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Functional interaural distance and high-frequency hearing in the elephant [43.80Lb, 43.66.Gf]

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Auditory thresholds were determined for a 7-year-old Indian elephant. The animal could hear only as high as 10.5 kHz (at an intensity of 60 dB SPL) and was unable to respond to frequencies above 12 kHz at intensities exceeding 90 dB. 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.

INTRODUCTION

Ever since the latter half of the nineteenth century it has been apparent that there is wide variation in the ability of different species of mammals to hear high-frequency sounds.[1] For example, while humans are generally capable of hearing up to 19 kHz, dogs can hear 44 kHz, rats 72 kHz, and bats 115 kHz.[2,3] Thus the high-frequency hearing limit of mammals is not uniform, but 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.[4,5] More recently, however, statistical analysis has 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.[3,6] 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 habits—even those such as of bats or dolphins. Instead, high-frequency hearing seems to vary predictably with interaural distance.

Though the relationship between functional interaural distance and high-frequency hearing has been established for over 30 different species, all of the mammals examined so far have been relatively small. Indeed, until now the largest mammal whose hearing was known is man, and it has often been suggested that the inability of humans to hear above 20 kHz is an abberation due to the development of good low-frequency hearing for the perception of speech sounds.[6,7] Thus, to determine if the relationship applied to all mammals, large and small, we decided to test the hearing of an elephant.

I. METHOD

A. Subject

The subject was a 7-year-old (adolescent) female Indian elephant (*Elephas maximus*) located at the Ralph Mitchell Zoo in Independence, KS.

B. Apparatus and procedure

The audiogram of the elephant was determined by use of a two-choice 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 (see Heffner and Heffner[2] for details). Briefly, a response panel with three response buttons mounted in a horizontal row and a small drinking trough located directly below the center button was mounted on a wall in the elephant house. The animal was tethered in front of the panel and trained to press the center button with its trunk in order to initiate a trial. Once a trial had begun, the elephant was required to wait at least 2 s and then press the left button if a tone had been presented or the right button if no tone has been presented. A correct response was rewarded with 30 ml of a fruit-flavored sugar solution dispensed into the trough. An incorrect response was not rewarded and was followed by a 5-s wait before a new trial could begin. Tone pulses were presented randomly on half of the trials, and thresholds were obtained by lowering the intensity of the tones until the animal could no longer distinghish tone trials from no-tone trials.

II. RESULTS

The results of the threshold tests indicate that the elephant had the lowest high-frequency hearing limit of any mammal yet tested. Above 4 kHz, the sensitivity of the animal decreased rapidly as frequency was increased to 12 kHz at which the animal's threshold was 72 dB (*re* 20 $\mu N/M^2$). Above 12 kHz no response could be obtained even at intensities exceeding 90 dB. Thus, while humans can hear 19 kHz at an intensity level of 60 dB, the elephant can hear only as high as 10.5 kHz at that intensity.

III. DISCUSSION

The high-frequency hearing ability 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. 1). Where interaural distance is represented by maximum Δt, that is, the interaural distance divided by the speed of sound, the correlation between maximum Δt and the high-frequency hearing limit is -0.89 ($p < 0.001$). This correlation is now based on audiograms for 32 genera ranging in size from mouse and bat to elephant and killer whale. This high correlation implies that about 80% of the variance in the upper limit of hearing is accounted for by the variance in functional interaural distance alone.

As was previously noted, small mammals tend to have better high-frequency hearing than large mammals. Yet body weight itself is not highly correlated with high-frequency hearing ($r = -0.49$, $p < 0.01$). Furthermore, it appears that the apparent relationship between body weight and high-frequency hearing is due to the fact that body weight is positively related to maximum Δt. That is, large mammals tend to have large maximum Δt's while small mammals tend to have small maximum Δt's. However, when maximum Δt is mathematically held constant by using partial correlational analysis,[8] the correlation between body weight and high-frequency hearing drops to chance ($r = 0.20$, $p > 0.05$). In contrast, the correlation between maximum Δt and high-frequency hearing remains statistically significant when the influence of body weight is removed. Thus it is maximum Δt, not body weight, which is correlated with high-frequency hearing.

It should be noted that maximum Δt in a given species is the maximum possible difference in the time of arrival of a sound at

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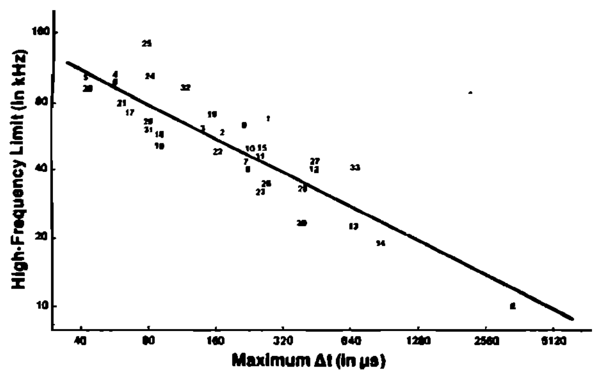

FIG. 1. Relationship between maximum Δt (maximum interaural distance divided by the speed of sound) and high-frequency hearing limit (highest frequency audible at 60-dB sound pressure level). Numbers and letter represent points for individual species (see Refs. 2 and 3 for a list of the audiograms). 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 unguiculatis*); 19, laboratory rat (*Rattus norvegicus*); 20, feral house mouse (*Mus musculus*); 21, laboratory mouse (*Mus musculus*); 22, guinea pig (*Cavia porcellus*); 23, chinchilla (*Chincilla* 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*) (from Heffner and Heffner[2]).

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, maximum Δt is the distance from ear to ear *around* the head divided by the speed of sound in air (340 m/s) for terrestrial mammals; and the distance from ear to ear *through* the head divided by the speed of sound in water and tissue (1500 m/s) for most marine mammals. In mammals which are well adapted to hearing in both aquatic and terrestrial environments, such as the harbor seal, an interesting situation arises in which the animal has two different maximum Δt's—one when it is underwater and another when it is in air (Fig. 1, points 29 and 30).

The existence of a strong inverse relationship between maximum Δt and high-frequency hearing has been ascribed to selective pressure for accurate sound localization. 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 (Δ fi), 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 Δ fi 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-localization 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 Δ fi 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 to an animal of 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.

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Practical acoustics in Finland [43.35.Yb, 43.80.Fv, 43.80.Jz, 43.80.Qf, 43.35.Sx, 43.85.-e]

A handheld device for detecting detached retinas and tumors in the eye, a system for measuring paper tension in a paper-processing or printing machine, are among the devices and systems that have been developed or are under study by Professor M. Luukkala and his group in the Physics Department of the University of Helsinki.

Several of the projects of Luukkala's group are in the field of medical electronics and employ ultrasonic waves. One that has recently passed from the research to the commercial stage is an instrument used for examining internal structure of the eye, which is now being manufactured at a Finnish company. In operation, a held-held portion of the instrument contacts the outer surface of the patient's eyelid, while an intervening jelly layer provides the medium for transmitting ultrasonic pulses into the eye's interior. The 6-MHz transducer which transmits echo pulses into the