

LETTERS TO THE EDITOR

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High-frequency hearing in phocid and otariid pinnipeds: An interpretation based on inertial and cochlear constraints (L)

Simo Hemilä

Department of Biological and Environmental Sciences, University of Helsinki, FI-00014 Helsinki, Finland

Sirpa Nummela^{a)}

Department of Anatomy, Northeastern Ohio Universities College of Medicine, Rootstown, Ohio 44272-0095 and Department of Biological and Environmental Sciences, University of Helsinki, FI-00014 Helsinki, Finland

Annalisa Berta

Department of Biology, San Diego State University, San Diego, California 92182-4614

Tom Reuter

Department of Biological and Environmental Sciences, University of Helsinki, FI-00014 Helsinki, Finland

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Audiograms in air and underwater, determined by previous workers for four pinniped species, two eared seals (Otariidae) and two phocids (Phocidae), are supplemented here by measurements on their middle ear ossicular mass, enabling mechanistic interpretations of high-frequency hearing and audiogram differences. Otariid hearing is not largely affected by the medium (air/water). This indicates that cochlear constraints limit high-frequency hearing in otariids. Phocids, however, have massive middle ear ossicles, and underwater hearing has radically shifted towards higher frequencies. This suggests that the high-frequency hearing of phocids in air is constrained by ossicle inertia. © 2006 Acoustical Society of America. [DOI: 10.1121/1.2372712]

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Pinnipeds are adapted to hearing in both air and water,^{1–4} two media with radically different acoustic properties. In air pinnipeds probably hear like terrestrial mammals; sound waves enter through the external auditory meatus and set the tympanic membrane and the middle ear ossicles into vibration, producing movements of the oval window and pressure fluctuations in the cochlear fluid. In this situation the middle ear acts as a filter limiting the hearing range, and the inertia of the middle ear ossicles is relevant as it may affect the high frequency hearing limit (HFHL).^{5–8} Cochlear factors may also limit high frequency hearing.⁹

While the detailed mechanism for pinniped hearing underwater still remains unknown, it is well-known that these animals close their outer ear canal in water,^{10,11} and that several options for hearing through bone conduction are possible. Sound may, for instance, set the whole head into vibration and then the inertia of massive ossicles has a very different role, leading to differential motion between the

stapes and the vibrating cochlear capsule.^{11–15} In such a situation massive ossicles are of great advantage. Skull vibrations may also cause movements and deformations of the cochlea, producing fluid movement and hair cell stimulation.^{11,12,14} Direct recordings of skull and ossicle vibrations suggest, however, that ossicle rather than fluid inertia is the main mechanism behind bone conduction in humans.¹⁶

In order to appreciate the different roles of inertia in air and water it is useful to consider the differences in sound dissipation in these media. Let us compare two plane waves of equal intensity and frequency, one in air and the other in water. As the ratio of the characteristic acoustic impedances between water and air is ≈ 3700 , the sound pressure ratio is $\sqrt{3700}=61$, and the ratio of particle velocities and accelerations is $1/61$. In water, sound can bring heavy masses into vibration, as a result of the large sound pressure, but due to the small particle velocity and acceleration the inertial forces are much reduced. Thus it is understandable that in water sound can set an animal's head into vibration, even at fairly high frequencies, and lead to bone conduction hearing.

^{a)}Author to whom correspondence should be addressed. Electronic mail: nummela@fastmail.fm

TABLE I. Data on hearing and middle ear ossicles for four pinnipeds. High-frequency hearing limit in air (f_{Ha}), and underwater (f_{Hw}), predicted high-frequency hearing limit in air (f_H), combined mass of malleus and incus (m , mean value for several ears, sex and side given when available). For institutional abbreviations, see the Acknowledgments.

Taxon	f_{Ha} kHz	f_{Hw} kHz	f_H kHz	m mg	Material studied
Phocidae					
<i>Phoca vitulina</i>	22	100	17	164	(see Ref. 18)
<i>Mirounga angustirostris</i>	24	80–100	8	1390	LACM 54767 (female, right and left)
Otariidae					
<i>Callorhinus ursinus</i>	35	40	39	13.0	AMNH 245298 (left), NMNH 286106 (female), 286149 (male), SDSNH 16326 (right)
<i>Zalophus californianus</i>	31	34	33	21.9	SDSNH 22862 (male, left), 22981 (left)

Phocid ears differ anatomically from otariid ears in several respects. In phocids, the auditory bulla is inflated, the tympanic membrane and oval window are relatively large, and the round window and the fossula into which it opens are immense. Further, the round window is partly shielded from direct access to the middle ear, and in extreme cases (*Mirounga*) it opens outside the middle ear cavity, external to the skull.¹² Phocid middle ear ossicles are bulbous and massive, ten times larger than in terrestrial mammals with a similar skull size, whereas the otariids ossicles do not deviate in size from those of their terrestrial carnivore relatives, indicating that the phocid hearing system is clearly more specialized for aquatic hearing.^{11,12,17,18}

Consequently, it is possible that in air the interaction between the middle and inner ear in seals is very different from that in water. However, given the current knowledge of cochlear physiology, there is no reason to expect significant changes, when the animal's head is submerged just below the surface. Thus a comparison of phocid and otariid audiograms measured in air and underwater^{1,17,19–25} may provide valuable information on the relative roles of the middle and the inner ear in shaping the high-frequency part of the audiograms. To study various functional interpretations previously published audiogram data are here supplemented by the middle ear ossicular mass (malleus+incus) for several phocids and otariids (Table I). The stapes mass is not included; it forms a constant fraction of 5% of the combined mass of malleus and incus.¹⁸

When a bone with mass m vibrates with angular frequency ω , acceleration a , and velocity v , the inertial force is $ma = m\omega v$. Thus the role of inertial forces increases with an increasing frequency. The ossicle inertia in air-conducted hearing and the inertia of the skull bones in bone-conducted hearing most likely limit the hearing sensitivity at high frequencies. The inertia may, however, lose its physiological relevance for high-frequency hearing in case the tonotopic organization of the basilar membrane, or the molecular mechanisms of the individual hair cells prevent the cochlea from following high frequencies.^{9,26,27} This means that cochlear factors may set limits to hearing already at somewhat lower frequencies, well before the inertia becomes a critical

factor that would limit the hearing sensitivity. While inertia causes the hearing threshold to rise rather steadily toward higher frequencies, cochlear effects apparently result in an abrupt high-frequency cutoff.^{8,28,29}

Behavioral audiograms of four pinniped species are of interest here (Fig. 1). Instead of sound pressure levels the corresponding plane wave intensity levels are being used. This quantity enables direct comparison of results from the

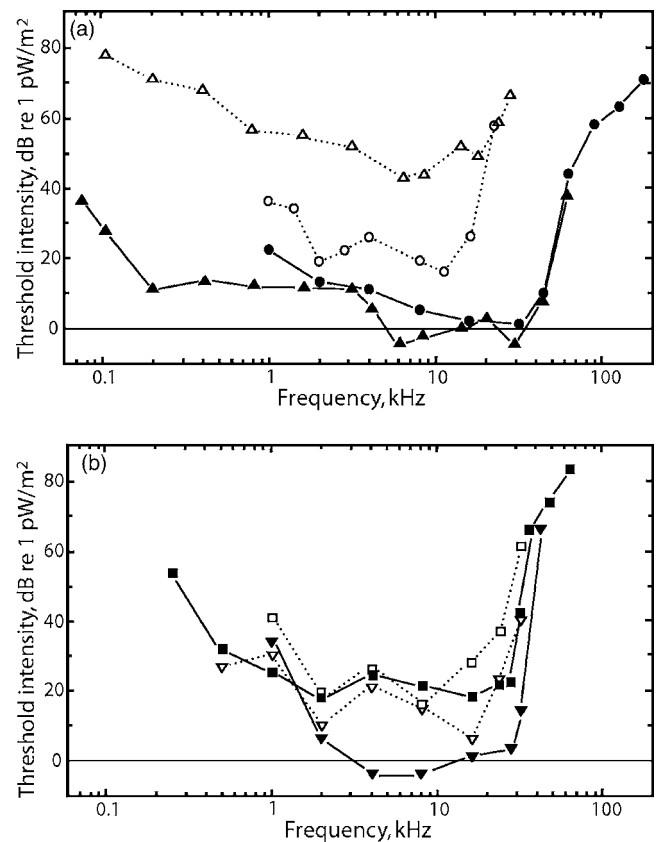


FIG. 1. Audiograms for phocids (a) and otariids (b). All threshold intensities are given in decibels relative to 1 pW/m², in order to compare thresholds in water and air. Open symbols in-air, filled symbols underwater. ○, ● *Phoca vitulina* (Ref. 1); △, ▲ *Mirounga angustirostris* (Ref. 23); □, ■ *Zalophus californianus* (Refs. 19 and 20); ▽, ▼ *Callorhinus ursinus* (Ref. 20, the values for Lori).

two media.^{1,11,23,28} All threshold intensities are given in decibels relative to 1 pW/m². In-air and underwater audiograms are shown for two phocids, *Phoca vitulina* (harbor seal) and *Mirounga angustirostris* (northern elephant seal) [Fig. 1(a)], and for two otariids, *Callorhinus ursinus* (northern fur seal) and *Zalophus californianus* (California sea lion) [Fig. 1(b)]. The high frequency hearing limits (HFHLs) of each pinniped in air and underwater are given in Table I; the HFHL is taken to be the frequency where the curve crosses the threshold of 60 dB at the high-frequency part of the curve.

The phocid underwater audiograms, with high sensitivities up to 50 kHz [Fig. 1(a)], are amply supported by similar audiograms for three other phocid species, the harp seal (*Pagophilus groenlandicus*), the ringed seal (*Pusa hispida*), and the grey seal (*Halichoerus grypus*).^{17,24,25} These species also have massive ossicles, the malleus+incus mass is ≈ 200 , 150 and 300 mg, respectively,¹⁸ similar to that of *Phoca vitulina* (164 mg, Table I). The harp seal shows a slight deviation from the other phocids; within the frequency range 16–32 kHz the hearing threshold in air remains constant, as opposed to the rising threshold in *Phoca* and *Mirounga*.²⁵ It is possible that in air the harp seal uses a somewhat different hearing mechanism than other phocids.

According to current understanding the middle ear remains air-filled when a seal is submerged just below the surface.^{11,12} This implies that in typical behavioral experiments where the animal's head is usually about 1 m below the water surface and the static pressure increase is approximately 10%, no radical changes in the cochlear physiology are to be expected. Thus the large difference between the phocid HFHL values in air and underwater [Fig. 1(a)] hardly reflect any cochlear changes but more likely differences between sound transmission in air and in water, and the different mechanisms by which these sound stimuli reach the cochlea. The inertia of the middle ear ossicles limits high-frequency hearing in air,^{5–8} but in water the bone conduction mechanism described above may stimulate the cochlea at higher frequencies. The effect of inertia thus explains the differences of HFHL values of phocids underwater and in air.

The otariid HFHL values in air and underwater are almost equal [Fig. 1(b)]. A parsimonious explanation for this is that in otariids the high-frequency hearing limit has a cochlear origin at sound frequencies around 35 kHz. This limit constrained by the cochlea is thus responsible for the final cutoff in air, and for a very sharp sensitivity cutoff underwater at about the same frequency. It is plausible that even in otariids the cochlea might be stimulated through bone conduction at higher frequencies, but according to the hypothesis presented above their cochlea is not evolutionarily adapted for high-frequency hearing in air or in water.

These pinniped results support the notion that both the middle ear and the inner ear contribute to the threshold rise toward high frequencies, the middle ear causing an inertial effect, mostly seen in phocids, and the inner ear producing an absolute cochlear cutoff, encountered in otariids. In terrestrial mammals, adapted to hearing in air, and whales, adapted to hearing underwater, the contributions of the middle and inner ear to the HFHL apparently overlap.^{9,26,28} Middle ear and inner ear have coevolved, and we cannot expect high

cochlear sensitivity to frequencies which cannot reach the inner ear.

If the middle ears of different mammals are isometric and certain other conditions are met, the HFHL values limited by inertia are inversely proportional to the cubic root of ossicle mass m .⁸ The middle ears of terrestrial mammals are approximately isometric, and indeed the experimental HFHL values as a function of $1/\sqrt[3]{m}$, where m is given in milligrams, follow approximately the line $f_H = 91 \text{ kHz}/\sqrt[3]{m}$.^{8,18} Table I shows the experimentally determined high-frequency hearing limits of seals in air (f_{Ha}) and the values calculated using the equation above (f_H). In *Phoca*, *Callorhinus*, and *Zalophus* f_{Ha} and f_H agree reasonably well, suggesting that the middle ears of these seals are functionally isometric with the middle ears of terrestrial mammals.^{8,18} The effect of inertia is also apparent in the otariid audiograms in air. The ossicles of *Zalophus* are heavier than those of *Callorhinus*, and indeed the threshold of *Zalophus* starts to rise at a lower frequency than the threshold of *Callorhinus*.

The experimental HFHL value of *Mirounga* in air, 24 kHz, is much higher than the value 8 kHz predicted on the basis of its heavy ossicles. However, the absolute sensitivity of *Mirounga* in air is poor, 27 dB lower than in *Phoca*, suggesting a functional difference between the hearing mechanisms of these species. Thus deviations from isometry and possible contributions from bone conduction may explain the exceptional HFHL of *Mirounga*.

It remains to be studied whether anatomical or functional differences exist in the inner ear of otariids and phocids. Our future work on pinnipeds will focus on the evolutionary aspects of the middle ear and hearing (in preparation).

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