Elephant hearing

Tom Reuter[a)] and Sirpa Nummela
University of Helsinki, Department of Ecology and Systematics, Zoological Laboratory, P.O. Box 17, FIN-00014 Helsinki, Finland

Simo Hemilä
Helsinki University of Technology, Laboratory of Physics, Otakaari 1, FIN-02150 Espoo, Finland

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Elephants' vocalizations and movements have recently been shown to produce seismic waves (Rayleigh waves). This may be relevant for the well-known long-distance communication of these animals. It is suggested here that elephants may sense ground vibrations as a result of bone conduction producing a differential vibration of the middle ear ossicles in relation to the skull. This hypothesis is supported by the exceptionally massive ossicles of the Indian and African elephants. The acoustics of bone conduction is reviewed and related to the anatomy of the elephant middle ear.
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We would like to comment on the observations presented by O'Connell, Arnason and Hart at the 134th meeting of the Acoustical Society of America in San Diego in December 1997.[1] O'Connell *et al.* suggest that elephants could base their acoustic long-distance communication on Rayleigh waves propagated in the surface layer of the ground. Such waves could be produced both by stomping the ground and by body vibrations produced by vocalization. In support of this hypothesis we would like to point out that the anatomy of the elephant middle ear shows morphological adaptations suitable for sensing ground vibrations.

Sound information can reach the mammalian inner ear through two main routes. In normal air-conducted hearing sound waves set the tympanic membrane and the middle ear ossicles in vibration, thus producing movements of the oval window and changing pressure gradients in the cochlear fluid. Bone-conducted hearing, on the other hand, is effective in water-living and fossorial mammals for which the difference between the acoustic impedances of the surrounding medium and the body is small. Thus the sound energy efficiently leads to skull vibration. For producing a hearing sensation, clearly a *differential* motion between the skull surrounding the inner ear fluid and the ossicles is needed. If the center of gravity of the ossicular chain lies on the axis of ossicle rotation, then skull vibration produces no such differential motion and no hearing sensation is achieved. Bárány[2] has suggested that such a prevention of bone conduction would be the main evolutionary reason for the mammalian middle ear hinge—it would save them from the noise created by chewing. But if the center of gravity does *not* lie exactly on the rotation axis, then the inertia produced by large ossicles brings about a rotatory movement of the ossicles, and inner ear stimulation and hearing are possible. This type of hearing is analogous to the otolith hearing in some fish.[3,4] In both cases sound brings the whole body into vibration, and the animal detects a motion difference between the head and the stapes or the otolith, respectively.

We have earlier suggested that the true seals (Phocidae) use both air-conducted and bone-conducted hearing, the former in air and the latter in water.[5,6] Among mammals, the ossicles of phocids are very massive and of an unusual shape, suggesting that the ossicle inertia is functional (provided that the rotation axis and the center of gravity do *not* coincide). The middle ear ossicles of the elephants are even more massive than those of the phocids; the combined mass of malleus, incus and stapes (m_{MIS}) is about 650 mg for the Indian elephant, compared with 160–320 mg for five species of phocids.[7] The ossicles of other large herbivores are generally one order of magnitude lighter; the m_{MIS} is 50 mg for the cattle, and 74 mg for the horse,[7] to mention two species for which complete audiograms have been determined.[8] The amphibious hippo might benefit from bone-conducted hearing in water, and indeed morphologically its middle ear ossicles somewhat resemble those of phocids, although they are clearly lighter (125 mg).[6,9]

Light ossicles are a condition for high-frequency hearing in air.[5] However, such ossicles do not *per se* impede low-frequency hearing. The horse and the cattle, for instance, combine rather light ossicles with a reasonably good sensitivity at low frequencies. Massive ossicles seem to occur in animals which receive acoustic information through body vibrations,[10,11] and for this they pay the price of radically reduced hearing at high frequencies.

Elephants have good low-frequency hearing (best sensitivity at 1000 Hz) extending into the infrasound region.[12] Further, they are known to produce infrasounds at high intensities,[13,14] and to use them for instance in mate searching.[15] Low frequencies attenuate less than higher frequencies and they apparently reach especially far when they propagate as Rayleigh waves. This is because Rayleigh waves attenuate as $1/r$, where r is distance, while the intensity of air-borne sound attenuates as $1/r^2$.

The elephant's body with a massive skeleton and pillar-like bones might be suitable for conducting the surface waves to the inner ear. In an elephant's audiogram measured with air-borne sound, the threshold at 100 Hz is quite high,

[a)]Electronic mail: tom.reuter@helsinki.fi

ca. 40 dB.[12] However, this high threshold at low frequencies is mainly caused by the limited middle ear air volume and the elastic couplings of the middle ear. In bone-conducted hearing these factors are less relevant. Provided a good inner ear sensitivity, an elephant could use bone conduction in hearing low frequencies. Its heavy ossicles provide the large inertia needed, and the freely mobile type of its middle ear[16] provides soft elastic couplings between the ossicles and the skull. Thus we postulate that an elephant using bone conduction is more sensitive to low frequencies than revealed by ordinary audiogram techniques.

Low-frequency surface waves could act as arousal signals over long distances. For precise sound localization elephants rely on their large pinnae and air-borne sound of higher frequencies.[17,18]

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