

Audiograms of Whales and Dolphins: Effects of Ear Size and Predictions Based on a Middle Ear Model

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THE HEARING MECHANISM OF DOLPHINS

The hearing sensitivity of odontocetes is very high: the absolute threshold of hearing in the Bottlenose Dolphin, *Tursiops truncatus*, is c. 0.013 pW m⁻², about equal to the sensitivity of a sensitive domestic cat, one of the most sensitive terrestrial mammals. Three factors contribute to the high sensitivity of the cat. Firstly, the outer ear efficiently funnels sound energy from an optimum direction into the meatus and on to the tympanic membrane, thus amplifying sound intensity. Secondly, in the middle ear the vibration energy is transmitted from the large tympanic membrane to the small oval window of the inner ear, leading to additional intensity amplification. Moreover, the cat middle ear minimizes sound reflection by increasing pressure and decreasing particle velocity, matching the acoustic impedance of external air to that of the inner ear. Thirdly, the cat cochlea is very sensitive.

The cochlea of the Bottlenose Dolphin is apparently also very sensitive. However, even assuming that it is as sensitive as the cochlea of the cat, a large intensity amplification is needed. Anatomical, physiological and theoretical studies indicate that the lower jaw of the dolphin acts as a wave guide, focusing sound energy to the middle ear. This corresponds to the effect of the outer ear of the cat. However, in the dolphin as well as in cat the middle ear has to amplify intensity and bring about an acoustic matching between the external medium and the cochlea.

Two elastically coupled bones surround the air-filled middle ear cavity of the dolphin: the tympanicum facing the incoming sound and the perioticum enclosing the cochlea. These bones are detached from the skull and protected from vibrations by air cushions making echolocation possible. In our model (NUMMELA et al. 1999) the large and thin part of tympanicum, the tympanic plate, has taken over the sound-receptive role of the tympanic membrane. The sound wave entering in blubber causes vibration of the large tympanic plate, and the ossicular chain malleus-incus-stapes transmits the vibrational energy to the small oval window. Thus intensity is amplified, provided that the reflection of sound waves at the tympanic plate can be prevented.

In contrast to acoustic impedance matching between air and the cochlea in terrestrial mammals, matching between water and the cochlea calls for a large increase of the particle velocity. In fact, this increase should be somewhat larger than the pressure increase, because the specific acoustic impedance of the cochlea is smaller than the characteristic acoustic impedance of water and blubber. A rigid coupling of the large

tympanic plate to the small oval window would increase pressure but not particle velocity. Three middle ear structures may contribute to acoustic matching in dolphins: the lever action of the rotatory movement of the tympanic plate, the lever action of the rotatory movement of the malleus-incus complex, and damped resonance vibrations of the elastic couplings between the middle ear bones.

We have presented a quantitative mechanical model of the odontocete middle ear function (HEMILÄ et al. 1999). The bone masses, the areas of the tympanic plate and the oval window, and characteristic lengths of bones were determined from middle ear samples obtained from museums, while the elastic constants of the bone couplings were adjustable parameters of the model. Simulations carried out with this model predicted audiograms and absolute sensitivities in reasonably good agreement with published experimental audiograms of six odontocete species.

The suggested mechanism of odontocete hearing is firmly based on anatomical features of the dolphin head and middle ear, and the quantitative simulations demonstrate that the suggested mechanism can be sensitive enough and can bring about a correct frequency dependence. It should be understood that a model including several adjustable parameters is hypothetical and cannot present unique solutions. The model, however, represents a physically realistic possibility.

ISOMETRY OF MIDDLE EARS OF DIFFERENT DOLPHIN SPECIES

Let us assume that middle ears of different size are strictly isometric (have the same shape), that the threshold intensities of the cochleae are equal, and that the intensity amplifications occurring in the structures preceding the middle ear are equal. Then it may be shown that the absolute hearing thresholds of these ears are equal. Moreover, if frequencies are scaled according to ear size, the audiograms (sound pressure level at threshold versus log scaled frequency) have the same shape and overlap. Thus, a common audiogram based on scaled frequency can be constructed. The middle ears of different terrestrial mammals are fairly isometric and indeed the predictions based on isometry are approximately valid (NUMMELA 1997).

Odontocete middle ears are also fairly isometric. Thus we were able to construct an universal odontocete audiogram (HEMILÄ et al. 2001). The universal audiogram can be used to predict the audiogram of any odontocete, if the bone masses are known and the isometry holds. With reservations, this universal audiogram gives rough estimates also of mysticete audiograms.

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Originally the Killer Whale audiogram and the Harbour Porpoise audiogram did not fit the universal audiogram very well. However, new experimental audiograms (Killer Whale: SZYMANSKI et al. 1999, and Harbour Porpoise: KASTELEIN et al. 2002) fit our universal audiogram quite well. Thus, the high frequency hearing of the animals used in earlier studies may have suffered some damage.

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