Biomechanical Evidence of Low to Infrasonic Hearing in Mysticetes: Implications for Impacts

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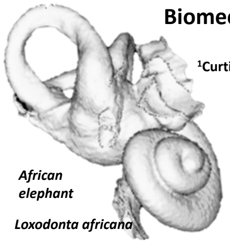
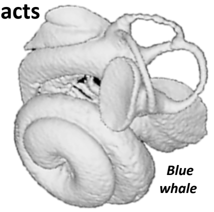


African elephant

Loxodonta africana



Blue whale

Balaenoptera musculus

INTRODUCTION

Knowing the hearing sensitivities of marine mammals is fundamental to mitigating noise impacts. There are no direct hearing measures for any mysticete. Vocalization data suggest they have acute low and infrasonic (LF/IF) hearing and may be especially sensitive to anthropogenic sources. To address this issue, we analyzed the anatomy and material properties of dolphin, whale, and land mammal ears to determine whether mysticetes, like elephants, have ears specialized for IF/LF hearing.

HYPOTHESIS

We hypothesize that IF and LF hearing abilities require cochlear biomechanical specializations that improve IF/LF reception and transduction.

METHODS

Siemens Volume Zoom UHRCT and X-Tec MicroCT: 12-100 μ isotropic voxel imaging; H&E and TEM histology; stiffness measures via nanoindentation (Zosuls et al 2012). Cochlear lengths, radii, and basilar membrane dimensions were obtained from 3D orthogonal projections and radial resections.

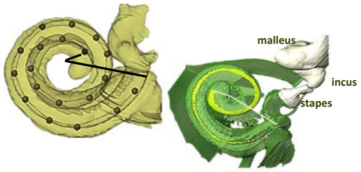
SPECIMENS: CT 30 Histology 18

PROBOSCIDAE

- *Loxodonta africana* (African) 3
- *Elephas maximus* (Asian) 1

CETACEA

- *Balaenoptera musculus* (Blue whale) 3
- *Balaenoptera physalus* (Fin whale) 1
- *Eubalaena glacialis* (Right whale) 3
- *Megaptera novaeanglia* (Humpback) 6
- *Balaenoptera acutorostrata* (Minke) 3
- *Phocoena phocoena* (porpoise) 5
- *Tursiops truncatus* (dolphin) 5



Minke whale (45.6 mm) and porpoise (22.5 mm) microCT showing basilar membrane paths and radii.

Equiangular vs Archimedean Cochlear Spirals

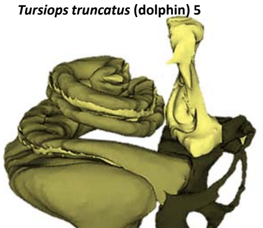
(Ketten 1985, Ketten et al. 1998)

$$r = a\theta$$

$$s = \left(\frac{a}{2}\right)\left[\theta\sqrt{\theta^2+1} + Ln\left(\theta + \sqrt{\theta^2+1}\right)\right]$$

$$r = e^{a\theta} \qquad s = \left(\frac{r}{a}\right)\sqrt{1+a^2}$$

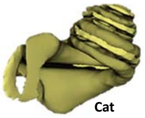
$$s = \int_{\theta_1}^{\theta_n}\sqrt{r^2 + \left(\frac{dr}{d\theta}\right)^2}\,d\theta \qquad z = \sqrt{s^2+h^2}$$



Grey Whale
60.2 mm

Harbour Porpoise
24.2 mm

Chinchilla
18.5 mm

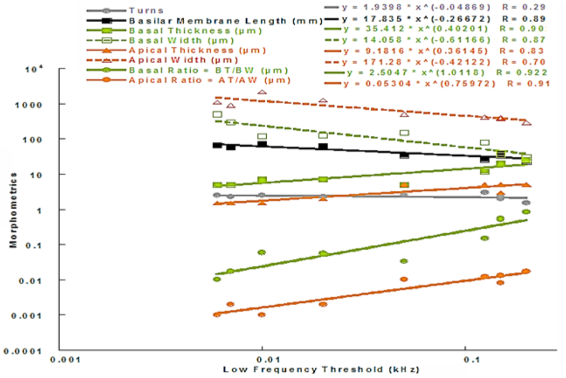


Cat
25.8 mm

Cochlear Morphometry: Cetaceans and Terrestrial Mammals

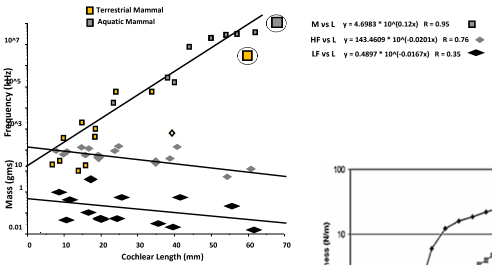
Species	Kg	Khz	Turns	BM (mm)	Base (t/w)	Apex (t/w)	Radii Ratio	LF Limit (Hz)
Porpoise	50	0.35-180	1.5	22.5	0.833	0.0172	4.3	250
Dolphin	155	0.15-160	2.25	39.24	0.714	0.0132	4.9	150
Minke whale	8,000	0.02-35	2.25	46.86	-	-	7.2	30*
Blue whale	100,869	0.01-18	2.25	72.3	0.058	0.0009	10.5	12*
Fin whale	-	0.01-0.75	2.5	64.7	0.050	0.0010	9.8	14*
Right whale	31,837	0.016-25	2.5	56.18	0.056	0.0017	9.2	9.2*
Humpback	30,000	0.018-30	2.0	59.61	0.056	0.0019	8.2	18*
Cow	500	0.14-22	3.5	38.0	-	-	7.5	29
Guinea pig	0.5	0.2-45	4.25	18.5	0.106	0.0082	7.4	40
Asian elephant	4,000	0.1-5.7	2.25	57.4	0.016	0.0017	8.7	16*
African elephant	7,000	0.01->8	2.5	65.1	0.01	0.0014	9.0	10*
Cat	3.0	0.125-70	3.0	25.8	0.150	0.0119	5.7	60
Human	75	0.05-16	2.5	34.78	-	-	7.0	30
Mouse	0.01	5-60	2.0	6.8	0.363	0.0063	4.0	1200
Rat	0.2	1-59	2.2	10.7	0.300	0.0106	4.3	400
Mustached Bat	0.012	25-115	-	14.3	0.440	0.022	4.0	25K
Horseshoe bat	0.018	30-90	3.25	16.1	0.388	0.0133	3.9	30K

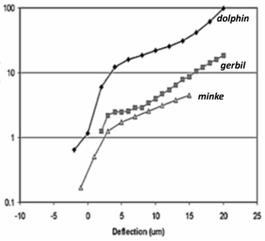
* Vocalization data

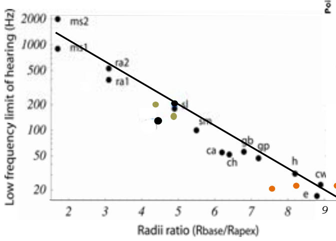


RESULTS

The analyses demonstrate 3 specializations in mysticetes vs. MF/HF adapted mammals: magnitude lower basilar membrane apical ratios (0.0014 vs. 0.015); membrane stiffness two magnitudes less; and cochlear radii ratios >8. Basilar membrane ratios correlate with stiffness. Basal:Apical radii ratios correlate with LF hearing limits. Cochlear length correlates with body mass, not HF or LF hearing limits.





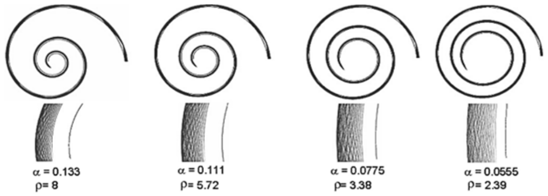


R=0.979, *P<0.001*

$$\left[f = 1354\exp[-0.609(R_{max}/R_{min} - 1)]\right]$$

DISCUSSION

Given Energy density is the product of pressure and velocity: $E_0 = PV_0$
Energy focusing is greatest at the apex where radius of curvature ratio differential is largest (Manoussaki et al. 2008):



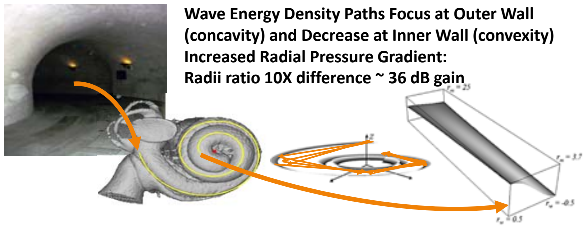
$$R(\theta) = Exp(-\alpha\vartheta)$$

Energy density focusing at the outer wall increases BM displacement, creating radial tilt T that increases base to apex, proportional to the difference in displacement between inner and outer walls/BM width at point x:

$$\frac{T_{apex} - T_{base}}{T_{base}} \approx \frac{\Lambda^{7/2}\rho}{W^2}\left(1 + \frac{w_{bm}^{\;2}}{10R_m^{\;2}}\right)_{apex} - 1$$

$$W = w_{base}/w_{apex} \qquad \Lambda = \lambda_{base}/\lambda_{apex}$$

$$\rho = R_{base}/R_{apex} \qquad R_m = x_{radiusbm}$$



Wave Energy Density Paths Focus at Outer Wall (concavity) and Decrease at Inner Wall (convexity)
Increased Radial Pressure Gradient:
Radii ratio 10X difference ~ 36 dB gain

LF "Whispering Gallery" Acoustic Energy Propagation (Manoussaki et al. 2008)

Mysticete basilar membrane ratios correlate with decreased apical stiffness and is consistent with better LF frequency response. Spirals with large radii ratios improve redistribution of LF wave energy towards the lateral wall, a biologic equivalent of a Whispering Gallery, that enhances intracochlear LF propagation. By contrast, odontocete cochleae approximate Archimedean spirals, tightly curved, with maximum radii ratios <5 and a double curved basal hook that may minimize LF energy transfer to the inner ear.

CONCLUSIONS

I. Spiral radii ratios predict low-frequency hearing thresholds in all mammals.
II. Increased basal radius of curvature is an adaptive feature for intracochlear LF energy density distribution.
III. HF cetaceans developed narrow radii and added unique basal arcs that minimize LF propagation

Implications for LF Impacts: HF and UHF marine mammal species' auditory responses may not be representative of sound impacts in IF/LF adapted ears.

This work was supported by ONR and LMRS. References: http://csi.whoi.edu