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Whale Hearing Models
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SCIENTIFIC AND TECHNICAL OBJECTIVES

The specific objective of this project was to develop biophysically based models of the inner and middle ear of a range of marine mammals to allow us to estimate audiograms from anatomical and mechanical measurements.

This project was designed to provide modular data to be integrated with the methodologies and partnership projects developed under the ONR Effect of Sound in the Marine Environment (ESME) Program.

The effort involved an integration of anatomical and physiological data. Anatomical analyses (WHOI/D.R. Ketten) characterized head, middle, and inner ear structures of represenative odontocete species. Physiological Modeling (BU/ David Mountain) implemented auditory response models using the anatomical data. This is the requisite first-step towards developing species-specific TTS models.

ACCOMPLISHMENTS AND RESULTS

The accomplishments consist primarily of the following:

- Completion of scans for representative species of porpoises, dolphins, humpback whales, sea lions, and beaked whales **(Ketten et al. 2003; Ketten 2004; Norman et al 2005; Chadwick et al 2006)**
- Biochemical analyses of fatty tissues associated with the lower jaw and ear regions for harbour porpoises and two beaked whale species **(Koopman et al 2006)**
- Sound speed measures for harbour porpoises **(Prasad, 2004)**
- Middle ear stiffness measures in porpoiscs, dolphins, and one beaked whale species **(Mountain et al 2003; Miller et al 2006)**
- Comparisons of fresh, fixed and frozen tissues from two control species to determine fidelity of measures across species and fixation conditions **(Miller et al 2006)**

WHOI and BU teams worked jointly to identify anatomical features that have the best predictive value for acoustic responses; e.g., range and sensitivity, for both marine and land mammal ears. Species-specific databases were developed for heads, middle ears and inner ears to facilitate export to ESME modules and web-based distribution as well as additions and revisions of prior, limited data on cetaceans as more individual and species hearing data become available.

Data obtained by the WHOI group (Ketten Lab) were directed at developing appropriate protocols to provide consistent interspecies data sets and at obtaining, via these protocols, complete head and inner ear anatomical descriptors that could be used for finite element modeling transmission characteristics for underwater signals.

Complete data sets were obtained for whole heads and/or ears of harbour porpoises, bottlenosed dolphins, humpback whales, right whales, and and sea lions. CT and MRI images as well light and electron microscopic measures were completed for 1 or more specimens of each species.

In addition, measurements of the inner ears of chinchillas and cats were obtained in order to provide comparative data of the inner ear scalae, basilar membrane, and organ of Corti elements in common laboratory animals.

Sound speed measurements were obtained via Time of Flight techniques for excised tissues of harbour porpoises in a system designed by Dr. David Brown of U Mass at Dartmouth, Bioengineering Dept.

Beaked whale specimens in this project were also analyzed by Dr. Heather Koopman during her tenure as a postdoctoral fellow at WHOI to determine whether there are significant variations in the biochemical and structural features of jaw fats in beaked whales vs other odontocetes.

Physiological Modeling

The BU team (D. Mountain laboratory) was successful in obtaining direct stiffness measures of the middle ear from 2 species and demonstrated comparable measures of some inner and middle ear structures were possible from fresh, formalin fixed, and previously frozen material, which substantially broadens the potential data base of ears. The BU team also adapted existing procedure and hardware for exposure of the basilar membrane in the exceptionally large and dense odontocete periotics and for direct displacement and stiffness measures of both the middle and inner ear components in odontocetes comparable to those previously obtained in land mammals.

Middle Ear Anatomy

A number of different hypotheses have been put forth about how the cetacean middle ear might function but many lack biophysical plausibility. To take a fresh look at the middle ear anatomy in odontocetes, we used microCT scanner to scan ears from our two control species, harbor porpoise and bottlenose dolphin.

The major attachment points for the malleus-incus complex are the processus gracilis and the minor process of the incus. These points define the most likely axis of rotation for the malleus-incus complex. Since the processus gracilis is fused with the tympanic bone, it appears that this structure acts as a torsional spring which may help to stiffen the middle ear. Although the shapes of the incus and malleus differ considerably from terrestrial mammals, this arrangement of the incus and malleus is very similar to that found in high-frequency terrestrial mammals.

The dolphin stapes is attached to the major process of the incus which acts as a lever arm. The tympanic ligament attaches to a longer lever arm on the malleus. The tensor tympani muscle attaches to the same point, but from the opposite side, and is oriented so as to pull on the tympanic ligament when it contracts. This orientation of the tensor tympani with respect to the tympanic ligament is the same as that found in terrestrial mammals. The stapedial muscle is oriented at right angles to the motion of the stapes which is also the same orientation as that found in terrestrial mammals. Our anatomical studies provide further support for the hypothesis that the cetacean middle ear works in a fashion very similar to that of high-frequency terrestrial mammals and that the tympanic ligament plays a major role in producing middle ear motion in response to sound.

The fact that the odontocete middle ear appears to function in a manner similar to that found in terrestrial mammals means that generic biophysical models of middle ear function can be used to predict middle ear function in cetaceans and get an estimate of low-frequency hearing sensitivity through simple measurements of middle ear stiffness.

.Middle ear measures that were completed in this grant employed a piezoelectric actuator that produces a sinusoidal displacement of the stapes. The force sensor measures the stapes force and stiffness is computed by taking the ratio of force to stiffness. The low-frequency cutoff of the audiogram is a power function of middle-ear acoustic stiffness in terrestrial mammals. Odontocetes follow the general mammalian trend for high frequency species; the middle-ear acoustic stiffness for bottlenose dolphin and for harbor porpoise is close to the regression line for terrestrial mammals. This suggests to us that the cetacean middle ear functions in a manner similar to that of other mammals

Basilar Membrane Mechanics

The range of hearing in mammals and especially the high-frequency limit is believed to be determined by the basilar membrane frequency-place map. In terrestrial mammals, the basilar membrane near the base of the cochlea is much stiffer than it is near the cochlear apex. As a result, the basal portion of the membrane responds best to high frequencies and the apical portion of the membrane responds best to low frequencies.

To measure basilar membrane stiffness in cetaceans, we have used a force probe that is similar in concept to that used for the middle ear measurements but which is much more sensitive. The dolphin stiffness gradient is very similar to that for gerbil but exhibits a higher stiffness. If basilar membrane mechanics in the two species are similar, the higher stiffness for dolphin is to be expected since the high-frequency limit for the bottlenose dolphin is about 2.5 times that for gerbil.

Von Bekesy (1960) published data for basilar membrane volume compliance from a number of different species. In Figure 5 we have converted our gerbil and dolphin stiffness data into volume compliance and plotted our data along with the von Bekesy data. All of the species show similar compliance gradients and the dolphin curve exhibits the lowest compliance (highest stiffness) as would be expected for a high frequency ear.

IMPACT/APPLICATIONS

Our mechanical and anatomical measurements in control species support the hypothesis that the cetacean middle ear and cochlea function in a manner very similar to that of terrestrial mammals. This means that the computational models that we have developed to predict hearing function in terrestrial mammals can be extended directly to cetaceans. Our next step is to extend the middle ear and cochlear measurements to species of special concern (c.g. beaked whales) and to use our computational models to predict audiograms for these species.

National Security

These data will assist in designing effective noise mitigation measures and may be useful in determining the mechanisms involved in beaked whale strandings in association with naval exercises.

Quality of Life

This research is a requisite step in determining how to avoid or ameliorate potential sound impacts from human generated noise, intentional as in sonar or seismic explorations, or auxillary as from ship generated noise, in our oceans.

Science Education and Communication

Both laboratories involved in this effort began development of web-accessible data bases and publicly accessible representative samples of this work.

The WHOI laboratory is developing a website featuring CT images and reconstructions for representative marine mammal species and can incorporate any new whale data that are releasable to the public. The scan data are archived in multi-platform compatible DICOM formats for broad application..

BU has already begun producing a web-site for review of available audiograms as part of their on-going EarLab project and has the infrastructure to extend their site to incorporate the inner ear models as a step towards a manageable, ESME-compatible model that can be run from the website that includes marine species for which there are reliable hearing data as well as sample sources with appropriate distance effects in their renditions, including biologic, commercial, exploratory, and military sources. The databases are expected to be open architecture and structured for ease of export and cross-application access

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Not applicable

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14. ABSTRACT
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