

Hearing in the Elephant (*Elephas maximus*)

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Abstract. Auditory thresholds were determined for a 7-year-old Indian elephant. The hearing range extended from 17 hertz to 10.5 kilohertz. The results indicate that the inverse relationship between functional interaural distance (that is, the distance between the two ears divided by the speed of sound) and high-frequency hearing limit is valid even for very large mammals.

Among vertebrates, only mammals can hear high-frequency sounds (1). Whereas other classes of vertebrates are unable to hear much above 10 kHz, the average mammalian high-frequency hearing limit is 55 kHz, and high-frequency limits near 100 kHz are not uncommon. Yet the ability of mammals to hear high frequencies is not uniform, but varies from one species to the next. For example, humans are generally capable of hearing 19 kHz, dogs 44 kHz, rats 72 kHz, and bats 115 kHz (2). Thus, high-frequency hearing among mammals varies over a range of nearly three octaves.

At first the variation in mammalian high-frequency hearing was thought to be related to the size of the animal, as small mammals seem better able to hear high-frequency sounds than larger ones (3). More recently, however, it has been shown that high-frequency hearing is directly correlated not with body weight,

but with the functional distance between the two ears, where functional distance (Δt) is defined as the distance between the ears (interaural distance) divided by the speed of sound (I). Mammals with small heads, and therefore close-set ears, are better able to hear high-frequency sounds than species with large heads and wide-set ears. More precisely, high-frequency hearing varies inversely with the functional distance between the ears and ultimately with the interaural time and intensity difference cues used for sound localization. Thus, the variation in mammalian high-frequency hearing is neither random nor, on the whole, the result of adaptations to specialized habitats—even those such as of bats or dolphins. Instead, high-frequency hearing seems to vary predictably with interaural distance.

The relationship between functional interaural distance and high-frequency hearing, however, has been established primarily for animals with small interaural distances. While there is no reason not to believe that this relationship is equally valid for all mammals, extrapolation to very large mammals leads to two somewhat unexpected conclusions. First, it predicts that a mammal as large as an elephant would hear sound only to about 10 kHz. Since this limit is no higher than that found in birds, this prediction suggests that mammalian high-frequency hearing may not always be superior to nonmammalian vertebrates. Second, humans have often been considered as aberrant because of their inability to hear above 20 kHz (1, 4). However, it would now appear that humans may not be unusual in this respect, but may even have better high-frequency hearing than certain other (larger) mammals. Thus, to determine if the relationship applied to very large mammals we decided to test the hearing of an elephant.

The elephant chosen for this study was a 7-year-old (adolescent) female Indian

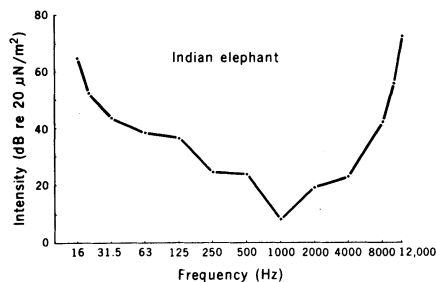


Fig. 1. Audiogram of the elephant. The thresholds represent the average of two audiograms, one obtained with the loudspeaker on the animal's left and the other with the loudspeaker on the right. Frequencies were tested in octave steps from 16 Hz to 8 kHz. Additional frequencies were 20 Hz, 10 kHz and 12 kHz. Sound pressure levels were recorded at the position of the opening of the elephant's auditory canal with and without the elephant in the sound field. To make the results comparable with previous audiograms, the thresholds reported here are based on measurements without the elephant in the sound field. (Sound pressure levels with the animal in the sound field were on average 2 dB higher, with the largest increase being 5 dB.)

elephant (*Elephas maximus*) with no history of serious illness. Her ears were carefully inspected and found to be free of any signs of obstruction or disease.

The audiogram was determined according to a two-choice or yes-no procedure, in which the elephant indicated the presence or absence of a tone by making one response when a tone was perceived and a different response when it was not perceived (5). Specifically, a panel (70 by 50 cm) had three Plexiglas response buttons (13 cm in diameter) mounted at the top in a horizontal row and a small drinking trough (13 by 15 by 7 cm) located at the bottom of the panel directly below the center button. The response panel was mounted on a cement-block wall 1.6 m high and topped by a chain fence. This wall and fence separated the elephant's room (6.7 by 5.6 by 4.6 m) from an adjacent room housing the test equipment. A loudspeaker was located 1 m to either the left or right side of the response panel and was pointed toward the elephant's ears (6).

The elephant was tethered 1.2 m in front of the response panel and trained to press the center button with its trunk. This response constituted an "observing response" which initiated a trial and also positioned the animal's head directly in front of the panel. Once a trial had begun, the elephant was required to wait at least 2 seconds and then press the left button if a tone had been presented or the right button if no tone had been presented. A correct response was rewarded with 30 ml of fruit-flavored drink dispensed into the trough. An incorrect response was not rewarded and was followed by a 5-second wait before a new trial could be begun. Tone pulses were presented randomly on half of the trials, and thresholds were obtained by presenting tones of various intensities (according to the method of constant stimuli). Threshold was defined as the intensity at which the animal could just distinguish tone trials from no-tone trials at the .01 level of statistical reliability (binomial distribution) for 50 trials (7). Testing was judged complete for a particular frequency when thresholds from two different sessions were within 3 dB of each other.

The elephant's audiogram exhibits the characteristic shape of mammalian audiograms (Fig. 1) (1). Beginning at the low frequencies, threshold decreased gradually to a relatively well defined point of best hearing in the midfrequency range followed by a steep increase in threshold at the high frequencies. The elephant's sensitivity was about average; the lowest threshold, 8-dB sound pressure level at

1 kHz, was well within the range of "best sensitivities" for mammals.

In spite of these similarities, the elephant's audiogram differs from those of other mammals in two major ways. (i) The elephant was unable to hear above 10.5 kHz at an intensity level of 60 dB. Though slightly higher frequencies could be heard at very high intensities, the animal was completely unable to respond to frequencies above 12 kHz at an intensity of 90 dB. (ii) The elephant was able to hear low-frequency sounds better than any mammal previously tested. At an intensity of 60 dB, the elephant could hear 17 Hz, nearly one octave below the comparable human threshold of 29 Hz. In sum, the elephant's audiogram was typically mammalian in form, but shifted toward low frequencies.

The audiogram of the elephant demonstrates the validity of the relationship between interaural distance and high-frequency hearing for all mammals large or small, land or water, echolocators or not (Fig. 2) (1). Where interaural distance is represented by maximum Δt , that is, the interaural distance divided by the speed of sound (8), the correlation between maximum Δt and the high-frequency hearing limit is $-.89$ ($P < .001$).

This correlation is now based on audiograms for 32 genera ranging from mouse and bat to elephant and killer whale. This high correlation implies that about 80 percent of the variance in the upper limit of hearing is accounted for by the variance in functional interaural distance alone.

The existence of a strong inverse relationship between these variables has been ascribed to selective pressure for accurate sound localization (1). Briefly, the two binaural cues for sound localization, the difference in time of arrival of a sound at the two ears (Δt) and the difference in frequency-intensity spectra of a sound reaching the two ears (Δfi), depend on the functional distance between the two ears and the sound shadow of the head and pinnae. That is, the farther apart the ears, the larger will be the Δt cue for any given direction of a sound source. Similarly, the Δfi cue is greater for animals with wide-set ears both because the sound attenuation is slightly greater over the longer distance between the ears and because animals with wide-set ears usually have large heads or large pinnae which effectively shadow the high-frequency content of sound. While the two binaural sound-lo-

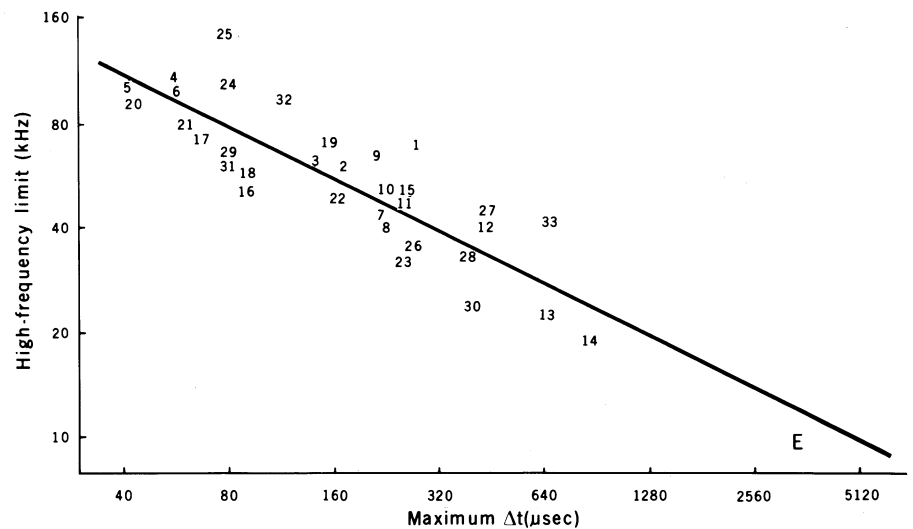


Fig. 2. Relationship between maximum Δt (maximum interaural distance divided by the speed of sound) and high-frequency hearing limit (highest frequency audible at 60-dB sound pressure level). Numbers and letter represent points for individual species (9). All high-frequency limits were determined in air except as noted. Key: E, elephant (*Elephas maximus*); 1, opossum (*Didelphis virginiana*); 2, hedgehog (*Hemiechinus auritus*); 3, tree shrew (*Tupaia glis*); 4, horseshoe bat (*Rhinolophus ferrumequinum*); 5, little brown bat (*Myotis lucifugus*); 6, big brown bat (*Eptesicus fuscus*); 7, slow loris (*Nycticebus coucang*); 8, potto (*Perodicticus potto*); 9, bush baby (*Galago senegalensis*); 10, owl monkey (*Aotus trivirgatus*); 11, squirrel monkey (*Saimiri sciureus*); 12, macaque (*Macaca* sp.); 13, chimpanzee (*Pan troglodytes*); 14, human (*Homo sapiens*); 15, rabbit (*Oryctolagus cuniculus*); 16, kangaroo rat (*Dipodomys merriami*); 17, cotton rat (*Sigmodon hispidus*); 18, gerbil (*Meriones unguiculatus*); 19, laboratory rat (*Rattus rattus*); 20, feral house mouse (*Mus musculus*); 21, laboratory mouse (*Mus musculus*); 22, guinea pig (*Cavia porcellus*); 23, chinchilla (*Chinchilla* sp.); 24, dolphin (underwater) (*Inia geoffrensis*); 25, porpoise (underwater) (*Tursiops truncatus*); 26, killer whale (underwater) (*Orcinus orca*); 27, dog (*Canis familiaris*); 28, sea lion (in air) (*Zalophus californianus*); 29, harbor seal (underwater) (*Phoca vitulina*); 30, harbor seal (in air) (*Phoca vitulina*); 31, ringed seal (underwater) (*Pusa hispida*); 32, harp seal (underwater) (*Pagophilus groenlandicus*); and 33, domestic sheep (*Ovis aries*).

calization cues are readily available to animals with large heads, the effectiveness of either cue is diminished in animals with functionally close-set ears. In the case of Δt , the available time difference may be so small that the nervous system can detect only gross changes in sound direction. However, an animal with a small head always has a Δf_i cue available, providing only that it is able to perceive frequencies which are high enough to be effectively shadowed by its head and pinnae. Therefore, given the ecological importance of an animal's localizing the sound of a stealthy intruder, animals with functionally close-set ears are subjected to more selective pressure to hear high frequencies than animals with more widely set ears.

Finally, the finding that the elephant is unable to hear significantly above 10 kHz has two immediate implications for ecological and evolutionary acoustics. (i) It suggests that when the selective pressure for high-frequency hearing is reduced as a consequence of evolving a large interaural distance, the upper limit of hearing is reduced to the point at which it does not greatly exceed that of non-mammalian vertebrates, such as birds, many of which hear up to 10 kHz. (ii) It appears that humans should no longer be considered aberrant among mammals for their lack of ability to hear above 20 kHz. Instead, restricted high-frequency hearing seems to be a consequence of a relatively large interaural distance and not the result of a special adaptation for the reception of speech sounds, as was once widely believed.

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References and Notes

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6. Loudspeakers used were a 15-inch (38-cm) woofer in a 0.45-m³ sealed enclosure and a piezoelectric tweeter. Sound production and measurement were by techniques described elsewhere [R. Heffner, H. Heffner, B. Masterton, *J. Acoust. Soc. Am.* **49**, 1888 (1971)].
7. Varying the definition of threshold over a wide range has no significant effect on the main conclusions.
8. Maximum Δt in a given species is the maximum possible difference in the time of arrival of a sound at the two ears. The value for maximum Δt depends on the path which the sound travels from ear to ear as well as the velocity of sound in the particular medium, that is, the distance from ear to ear divided by the speed of sound in air (340 m/sec) around the head in terrestrial mammals; and the distance from ear to ear through the head divided by the speed of sound in water and tissue (1500 m/sec) in most marine mammals.
9. For a list of the audiograms, see R. L. Francis [in *Sound Reception in Mammals*, R. J. Bench, A. Pye, J. D. Pye, Eds. (Academic Press, London, 1975), pp. 237-289], H. Heffner and B. Masterton (*J. Acoust. Soc. Am.*, in press) and the sources in (2).
10. We thank the Ralph Mitchell Zoo of Independence, Kans., for allowing us to study their elephant, and N. Stichman, for his help in training her. Supported by NSF grant BNS 58-07391.

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