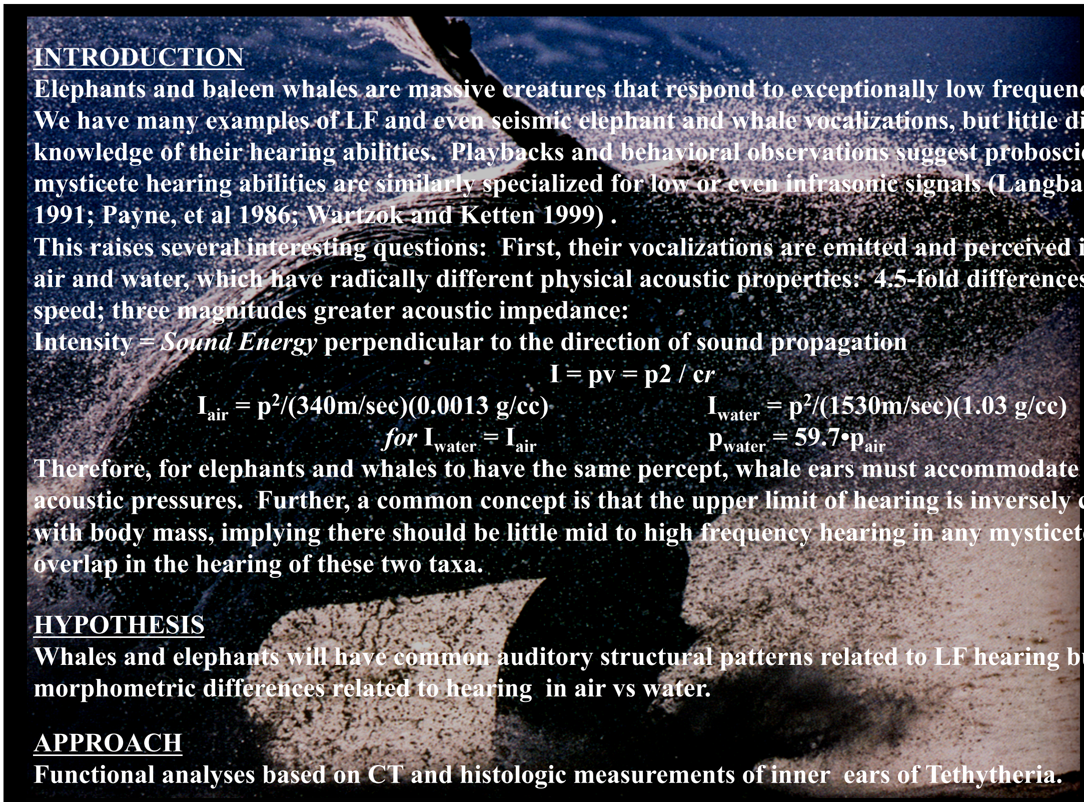


INTRODUCTION

Elephants and baleen whales are massive creatures that respond to exceptionally low frequency signals. We have many examples of LF and even seismic elephant and whale vocalizations, but little direct knowledge of their hearing abilities. Playbacks and behavioral observations suggest proboscidean and mysticete hearing abilities are similarly specialized for low or even infrasonic signals (Langbauer, et al 1991; Payne, et al 1986; Wartzok and Ketten 1999) .

This raises several interesting questions: First, their vocalizations are emitted and perceived in two media, air and water, which have radically different physical acoustic properties: 4.5-fold differences in sound speed; three magnitudes greater acoustic impedance:

Intensity = *Sound Energy* perpendicular to the direction of sound propagation

$$I = pv = p2 / cr$$

$$I_{air} = p^2/(340 m/sec)(0.0013 g/cc) \qquad I_{water} = p^2/(1530 m/sec)(1.03 g/cc)$$

$$\textit{for } I_{water} = I_{air} \qquad p_{water} = 59.7 \cdot p_{air}$$

Therefore, for elephants and whales to have the same percept, whale ears must accommodate 60-fold acoustic pressures. Further, a common concept is that the upper limit of hearing is inversely correlated with body mass, implying there should be little mid to high frequency hearing in any mysticete and little overlap in the hearing of these two taxa.

HYPOTHESIS

Whales and elephants will have common auditory structural patterns related to LF hearing but morphometric differences related to hearing in air vs water.

APPROACH

Functional analyses based on CT and histologic measurements of inner ears of Tethytheria.

MATERIALS & METHODS

PROBOSCIDAE (7)

Loxodonta africana (African)	3 CT / 2 histology
Elephas maximus (Asian)	4 CT / 2 histology

MYSTICETI (23)

Megaptera novaeanglia (Humpback)	6 CT / 1 histology
Balaenoptera musculus (Blue)	2 CT / 1 histology
Eschrichtius robustus (Grey)	2 CT / 1 histology
Eubalaena glacialis (Right)	5 CT / 2 histology
Balaenoptera acutorostrata (Minke)	6 CT / 1 histology
Balaenoptera physalus (Finback)	2 CT / 0 histology

IMAGING

WHOI CT FACILITY http://csi.whoi.edu

Specimens scanned on Siemens Volume Zoom as whole animals, heads, and intact temporal bones

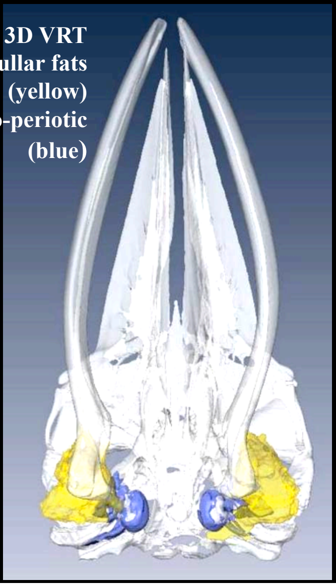
- spiral UHR submillimeter imaging
- 0.5 mm/sec acquisitions amd collimation
- UHR 90 (bone) to 40 (soft tissue) kernels
- 0.1 mm slice images
- 100 µ isotropic voxels

2D to 3D CT IMAGING, RECONSTRUCTION, AND MEASUREMENT (Siemens SSD -VRT, Amira)

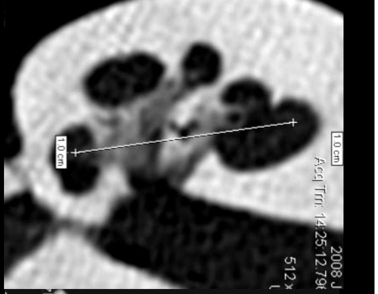
Representative CT Scan Series for 56 cm diameter, 120 cm length intact minke whale head

2D coronal CT

3D VRT peribullar fats (yellow) tympano-periotic (blue)



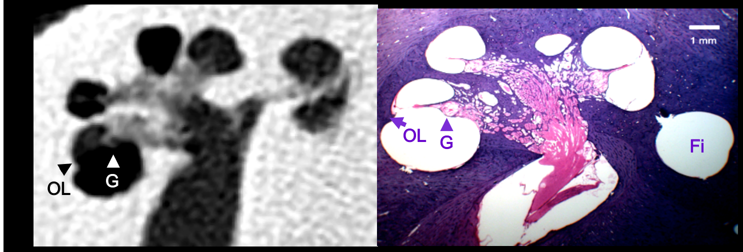
0.1 mm 2D modiolar section of cochlea



3D orthogonal view of inner ear canals

CT vs HISTOLOGY

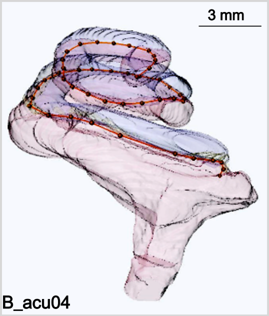
100 micron paramodiolar CT sections, 20-30 micron celloidin sections, hematoxylin-eosin stain

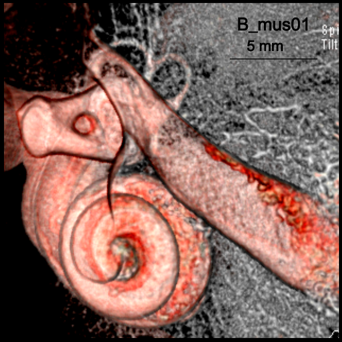


100 µ paramodiolar CT image (left) vs 25 µ celloidin H&E stained section (right) from the same minke whale ear. Cochlear canal dimensions are obtained from both. Histology is used for all basilar membrane measurements. Some micro-features; e.g., ganglion cell regions (G), and outer osseous lamina (OL) are visible and comparable in both the UHRCT and histology. A fiducial (Fi) marker necessary for accurate alignment of celloidin sections that is not required for 3D CT is also shown.

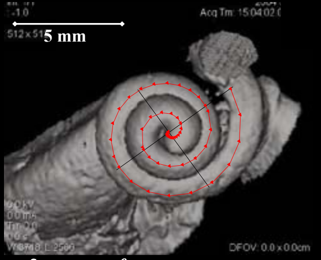
Cochlear Radii, Lengths, Basilar Membrane Morphometry, and Frequency Calculations (methods Ketten et al, 1998)

Multi-tissue segmentations from CT are compared with reconstructions from histology to determine shrinkage or distortion and verify calculations. The circles and subtended line represent basilar membrane positions .





Orthogonal projections are used for radii and length



Chadwick et al 2005

$$s=\int_{\theta_1}^{\theta_n}\sqrt{r^2+\left(\frac{dr}{d\theta}\right)^2}d\theta$$

and

$$z=\sqrt{s^2+h^2}$$

for $r=e^{a\theta}$

$$s=(r/a)\sqrt{1+a^2}$$

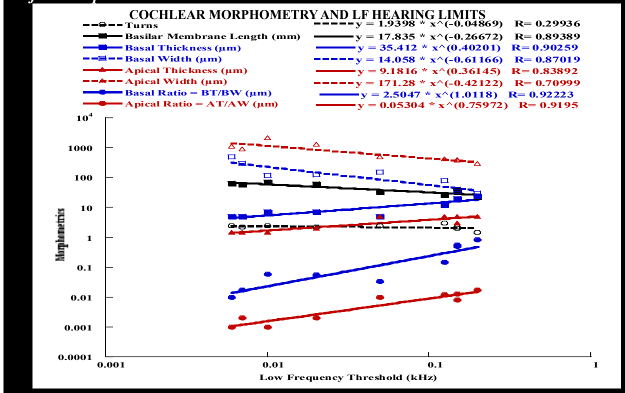
for $r=a\Theta$

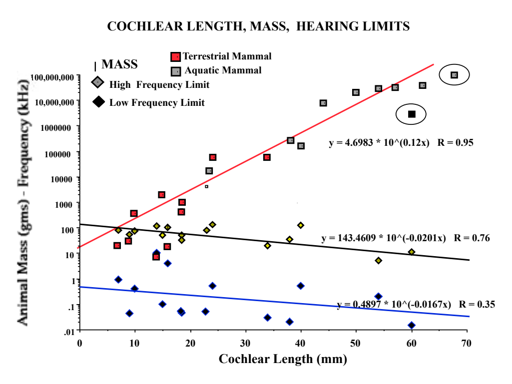
$$s=(a/2)\left[\Theta\sqrt{\Theta^2+1}+\mathrm{Ln}\left(\Theta+\sqrt{\Theta^2+1}\right)\right]$$

RESULTS

MAMMALIAN COCHLEAR MORPHOMETRY (Firbas 1972; West 1985; Echteler et al. 1994; Ketten 2000)

Species	Common Name	Hearing range (kHz)	Turns	Membrane Length (mm)	Basal Thickness (µm)	Basal Width (µm)	Apical Thickness (µm)	Apical Width (µm)
Phocoena phocoena	Harbor porpoise	0.3 - 180	1.5	22.5	25	30	5	290
Lagenorhynchus obliquidens	White-sided dolphin	0.2 - 140	2.0	33.8	20	40	3	400
Tursiops truncatus	Bottlenosed dolphin	0.2 - 160	2.25	38.9	20	35	5	380
Balaenoptera musculus	Blue whale	0.01 - 18	2.5	72.3	7	120	<2	2200
Megaptera novaeangliae	Humpback whale	0.02 - 30	2.25	61.65	7	125	2	1,300
Loxodonta africana	African elephant	0.006 - 8	2.5	65.1	5	500	2	>1100
Elephas maximus	Asian elephant	0.007 - 9	2.25	57.4	-	>300	-	>900
Felis domesticus	Cat	0.125 - 60	3.0	25.8	12	80	5	420
Homo sapiens	Human	0.05 - 16	2.5	33.5	5	150	5	504
Spalax ehrenbergi	Mole rat	0.1 - 10	3.5	13.7	9	120	18	200
Pteronotus parnellii	Mustached bat	16 - 110	2.75	14.3	22	50	2	110
Rhinolophus ferrumequinum	Horseshoe bat	7 - 90	3.25	16.1	35	80	2	150





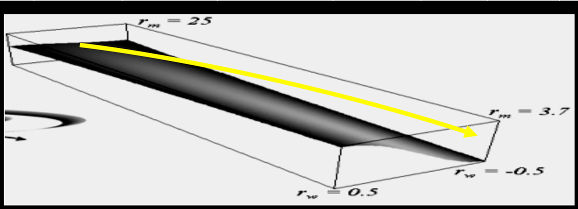
Both whales and elephants have generalist ear formats. Cochlear length is correlated with mass but is not significantly correlated with high or low frequency hearing limits. The most significant correlations for LF and HF limits of hearing are the thickness to width ratios of the basilar membrane.

Functional Effect: “Whispering Gallery” Propagation (Manoussaki et al, 2008)

Broader basal curvatures and greater radii provide better propagation of LF energy to the cochlear spiral apex

Radii ratios and low-frequency threshold.

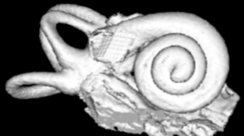
Species	blue whale	right whale	humpback whale	bottlenose dolphin		harbor porpoise	
R_{max}/R_{min}	10.7	9.1	8.1	4.4		3.5	
LF Hz	12	15	18	150		180	
Species	african elephant	asian elephant	cow	guinea pig	man	rat	mouse
R_{max}/R_{min}	9	8.7	7.5	7.4	7	4.3	4
LF Hz	6	7	20	40	50	400	800



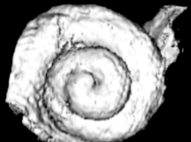
Implications: Parallel Cross-Media Strategies for LF Hearing

Megaptera novaeangliae

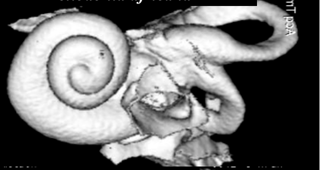
Elephas maximus



Gomphothere



Loxodonta africana

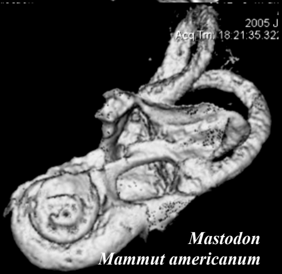


10 mm

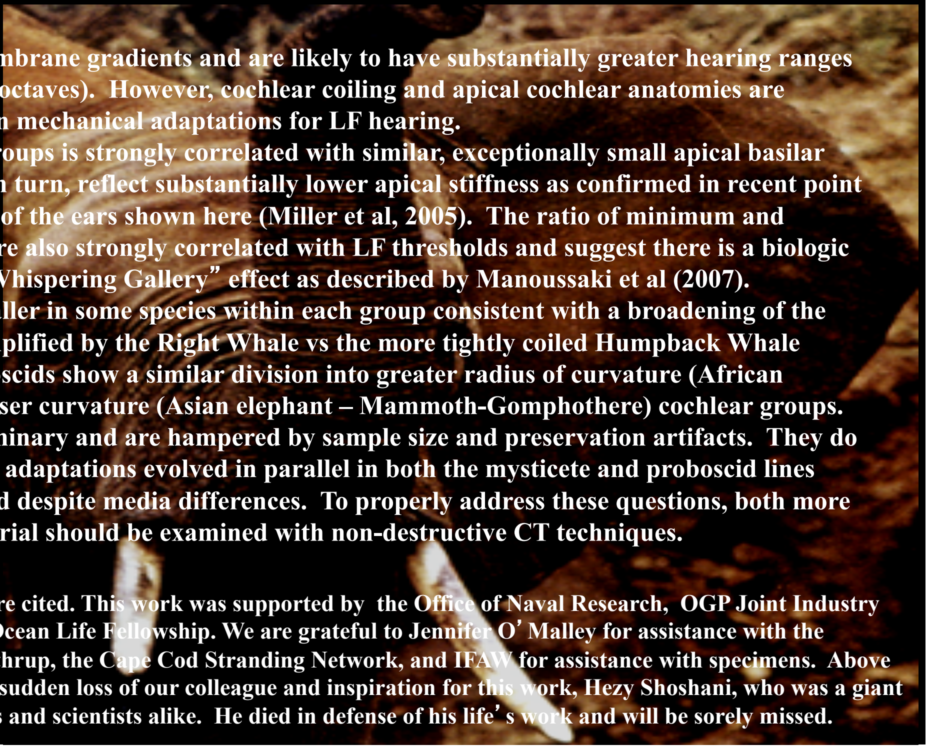
Balaenoptera musculus

Eubalaena glacialis

Mammoth
Mammuthus primigenius



Mastodon
Mammut americanum



CONCLUSIONS

Mysticetes have larger membrane gradients and are likely to have substantially greater hearing ranges than elephants (~10 vs 6-8 octaves). However, cochlear coiling and apical cochlear anatomies are similar, suggesting common mechanical adaptations for LF hearing.

LF sensitivity in both groups is strongly correlated with similar, exceptionally small apical basilar membrane ratios, which, in turn, reflect substantially lower apical stiffness as confirmed in recent point stiffness measures of some of the ears shown here (Miller et al, 2005). The ratio of minimum and maximum cochlear radii are also strongly correlated with LF thresholds and suggest there is a biologic equivalent of the classic “Whispering Gallery” effect as described by Manoussaki et al (2007).

The radii ratios are smaller in some species within each group consistent with a broadening of the basalmost regions, as exemplified by the Right Whale vs the more tightly coiled Humpback Whale shown above. Fossil proboscids show a similar division into greater radius of curvature (African elephant -Mastodon) vs lesser curvature (Asian elephant – Mammoth-Gomphothere) cochlear groups.

These results are preliminary and are hampered by sample size and preservation artifacts. They do suggest that low frequency adaptations evolved in parallel in both the mysticete and proboscid lines over similar time scales and despite media differences. To properly address these questions, both more fossil and rare extant material should be examined with non-destructive CT techniques.

ACKNOWLEDGEMENTS

Please see abstract for literature cited. This work was supported by the Office of Naval Research, OGP Joint Industry Program, NIH, and a WHOI Ocean Life Fellowship. We are grateful to Jennifer O’ Malley for assistance with the histology and to Clarinda Northrup, the Cape Cod Stranding Network, and IFAW for assistance with specimens. Above all, we mourn the terrible and sudden loss of our colleague and inspiration for this work, Hezy Shoshani, who was a giant amongst his beloved leviathans and scientists alike. He died in defense of his life’ s work and will be sorely missed.