hearing in animals that do not use the binaural spectral-difference cue, we turned to the third type of sound-localization cue which is produced by the external ear, namely the pinna cues.

Pinna Localization Cues

Although the role of the pinna in sound localization was demonstrated during the late 19th century, most 20th century studies focused on the binaural locus cues (Butler, R. A., 1975). This resulted in the use of headphones for presenting stimuli thereby eliminating the pinnae, making it easy to lose sight of their importance. Over the years, the work of Robert Butler and others has demonstrated that the directionality of the pinna not only provides the primary cues for vertical localization and for preventing front--back confusions, but also provides effective cues for localizing sound in the horizontal plane (e.g., Butler, R. A., 1975; Musicant, A. D. and Butler, R. A., 1985a,b). Indeed, as noted by Butler, R. A. (1999), "We live in a world where many sounds emanating from the side are not sufficiently intense to stimulate the opposite ear", in which case a binaural comparison only indicates that

the sound source is somewhere within the hemifield of the ear receiving the sound and, in the absence of pinna cues, may result in the perception of the sound being located within the ear itself. Thus, there are situations in which the pinnae provide the only locus cues as to the horizontal and vertical location of a sound source within a hemifield. For pinna cues to be effective in humans, the sounds must contain frequencies above 4 kHz and even sounds as high as 15 kHz have been shown to be necessary for optimal localization performance. Thus, the upper two octaves of human hearing (from 4 to 16 kHz) appear to be used primarily, if not exclusively, for sound localization, as they are not necessary for the perception of speech.

Other mammals also require high frequencies for localizing in the vertical plane, as well as for preventing front-back confusions. For example, filtering out high frequencies from a broadband noise signal degrades sound-localization performance for front-back and vertical localization in chinchillas and for vertical localization in monkeys (Brown, C. H., *et al.*, 1982; Heffner, R. S., *et al.*, 1996). Horses, which lack the ability to use the binaural spectral-difference cue, still require high frequencies to use pinna cues for front-back localization (Heffner, H. E. and Heffner, R. S. 1983). Thus, although most mammals use their high-frequency hearing to obtain both binaural spectral differences and pinna cues, some, such as horses, pigs and cattle, use it only for pinna locus cues. In addition, it is likely that there are species that use their high-frequency hearing to obtain the binaural spectral-difference cue, but do not use pinna cues (such as cetacea and the pinnipeds that lack pinnae).

Subterranean Mammals

As previously noted, subterranean mammals do not have good high-frequency hearing and their upper limit of hearing does not fit the relation between functional head size and high-frequency hearing (Fig. 1). However, the existence of these animals does not weaken the theory that mammals evolved good high-frequency hearing for sound localization, but, instead, strengthens it. This is because not only do the pocket gopher, naked mole-rat, and blind mole-rat lack good high-frequency hearing, they also lack the ability to localize sound (Heffner, R. S. and Heffner, H. E., 1990, 1992a, 1993). Thus it appears that subterranean animals that are adapted to the one-dimensional world 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 cannot optimally localize sound without high frequencies, and those that relinquish the ability to localize sound also give up their high frequency hearing.

Bats

Although bats require good high-frequency hearing for passive sound localization (Koay, G. *et al.*, 1998b), the question arises as to whether selective pressure for echolocation has caused bats to increase their high-frequency hearing beyond that required for passive sound localization. This possibility was recently examined by comparing the high-frequency hearing limits of bats with those of other mammals. The results of this comparison indicated that echolocating bats hear on average about 0.5 octaves higher than expected from their functional head size. Thus, although echolocating bats appear to owe 3.3 octaves of their high-frequency hearing to selective pressure for passive sound localization, they seem to have added an average of half an octave to their hearing ranges for use in echolocation. In contrast, non-echolocating bats have not extended their high-frequency hearing beyond that expected for passive sound localization (Heffner, R. S., *et al.*, 2003).

Ultrasonic Communication

It is not unusual for small rodents to produce vocalizations that are above the range of human hearing, i.e., "ultrasonic" (e.g., Nyby, J. and Whitney, G., 1978), and it has been suggested that high-frequency hearing evolved in order for animals to communicate via ultrasound (e.g., Sales, G. D. and Pye, J. D., 1974). Indeed, it would seem advantageous for small animals to use high-frequency communication signals because they are more directional and attenuate more rapidly over distance than low frequencies making them less likely to be detected by predators (Wilson, D. R. and Hare, F., 2004). However, whether such calls are inaudible to a predator depends on the predator's proximity as well as its auditory sensitivity.

Although the use of high-frequency communication signals by small mammals is well-established, we have argued elsewhere that it appears to be a co-option of

high-frequency hearing that originally evolved for sound localization (Heffner, H. E. and Heffner, R. S., 1985; Heffner, R. S., and Heffner, H. E., 1985). One reason is that a species' upper limit of hearing often extends beyond that required for hearing its communication vocalizations, as in the case of cattle, dogs, and humans, which hear frequencies well above the dominant frequencies of their vocalizations. Another is that there is no clear sign that high-frequency communication has affected a species' auditory sensitivity. Although some species vocalize at frequencies corresponding to secondary peaks of sensitivity toward the midrange of their audiograms, these secondary peaks have been shown to result from the directionality of the pinnae and serve to enable animals to localize in the vertical plane (Kooy, G. *et al.*, 1998b). Finally, the fact that small animals produce high-frequency vocalizations is not surprising as it would require special adaptation for them to produce low-frequency calls, as is the case for frogs and toads that use specialized vocal sacs to produce low-frequency calls. (e.g., Bradbury, J. W. and Vehrencamp, S. L., 1998).

Conclusion

The primary source of selective pressure for mammalian high-frequency hearing appears to be its role in localizing sound through use of the binaural spectral-difference cue, pinna cues, or both. Most mammals hear higher than humans because they have functionally smaller heads and therefore require higher frequencies to localize sound—when compared to the elephant, which only hears up to about 10 kHz, even humans have “ultrasonic” hearing. Finally, it may be noted the understanding of high-frequency hearing is only one example of the insight that can be gained from a comparative analysis of hearing; other examples include low-frequency hearing (R. S. Heffner and Heffner, 2001) and sound localization (Heffner, H. E. and Heffner, R. S., 2003; Heffner, R. S., and Heffner, H. E., 1992b). Indeed, the view that mammals evolved high-frequency hearing for sound localization suggests that non-mammals, such as birds, which lack high-frequency hearing, either do not localize sound as well as mammals (especially off to the side and in the vertical plane where pinna cues predominate) or else

have evolved alternative mechanisms for sound localization, such as the facial ruff of the barn owl (Knudsen and Konishi, 1979).

References

- Bradbury, J. W., and Vehrencamp, S. L. 1998. Principles of animal communication. Sunderland MA: Sinauer Assoc.
- Brown, C. H., Schessler, T., Moody, D., and Stebbins, W. 1982. Vertical and horizontal sound localization in primates. *J. Acous. Soc. Am.* 72, 1804-1811.
- Butler, R. A. 1975. The influence of the external and middle ear on auditory discriminations. In: *Handbook of Sensory Physiology: Auditory System, Vol. V/2* (eds. W.D. Keidel and W.D. Neff), pp. 247-260. New York: Springer.
- Butler, R. A. 1986. The bandwidth effect on monaural and binaural localization. *Hear. Res.* 21, 67-73.
- Butler, R. A. 1999. The unfolding of an auditory illusion. *Perspectives in Biol. and Med.* 42, 157-173.
- Dooling, R. J., Lohr, B., and Dent, M. L. 2000. Hearing in birds and reptiles. In: *Comparative Hearing: Birds and Reptiles* (eds. R. J. Dooling, R. R. Fay, and A. N. Popper), pp. 308-359. New York: Springer-Verlag.
- Galton, F. 1883. *Inquiries in Human Faculty and its Development*. London: J. M. Dent and Sons.
- Heffner, H. E. 1983. Hearing in large and small dogs: Absolute thresholds and size of the tympanic membrane. *Behav. Neurosci.* 97, 310-318.
- Heffner, H. E., and Heffner, R. S. 1983. Sound localization and high-frequency hearing in horses. *J. Acous. Soc. Am.* 73, S42.
- Heffner, H. E., and Heffner, R. S. 1985. Hearing in two cricetid rodents: wood rat (*Neotoma floridana*) and grasshopper mouse (*Onychomys leucogaster*). *J. Comp. Psychol.* 99, 275-288.
- Heffner, H. E., and Heffner, R. S. 1998. Hearing. In: *Comparative Psychology, A Handbook* (eds. G. Greenberg and M. M. Haraway), pp. 290- 303. Garland: New York.
- Heffner, H. E. and Heffner, R. S. 2003. Audition. In: *Handbook of Research Methods in Experimental Psychology* (ed. S. F. Davis), pp. 413-440. Blackwell: Malden, MA.

- Heffner, R. S., and Heffner, H. E. 1982. Hearing in the elephant: Absolute sensitivity, frequency discrimination, and sound localization. *J. Comp. Physiol. Psychol.* 96, 926-944.
- Heffner, R. S., and Heffner, H. E. 1985. Hearing in mammals: the least weasel. *J. Mammal.* 66, 745-755.
- Heffner, R. S., and Heffner, H. E. 1986. Localization of tones by horses: Use of binaural cues and the superior olivary complex. *Behav. Neurosci.* 100, 93-103, 137.
- Heffner, R. S., and Heffner, H. E. 1989. Sound localization, use of binaural cues and the superior olivary complex in pigs. *Brain, Behav, and Evol.* 33, 248-258.
- Heffner, R. S., and Heffner, H. E. 1990. Vestigial hearing in a fossorial mammal, the pocket gopher, (*Geomys bursarius*). *Hear. Res.* 46, 239-252.
- Heffner, R. S., and Heffner, H. E. 1992a. Hearing and sound localization in blind mole rats. *Hear. Res.* 62, 206-216.
- Heffner, R. S., and Heffner, H. E. 1992b. Visual factors in sound localization in mammals. *J. Comp. Neurol.* 317, 219-232.
- Heffner, R. S., and Heffner, H. E. 1993. Degenerate hearing and sound localization in naked mole rats (*Heterocephalus glaber*), with an overview of central auditory structures. *J. Comp. Neurol.* 331, 418-433.
- Heffner, R. S., and Heffner, H. E. 2001. Audiograms of five species of rodents: Implications for the evolution of hearing and the perception of pitch. *Hear. Res.* 157, 138-152.
- Heffner, R. S., Koay, G., and Heffner, H. E. 1996. Sound localization in chinchillas, III: Effect of pinna removal. *Hear. Res.* 99, 13-21.
- Heffner, R. S., Koay, G., and Heffner, H. E. 2001a. Sound-localization acuity changes with age in C57BL/6J mice. In: *Handbook of Mouse Auditory Research: From Behavior to Molecular Biology* (ed. J.F. Willott) pp. 31-35. CRC Press: Boca Raton FL.
- Heffner, R. S., Koay, G., and Heffner, H. E. 2001b. Sound localization in a new-world bat, *Artibeus jamaicensis*: Acuity, use of binaural cues, and its relationship to vision. *J. Acous. Soc. Am.* 109, 412-421.
- Heffner, R. S., Koay, G., and Heffner, H. E. 2003. Hearing in American leaf-nosed bats. III: *Artibeus jamaicensis*. *Hear. Res.* 184, 113-122.
- Knudsen, E. I., and Konishi, M. 1979. Mechanisms of sound localization in the barn owl (*Tyto alba*). *J. Comp. Physiol. A.*, 133, 13-21.
- Koay, G., Heffner, R. S., and Heffner, H. E. 1998a. Hearing in a megachiropteran fruit bat (*Rousettus aegyptiacus*). *J. Comp. Psychol.* 112, 371-382.
- Koay, G., Kearns, D., Heffner, H. E., and Heffner, R. S. 1998b. Passive sound-localization ability of the big brown bat (*Eptesicus fuscus*). *Hear. Res.* 119, 37-48.
- Mann, D. A., Higgs, D. M., Tavalga, W. N., Souza, M. J., and Popper, A. N. 2001. Ultrasound detection by clupeiform fishes. *J. Acous. Soc. Am.* 109, 3048-3054.
- Masterton, B., Heffner, H., and Ravizza, R. 1969. The evolution of human hearing. *J. Acous. Soc. Am.* 45, 966-985.
- Musicant, A. D., and Butler, R. A. 1985a. Influence of monaural spectral cues on binaural localization. *J. Acous. Soc. Am.* 77, 202-208.
- Musicant, A. D., and Butler, R. A. 1985b. Erratum: "Influence of monaural spectral cues on binaural localization" [*J. Acoust. Soc. Am.*, 77, 202-208 (1985)]. *J. Acous. Soc. Am.* 77, 2190.
- Nyby, J., and Whitney, G. 1978. Ultrasonic communication of adult myomorph rodents. *Neuroscience and Biobehavioral Rev.* 2, 1014.
- Sales, G. D., and Pye, J. D. 1974. *Ultrasonic Communication by Animals*. London: Wiley.
- Wilson, D. R., and Hare, F. 2004. Ground squirrel uses ultrasonic alarms. *Nature*, 430, 523.

Relevant Website

<http://psychology.utoledo.edu/default.asp?id=50> – The University of Toledo Department of Psychology, Laboratory of Comparative Hearing.