

High-Frequency Hearing

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Glossary:

Azimuth – direction along the horizon relative to a listener

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

fi – 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 t), and the difference in the frequency-intensity spectra of the sound reaching the two ears (f_i). 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

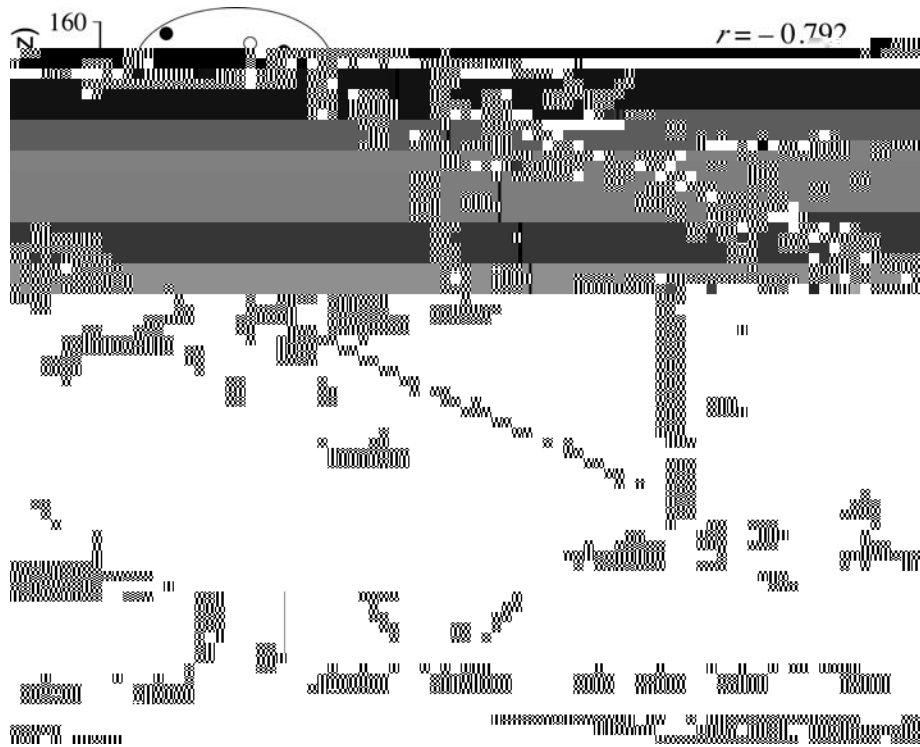


Figure 1. Relation between functional head size and high-frequency hearing (highest frequency audible at 60 dB sound pressure level) for mammals. This relationship is explained by the need of small mammals need to hear higher frequencies than larger mammals in order to use the binaural spectral-difference 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.

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*

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

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 (Koay, G.

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