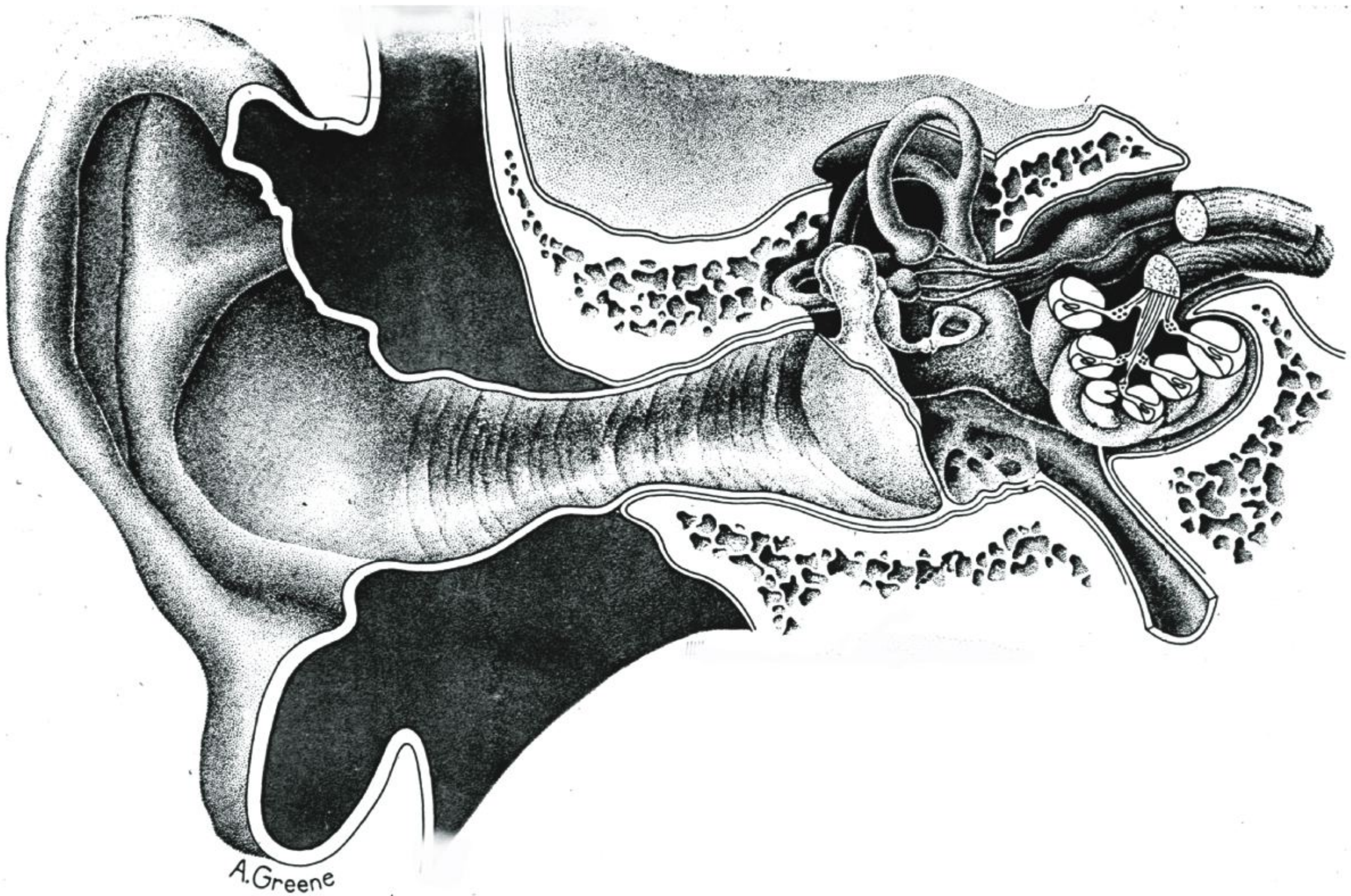
Slow to hear: Traveling waves on the eardrum

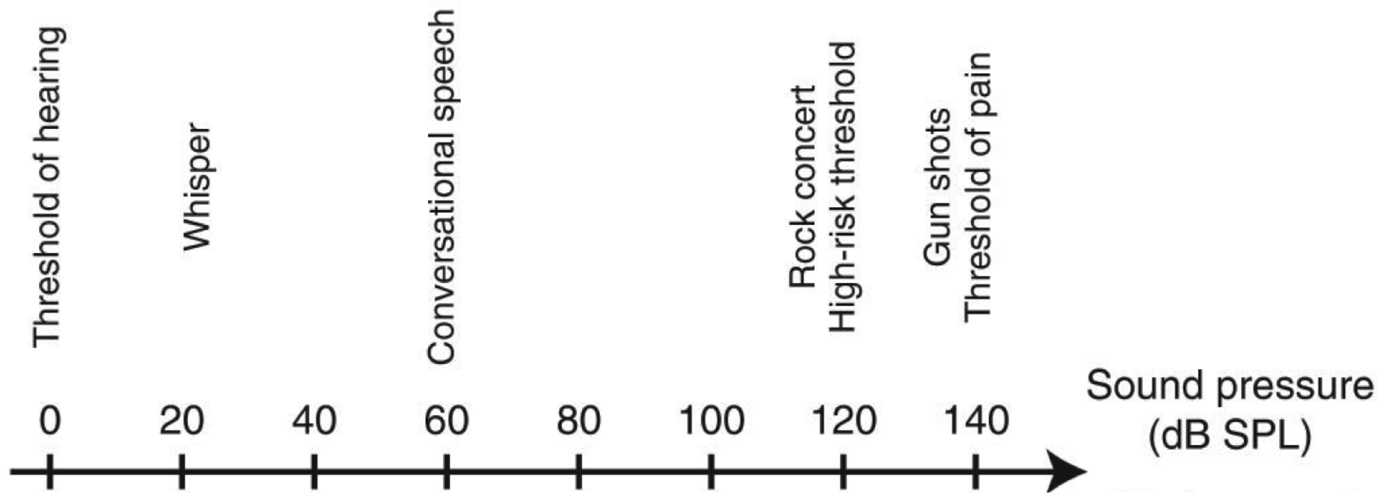
Christopher Bergevin (York University)
Sebastiaan Meenderink (University of California, Los Angeles)
Marcel van der Heijden (Erasmus MC, Netherlands)
Peter Narins (University of California, Los Angeles)

CAP 2014



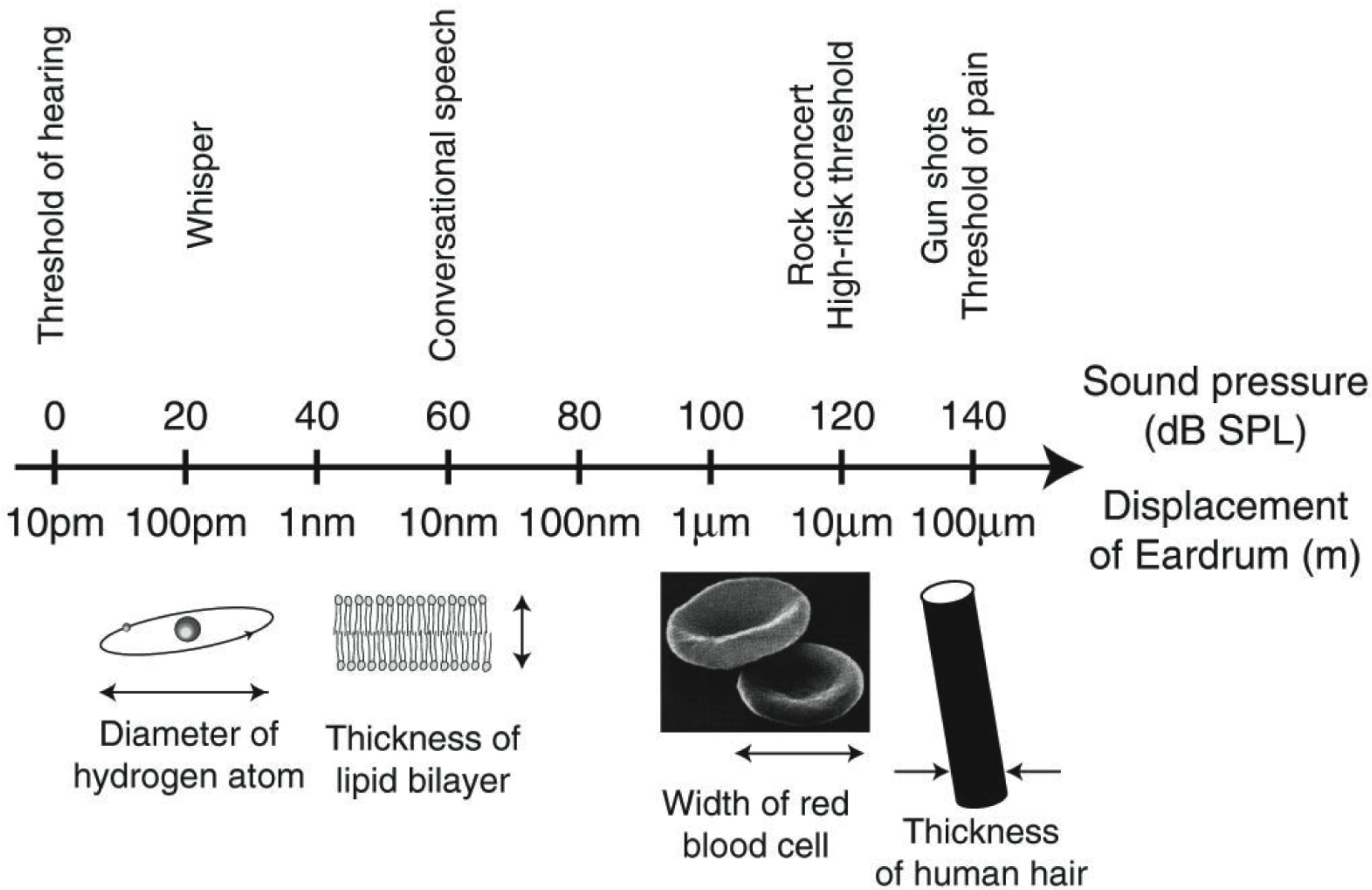
Dynamic Range

Humans hear over a pressure range of 120 dB [that's a factor of a *million*]



Dynamic Range

Humans hear over a pressure range of 120 dB [that’s a factor of a *million*]



D. Freeman

→ Ear actually **EMITS** sound!

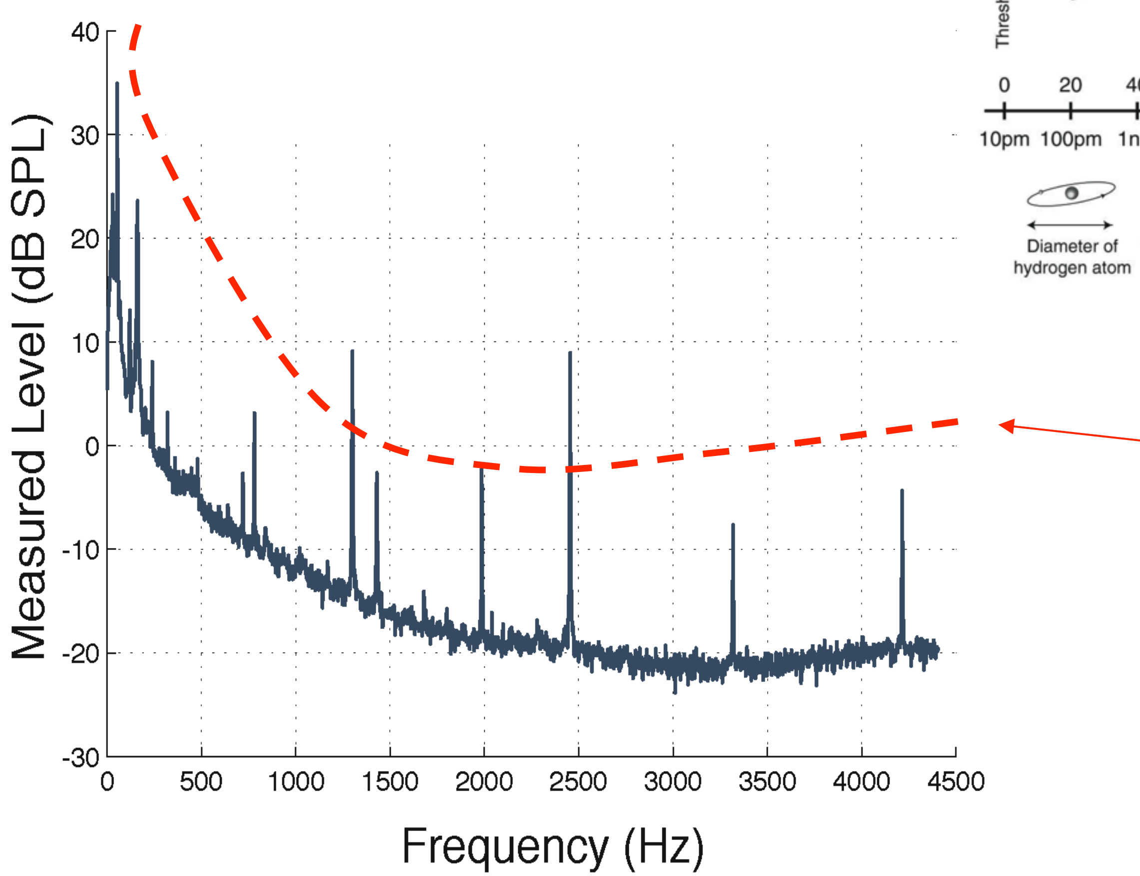
Otoacoustic Emissions – OAEs

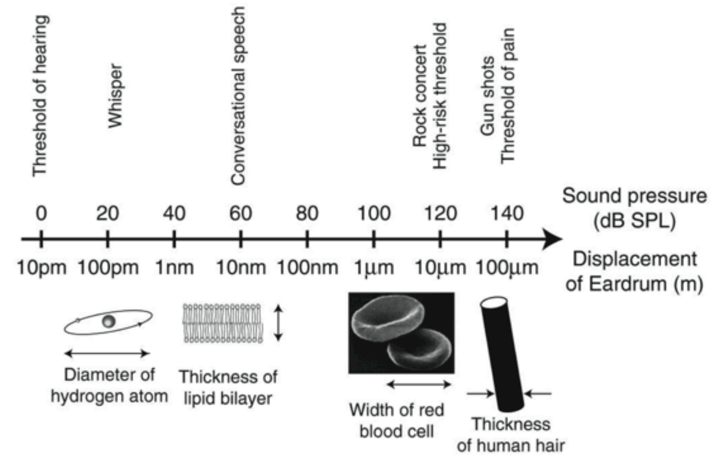
http://www6.miami.edu/UMH/CDA/UMH_Main/

➢ OAEs used for newborn hearing screening (only healthy ears emit)

➢ Much faster/easier than evoked potentials (i.e., Auditory Brainstem Response, ABR)

<u>Otoacoustic Emissions</u> (OAEs)





D. Freeman

- OAEs apparently a byproduct of the *amplification* mechanism
- Provide means to non-invasively probe inner ear

<u>Evoked OAEs & Delays</u>

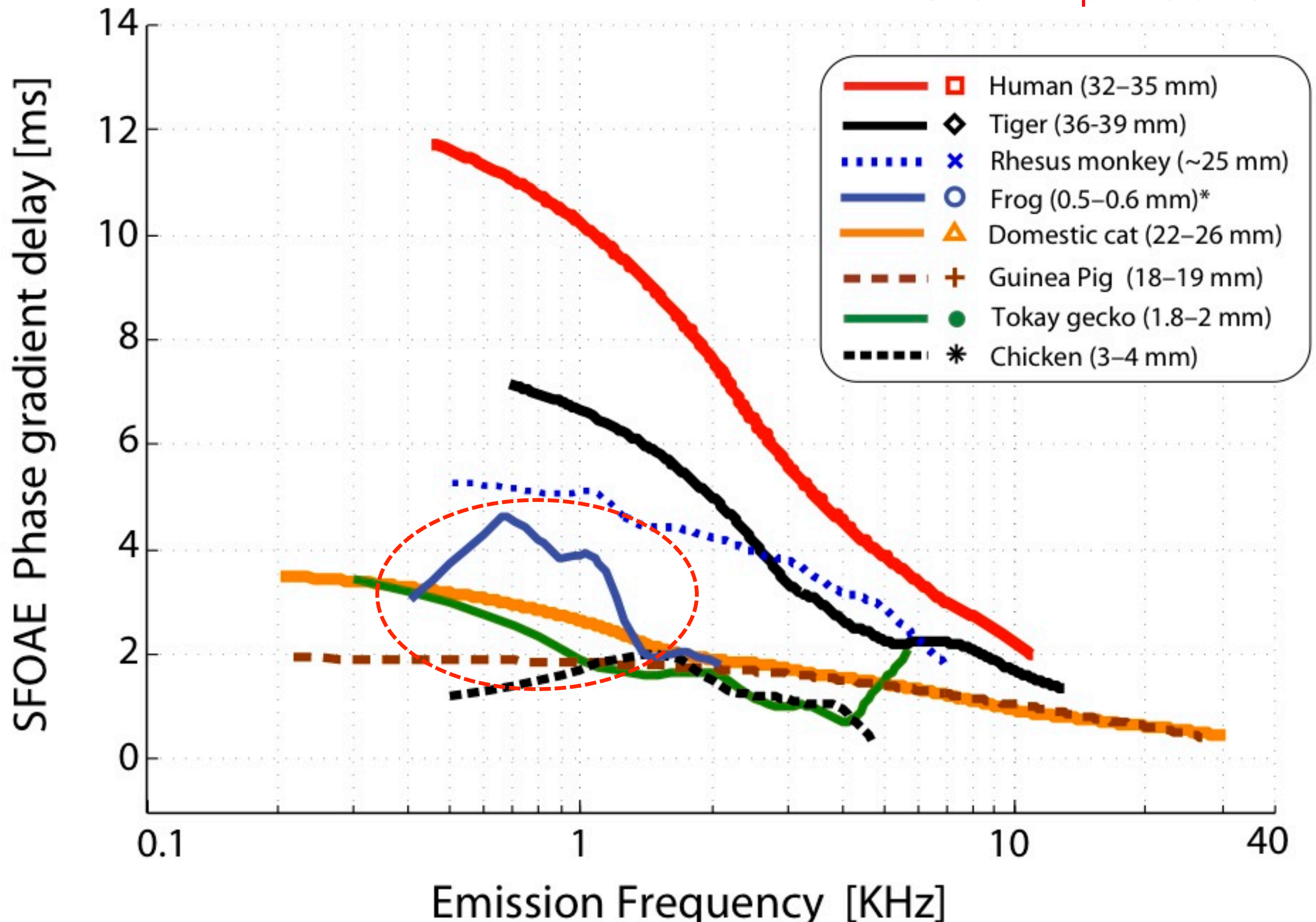
- Stimulate with single tone ('**S**timulus **F**requency') and an 'echo' returns (SFOAE)

- Delay of echo varies across species

- Delay tied to tuning
(i.e., resonant filter build-up)

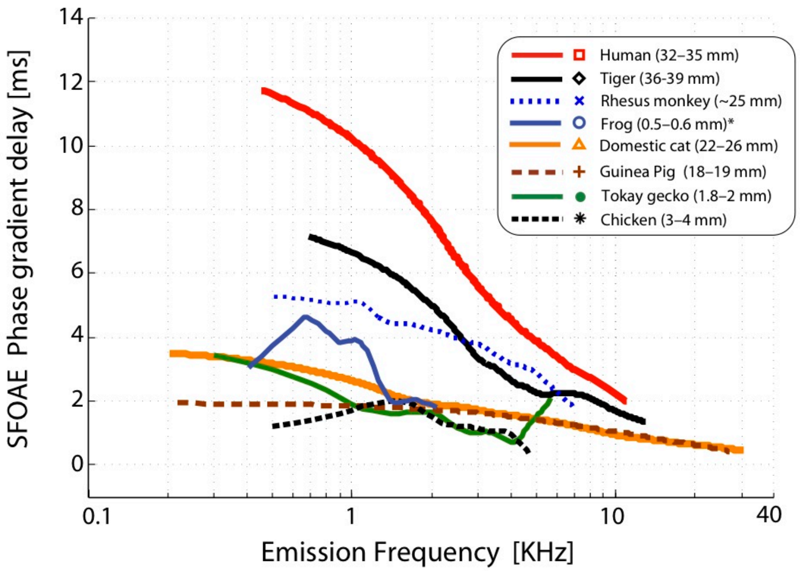
- Frog delays appears exceptional...

SFOAE: Lp = 40 dB SPL

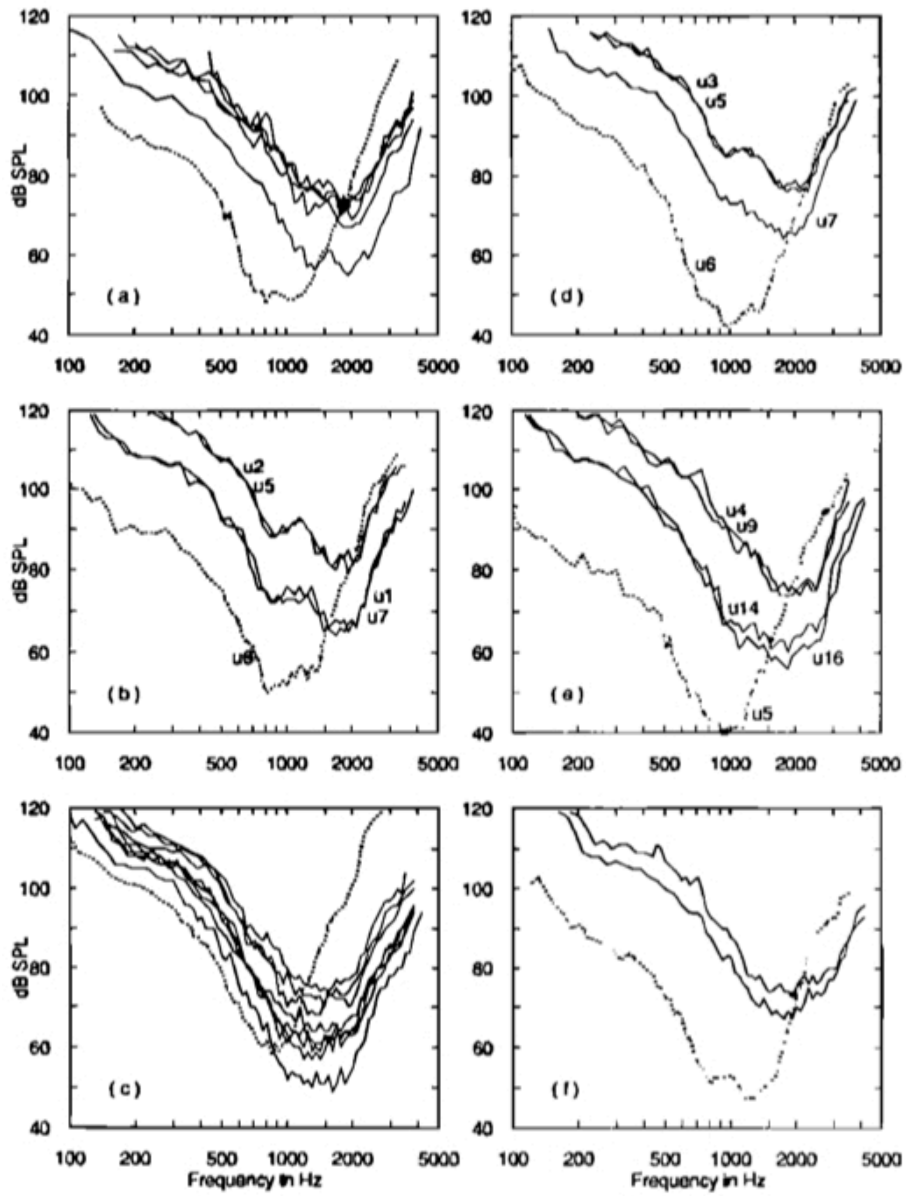


Shera & Guinan (2003)
Bergevin et al. (2008)
Joris et al. (2011)
Bergevin et al. (2011)

Frog Auditory Neurophysiology



Single-unit auditory nerve fiber tuning curves



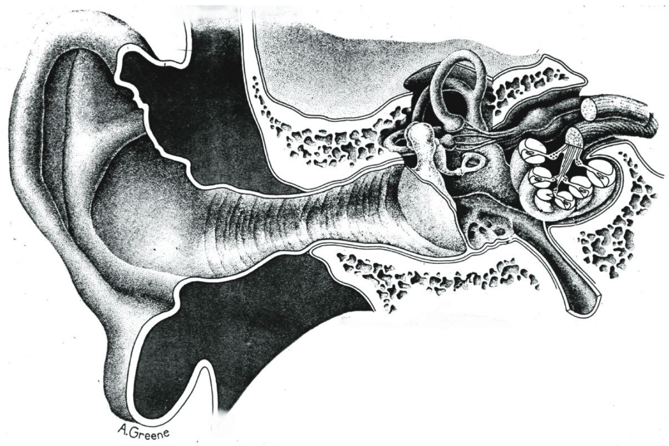
- Despite long SFOAE delays, frog neural tuning is relatively broad

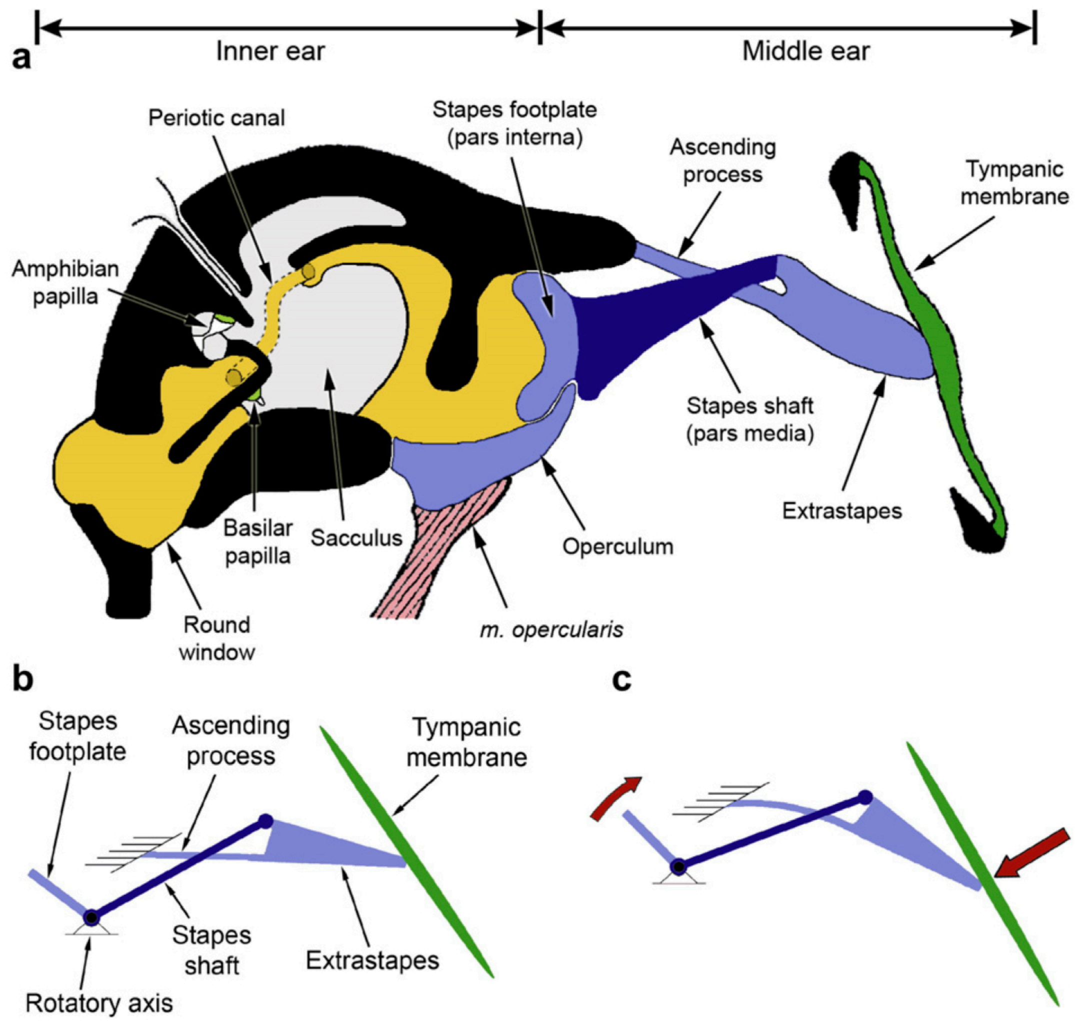
So where is the delay coming from in frogs?

Ronken (1991)

Artistic inspirations....

Amphibian Middle Ear

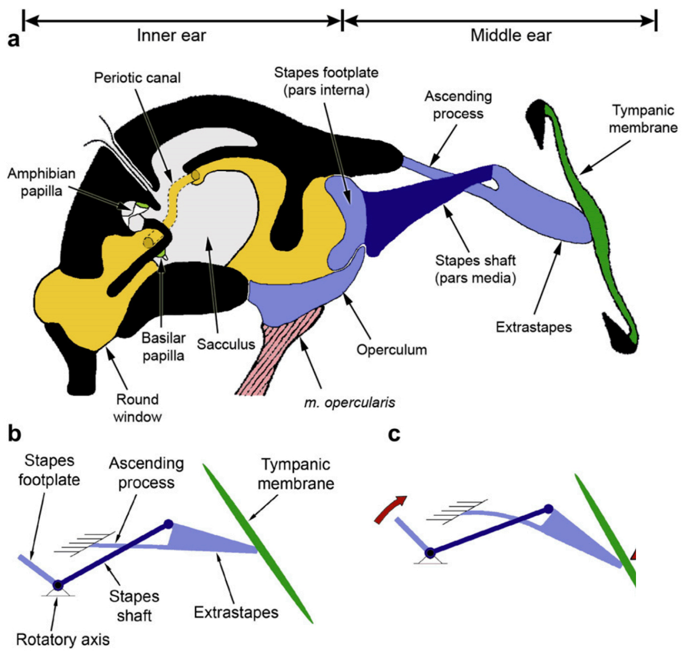




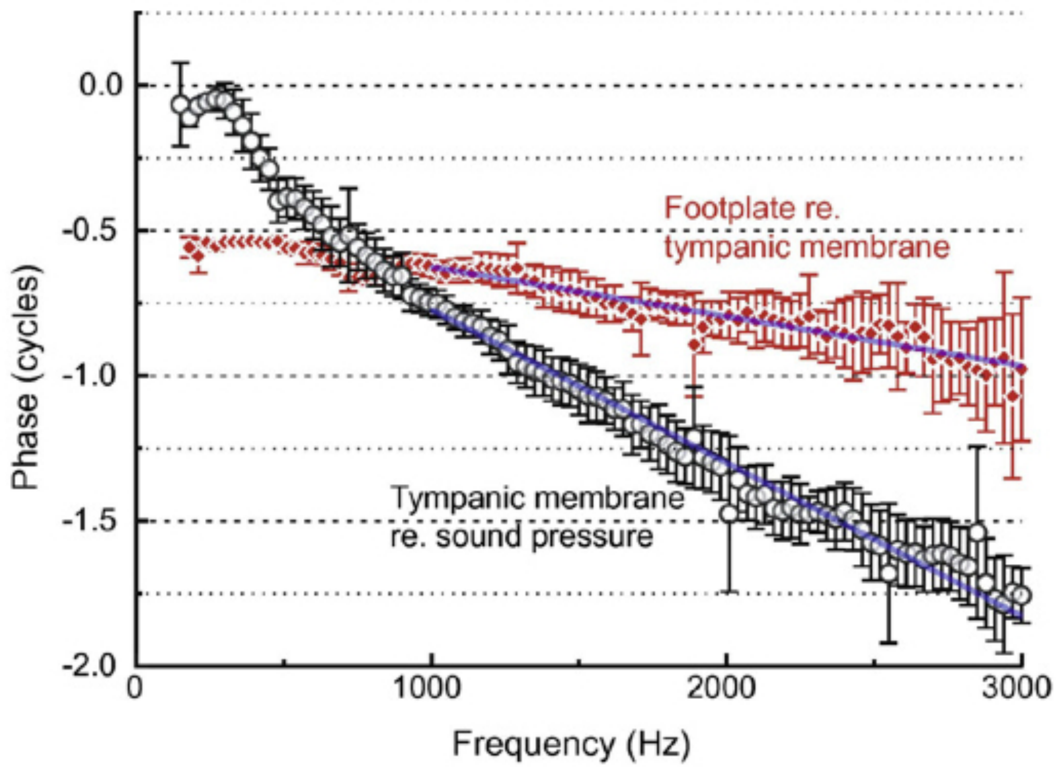
- Eardrum (TyM) is a (relatively) flat circular membrane
- Connection to middle ear (ossicular attachment) at center of membrane
- Ossicle funnels energy to/ from inner ear

van Dijk et al. (2011)

Amphibian Middle Ear → Long Delays



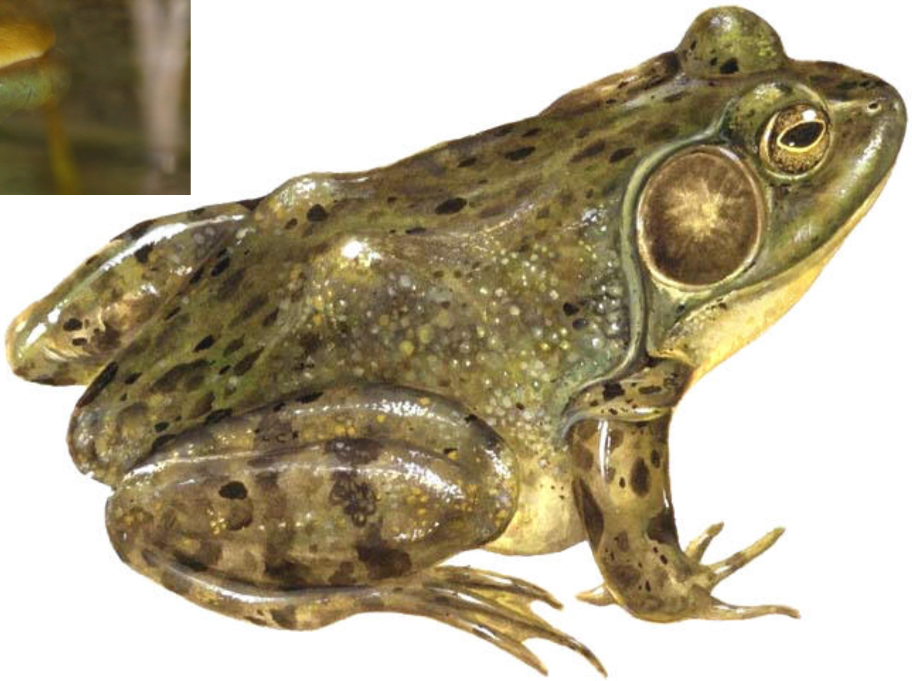
- Large delay through middle ear (~0.5 ms inwards)
- More than an order of magnitude longer than mammals



How does such a long middle ear delay arise?

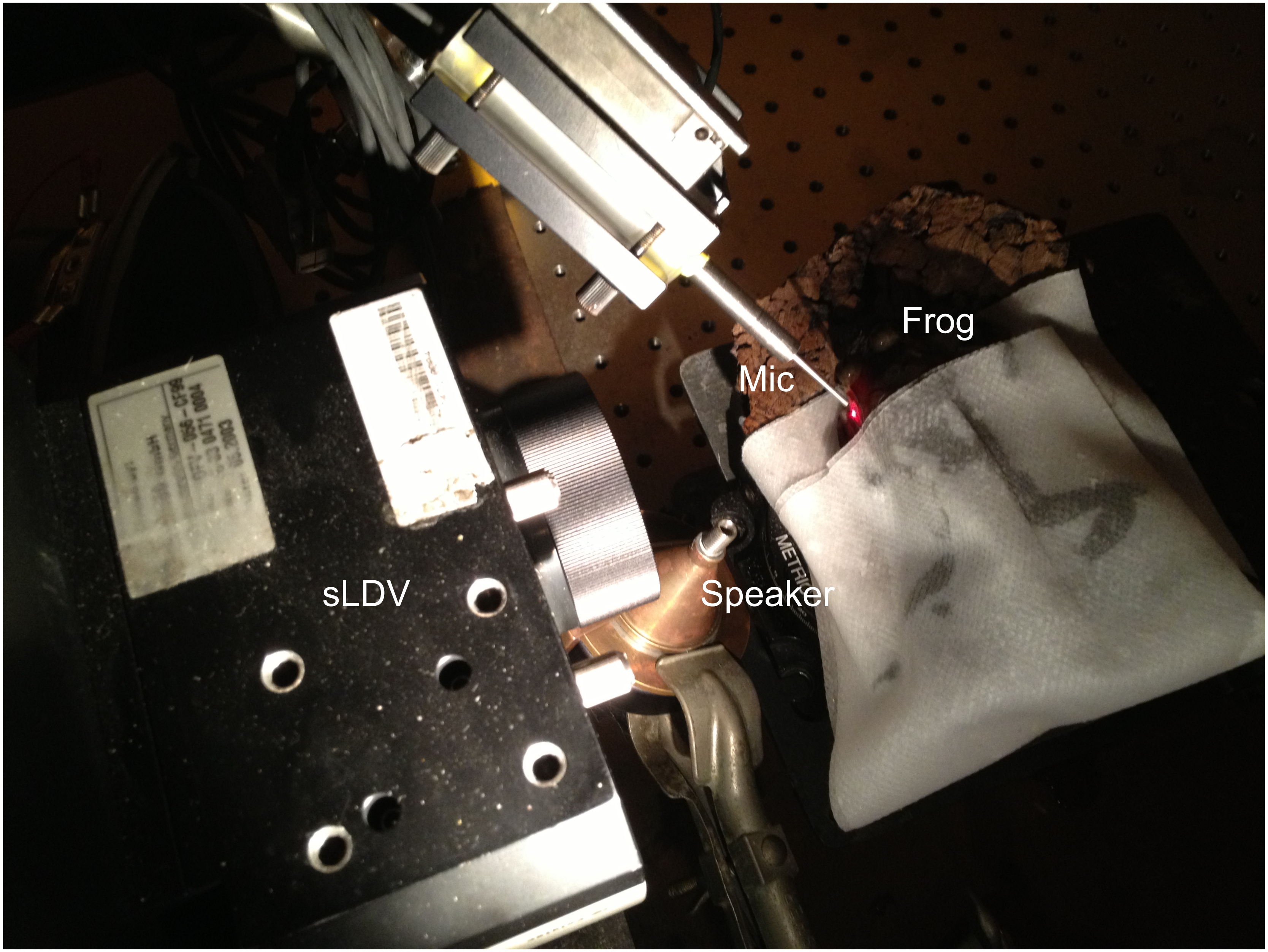
Mason & Narins (2002)

van Dijk et al. (2011)

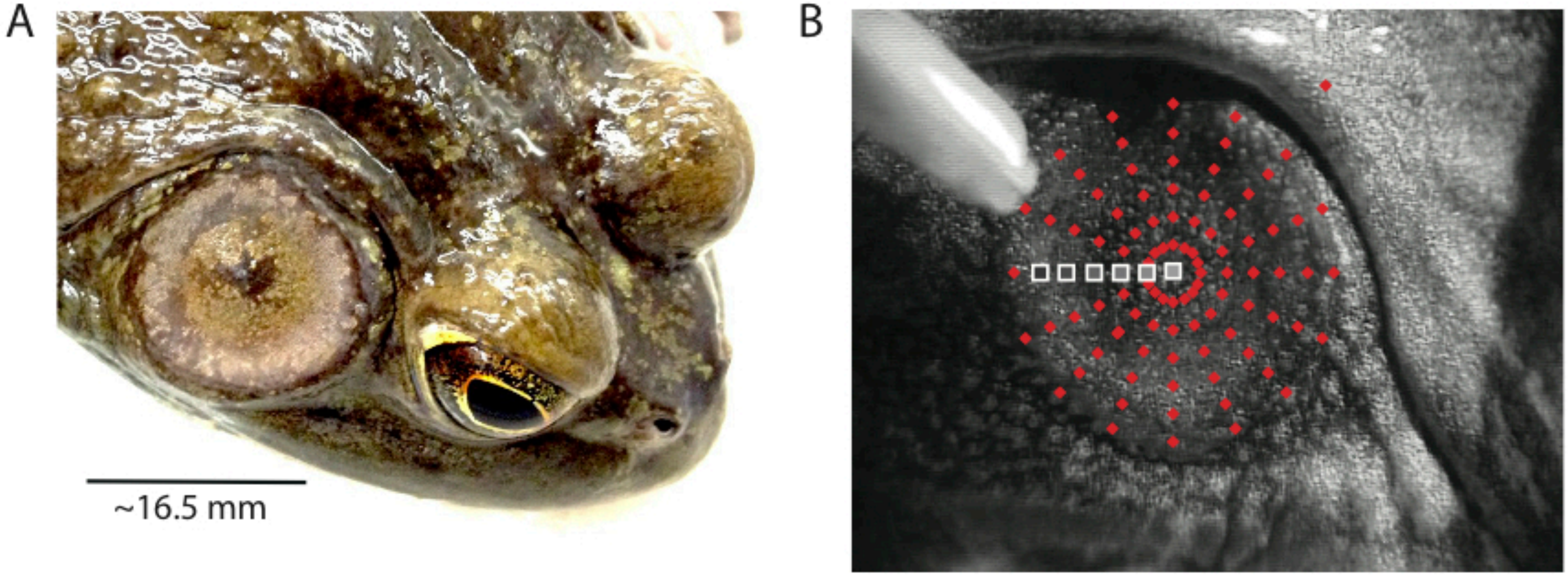


Eardrum as the source
of the delay?

Methods → Scanning Laser Doppler Vibrometry (sLDV)

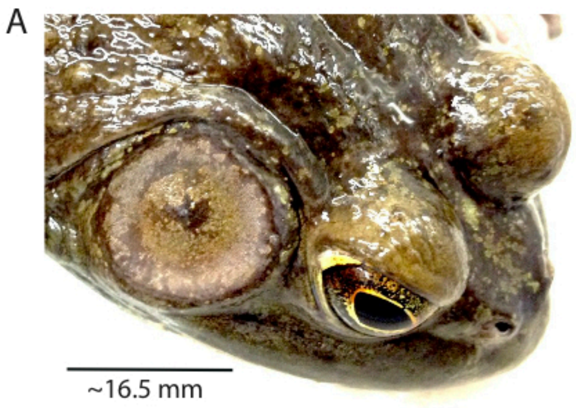


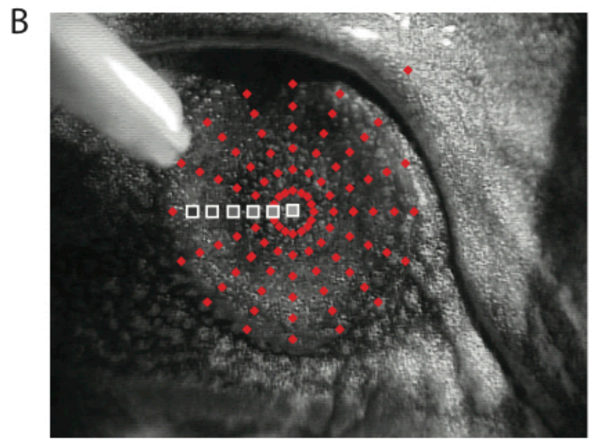
Methods → Scanning Laser Doppler Vibrometry (sLDV)



- ➢ Scan velocity (magnitude & phase) across eardrum surface
- ➢ Anesthesia required (otherwise non-invasive)

Results → Radial profile

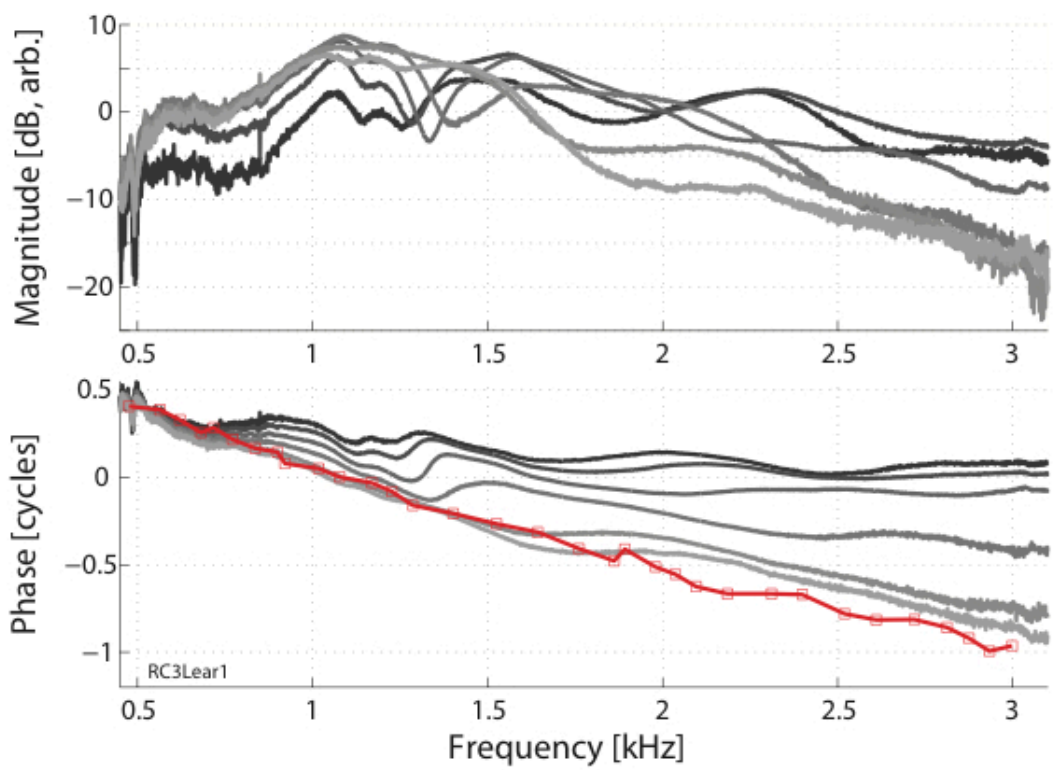




(Arbitrary) Radial profile:
- Darker = closer to edge
- Lighter = closer to center

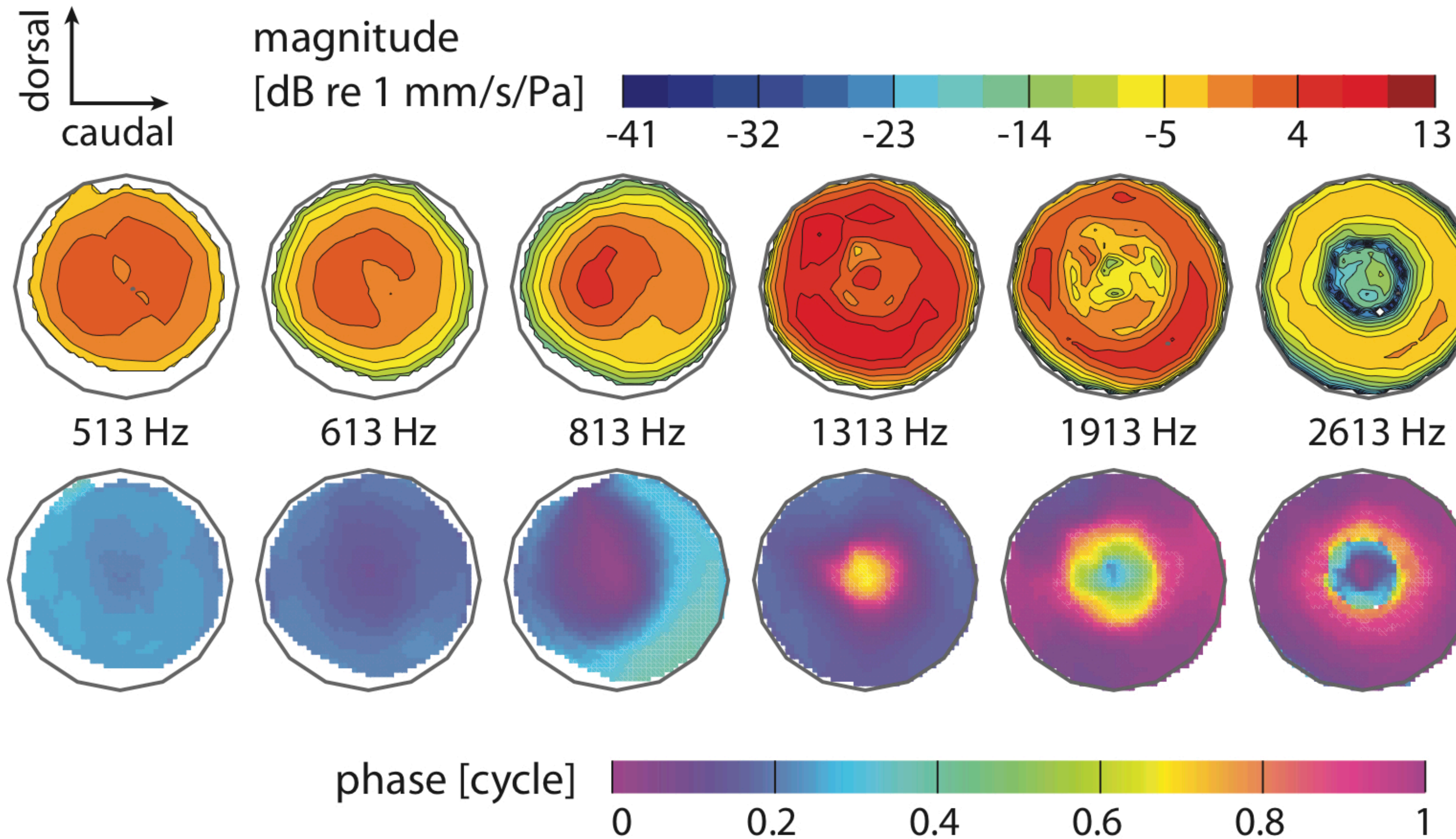
- Complex magnitude profile along radial path

- Progressive phase accumulation towards center



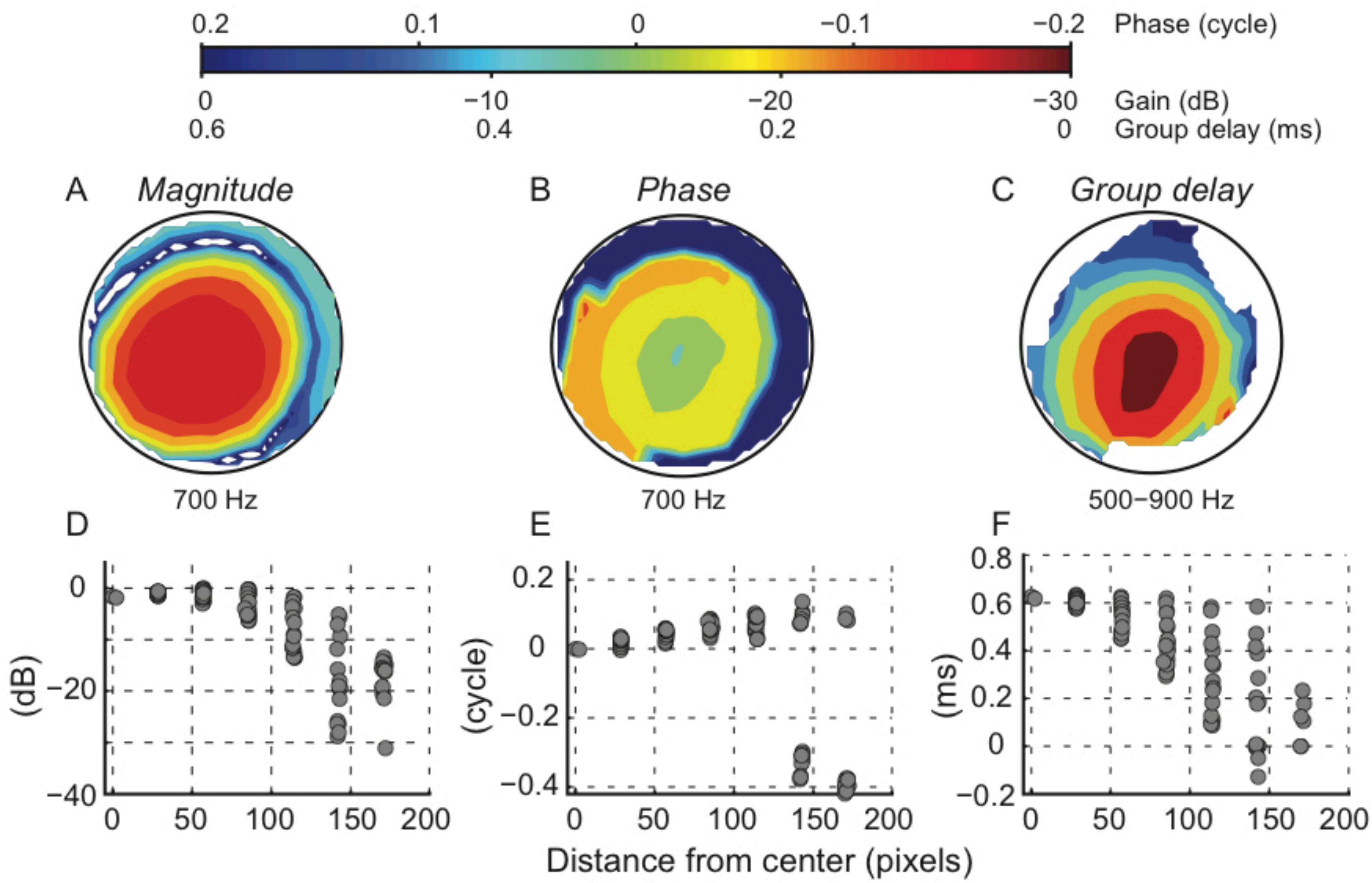
Results → Contour plots

Data shown here from one representative ear



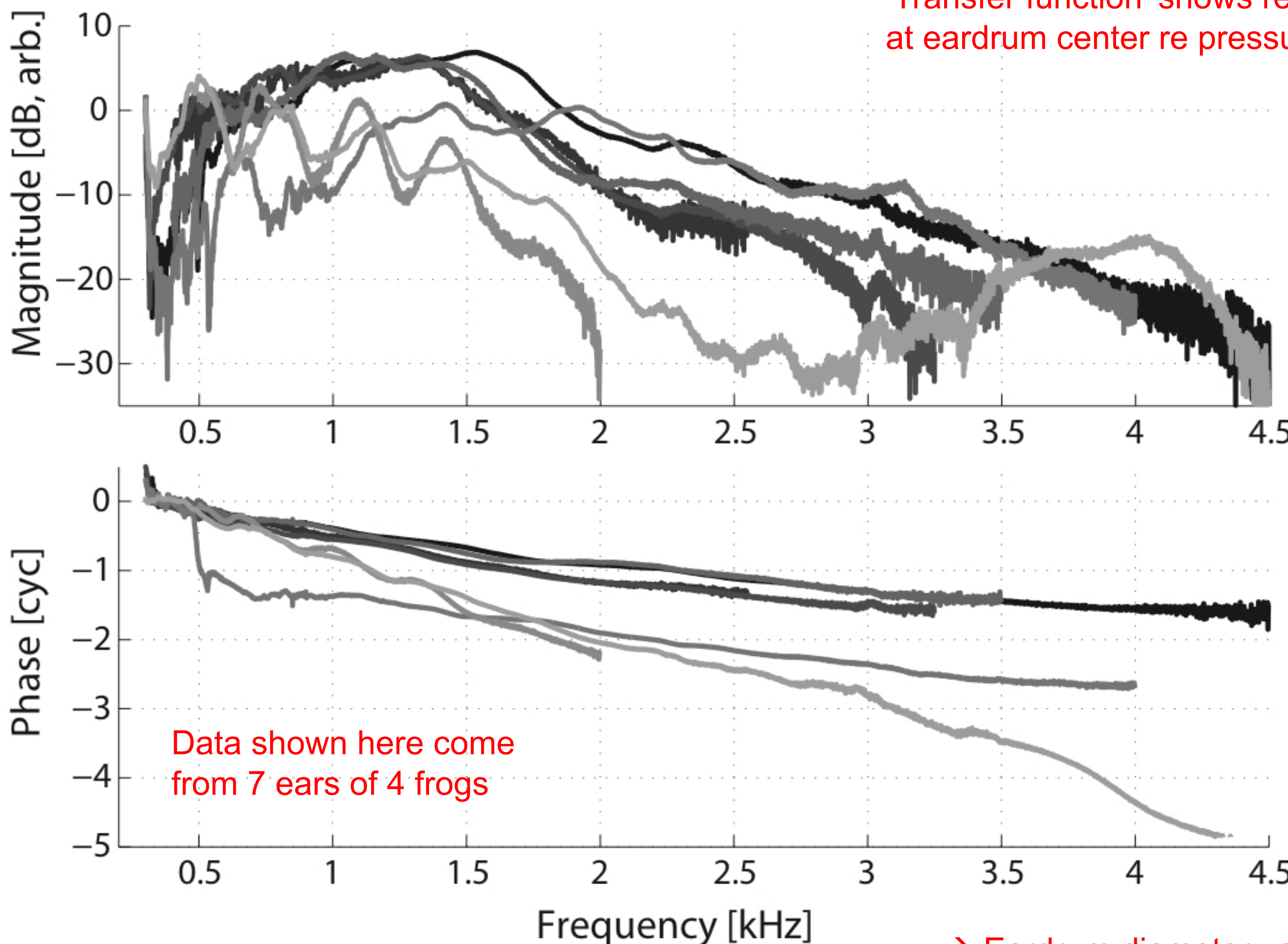
Results → Group delays

Data shown here from one representative ear



Results → Compiled responses

‘Transfer function’ shows responses at eardrum center re pressure

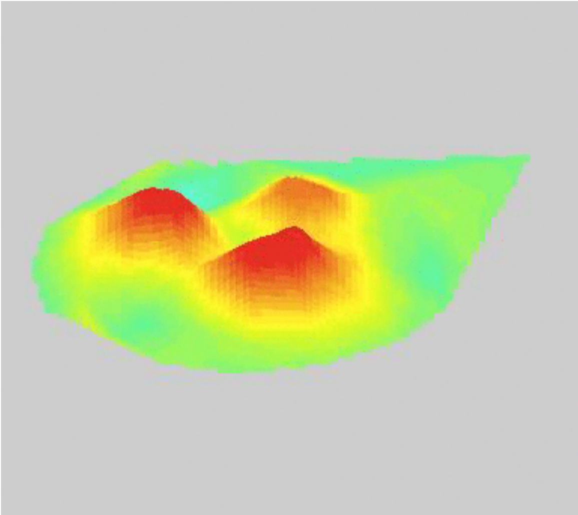


Data shown here come from 7 ears of 4 frogs

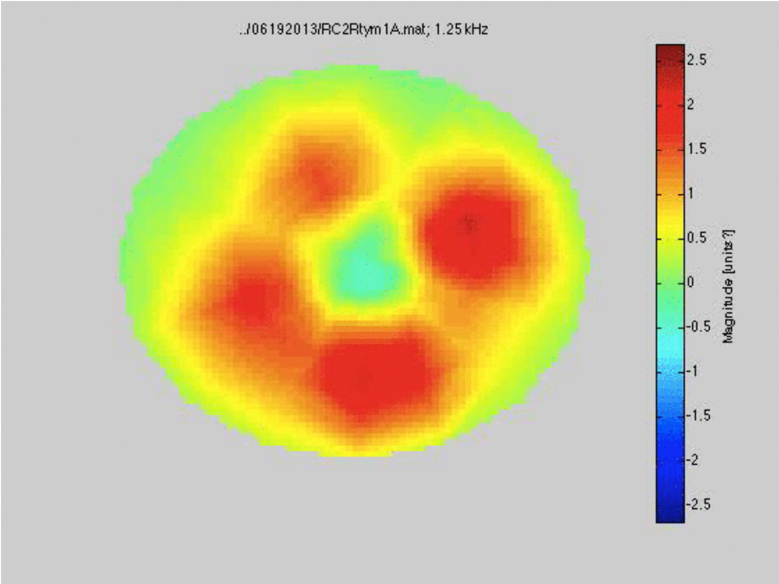
→ Eardrum diameter varied 6-16 mm, reflected in the differing delays

<u>Results</u> → Animation

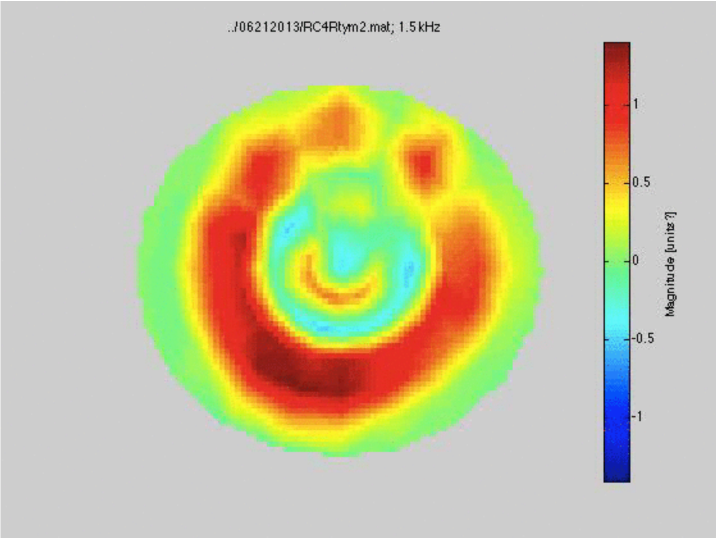
Female, 1.2 kHz



Female, 1.25 kHz



Male, 1.5 kHz



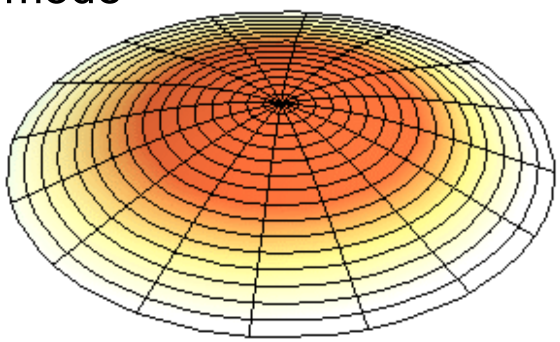
Note the lack of nodes

(i.e., these are inward-traveling waves, not standing waves)

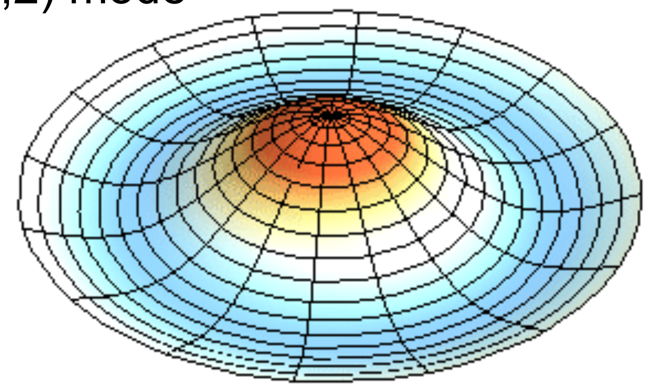
Circular membrane → Standing wave modes

e.g., drumhead

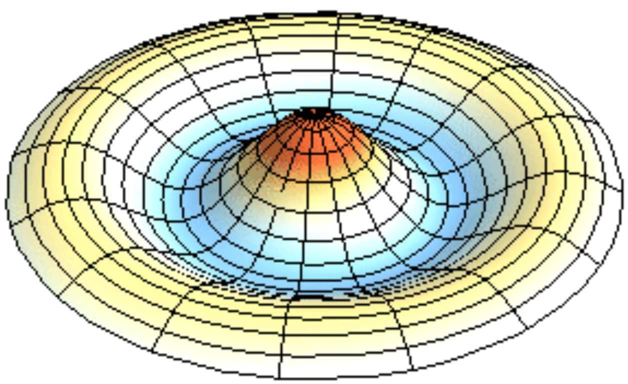
(0,1) mode



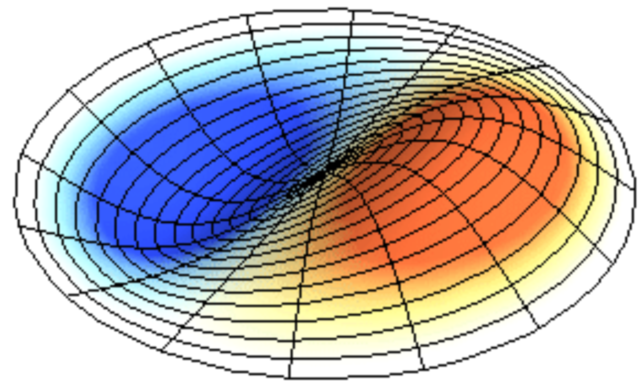
(0,2) mode



(0,3) mode



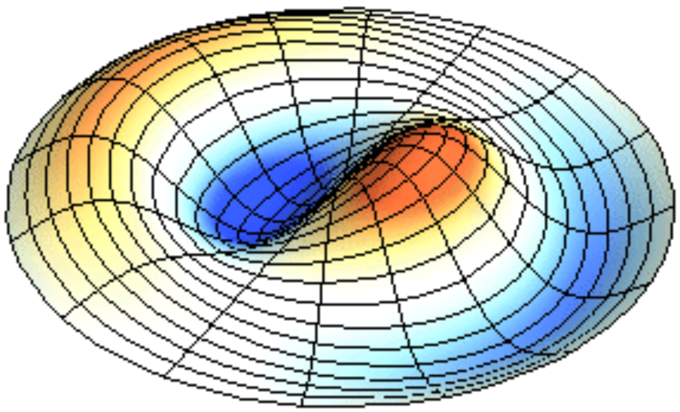
(1,1) mode

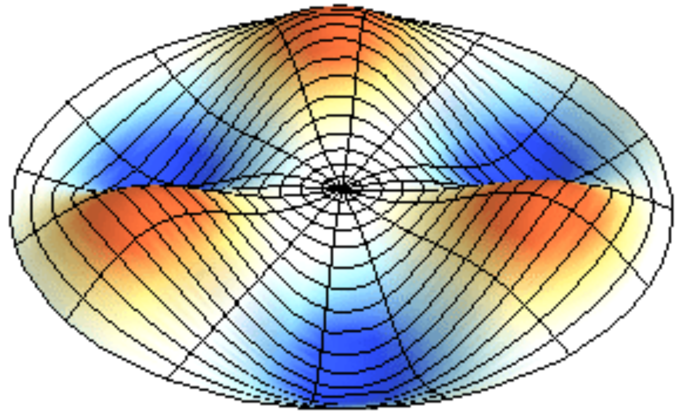


http://www.acs.psu.edu/drussell/demos/membranecircle/circle.html

<u>Circular membrane</u> → Standing wave modes

(1,2) mode





(3,1) mode

Note clear presence of nodes

http://www.acs.psu.edu/drussell/demos/membranecircle/circle.html

Summary

Inward traveling wave along eardrum surface is source of delay:
→ Energy (relatively) slowly propagates inwards to center point

Further questions raised:

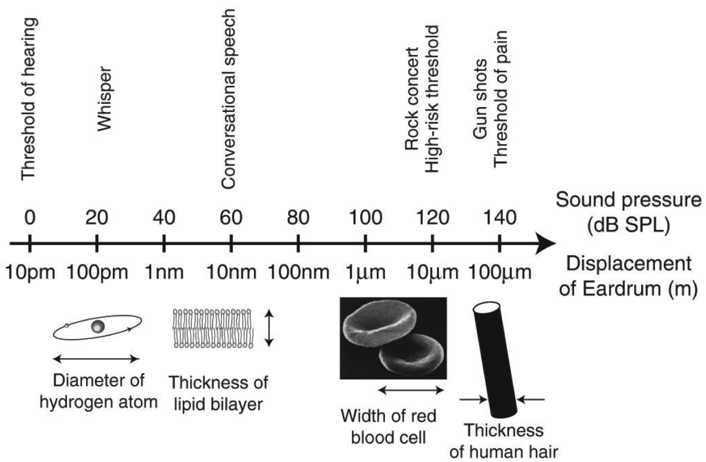
- Different from generic circular membrane (no nodes). What determines transition between traveling and standing waves?

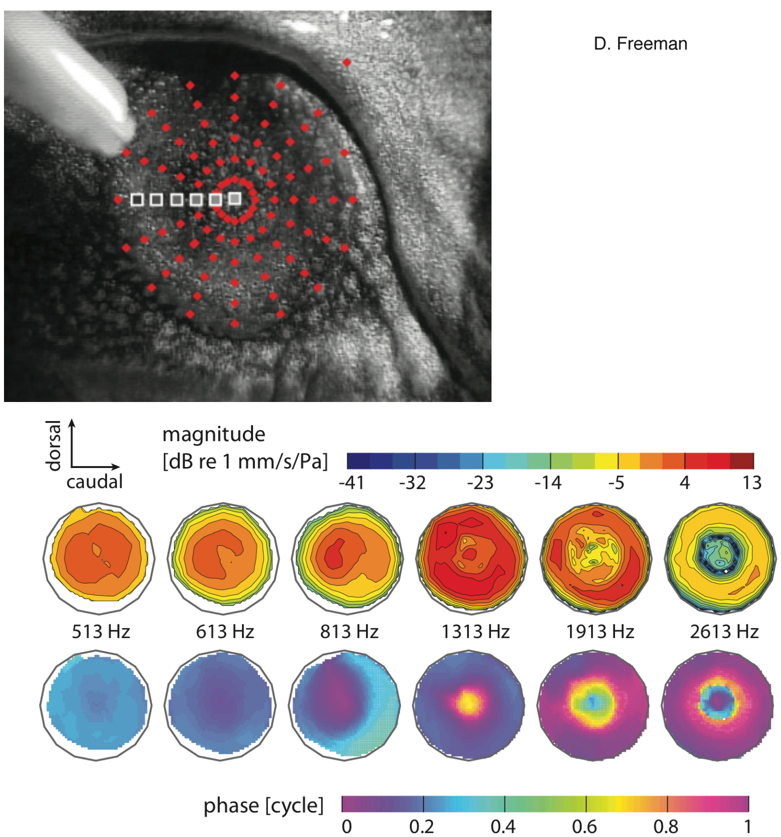
- Is the delay reciprocal (for OAE energy coming back out)?

- In terms of biomechanical design, is this optimal given ecological constraints (i.e., living both above and below water) to act as impedance matcher?

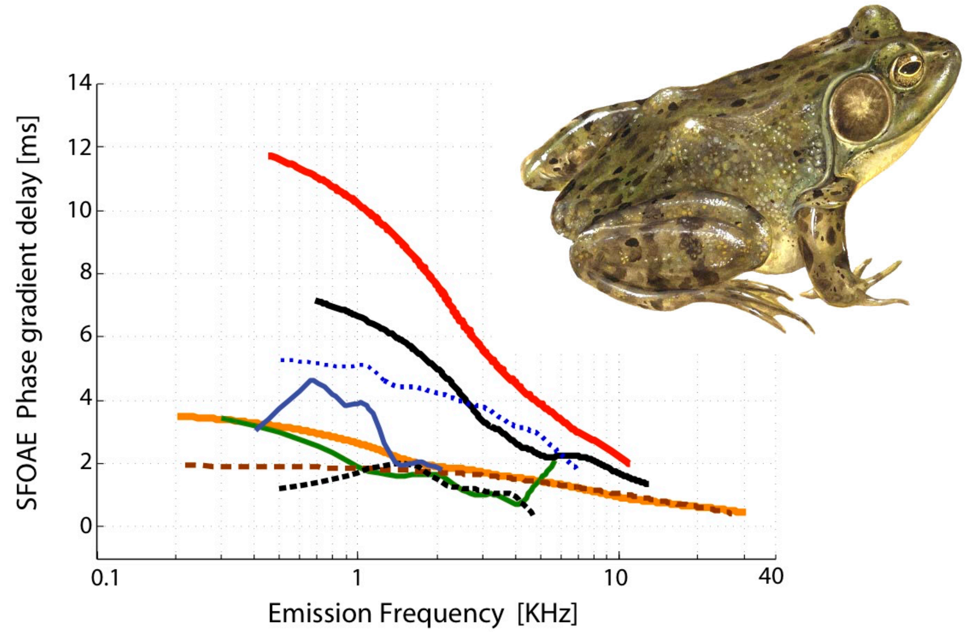
- Optimal strategies for modeling? (e.g., transmission line vs finite element)

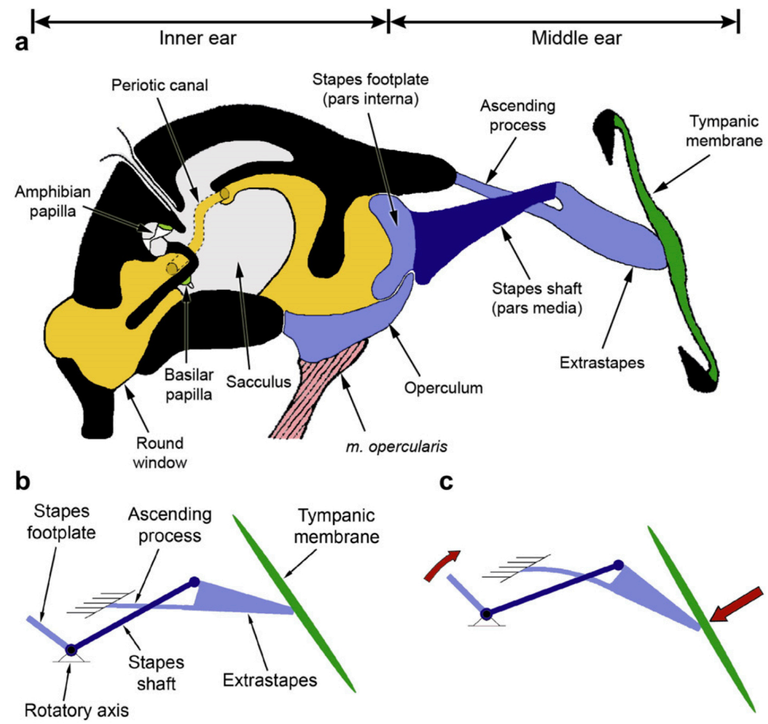
Summary

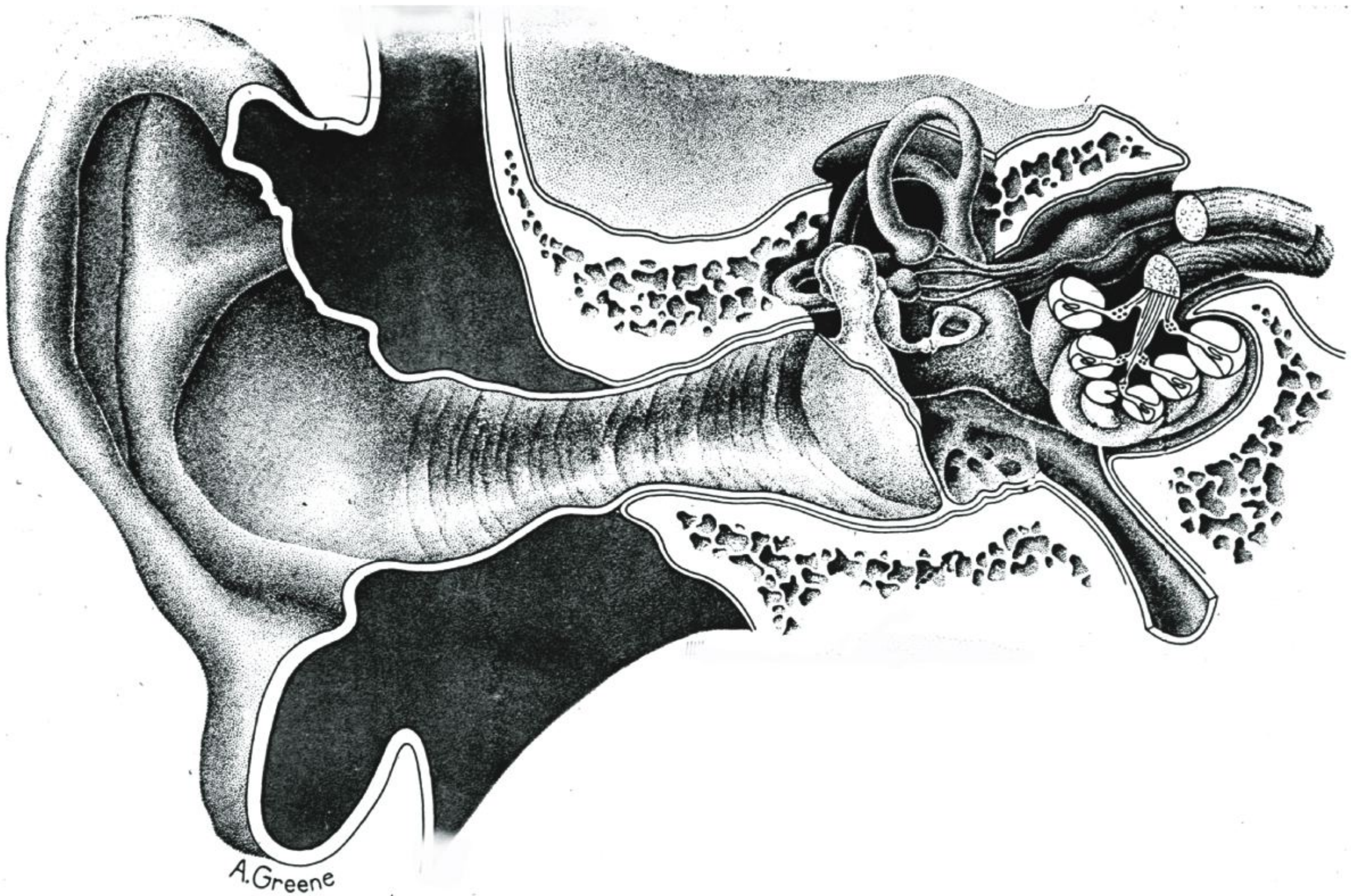




D. Freeman





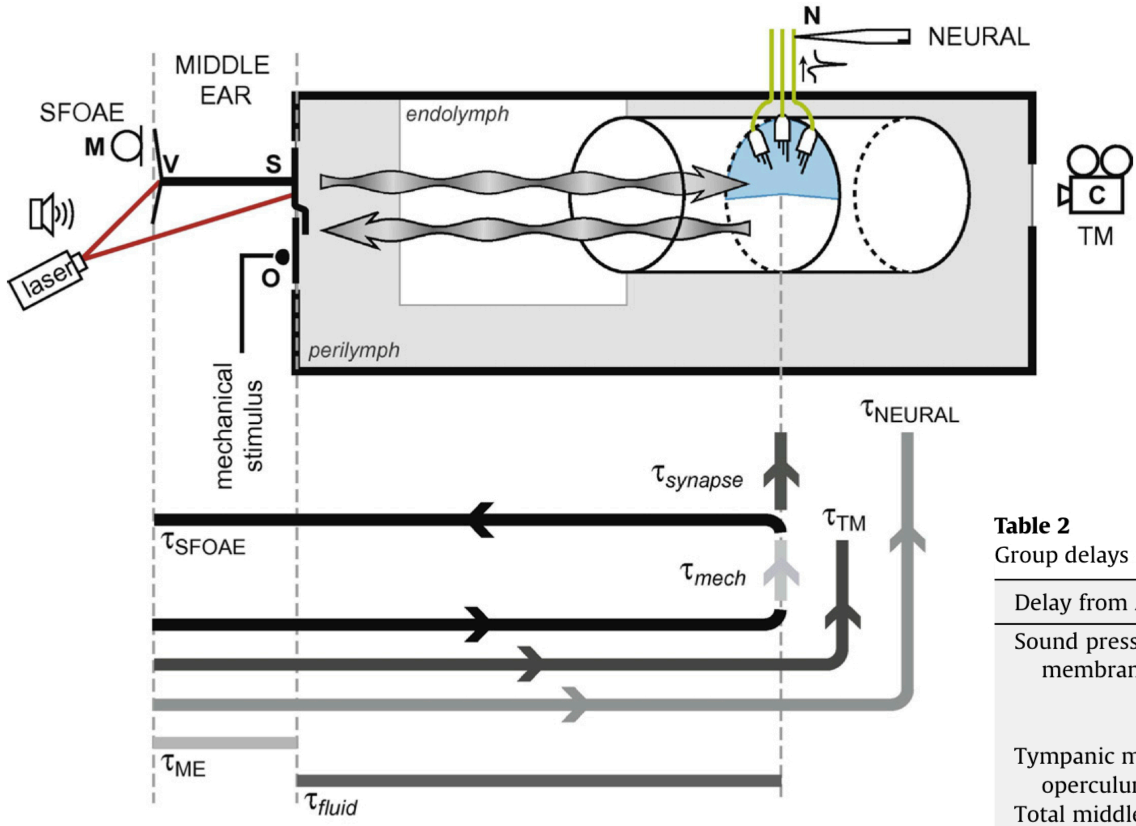

A.Greene

Fini

BIOPHYSICS @ YORK

UNIVERSITÉ
UNIVERSITY

redefine THE POSSIBLE.



$$\tau_{TM} = \tau_{fluid} + \tau_{mech}$$

$$\tau_{NEURAL} = \tau_{ME} + \tau_{fluid} + \tau_{mech} + \tau_{synapse}$$

$$\tau_{SFOAE} = 2x\ \tau_{ME} + 2x\ \tau_{fluid} + \tau_{mech}$$

τ_{fluid} : one-way delay of longitudinal waves in inner ear fluids ≈ 0

τ_{mech} : filter delay of mechanical response of the tectorial membrane

$\tau_{synapse}$: synaptic delay

τ_{TM} : tectorial membrane delay

τ_{ME} : middle ear delay

Table 2
Group delays in the middle ear and the basilar papilla.

Delay from A to B		Reference
Sound pressure to tympanic membrane	0.53 (±0.07) ms	Mason and Narins, (personal communication)
Tympanic membrane to footplate/ operculum**	0.170 (±0.005) ms	Mason and Narins (2002a)
Total middle ear delay (τ_{ME})	0.53 + 0.170 = 0.70 (±0.07) ms	
Operculum to tectorial membrane (τ_{TM})	0.60 (±0.08) ms	Schoffelen et al. (2009)
SFOAE delay (from stimulus sound pressure in front of the tympanic membrane to BP and back) (τ_{SFOAE})	2.0 (±0.1) ms*	Meenderink and Narins (2006)
Neural group delay from Wiener kernels (delay from sound pressure in front of the tympanic membrane to neuronal response) (τ_{NEURAL})	2.9 (±0.4) ms*	Van Dijk et al. (1997a,b)

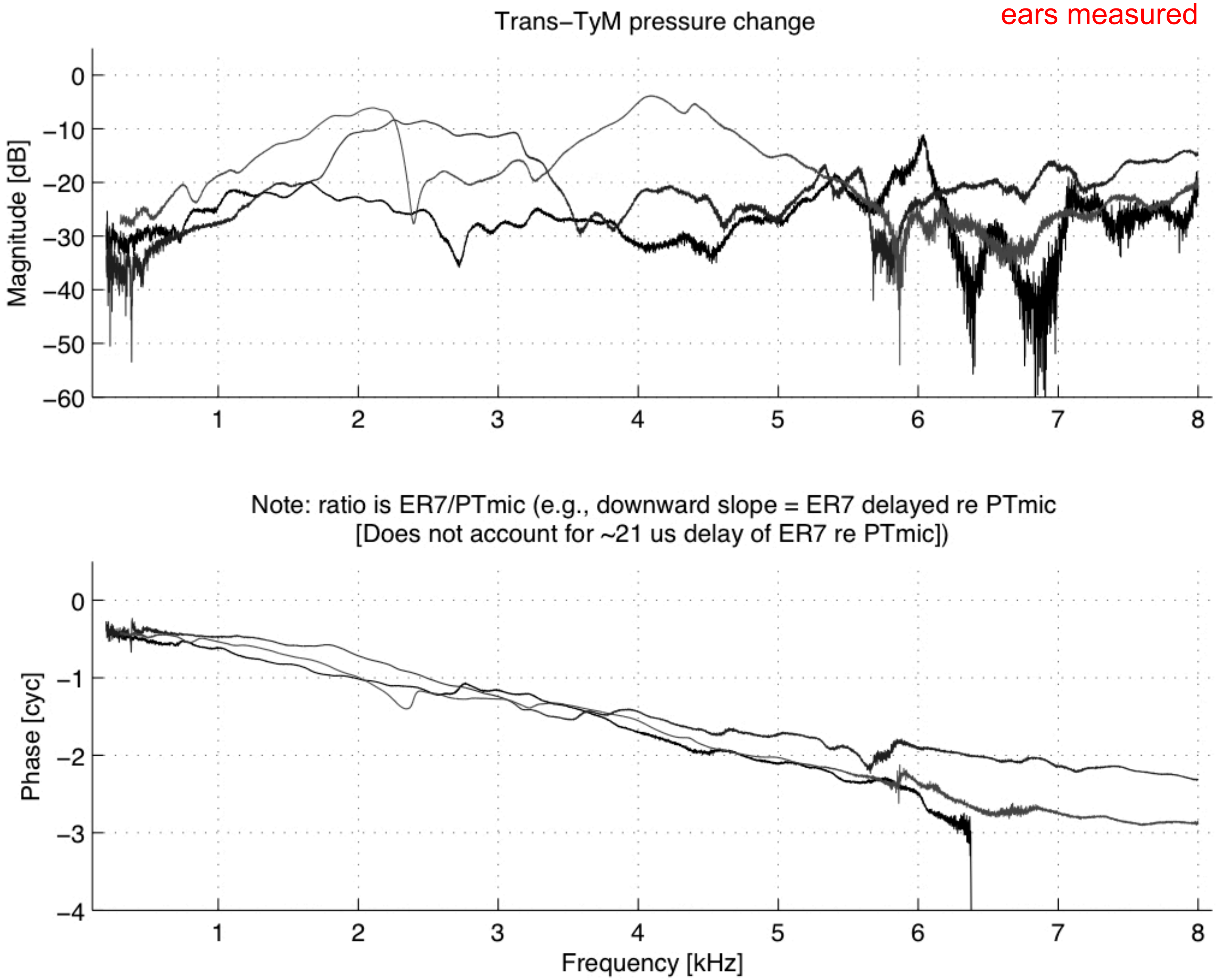
* Mean and standard deviation obtained by averaging across the values in the interval 1700–2300 Hz, excluding one outlier near 0.1 ms in the SFOAE data.

** There is essentially no phase lag between the footplate and operculum response (Mason and Narins, 2002b).

van Dijk et al. (2011)

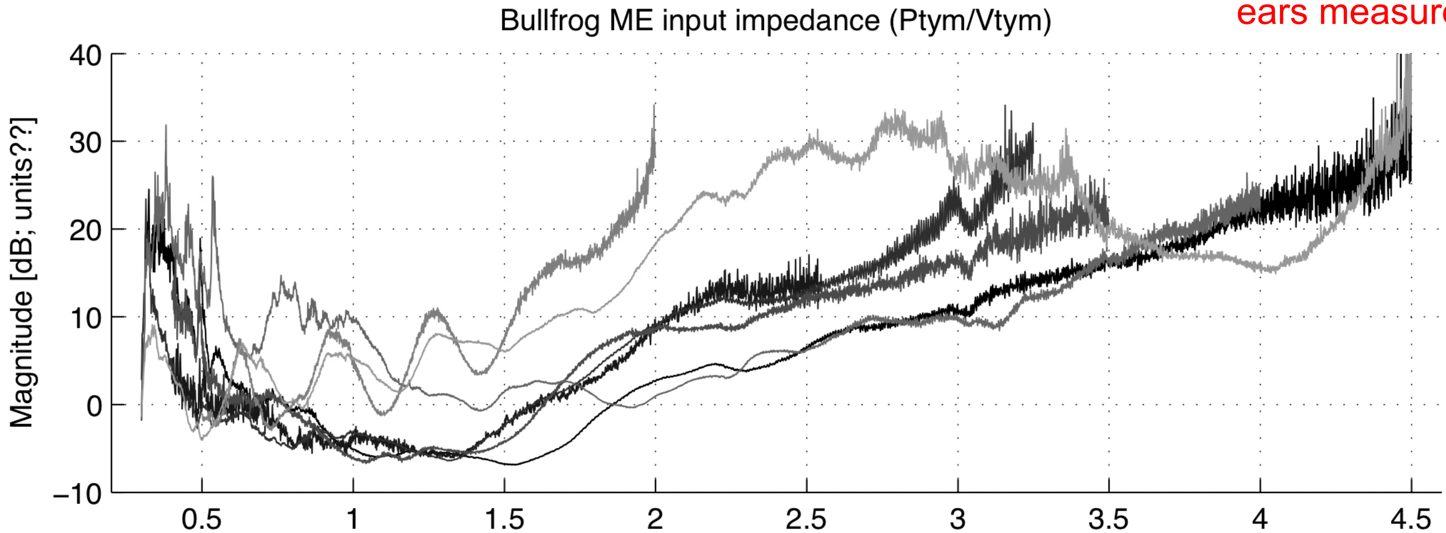
Results → Trans-TyM pressure change

Data compiled from all ears measured

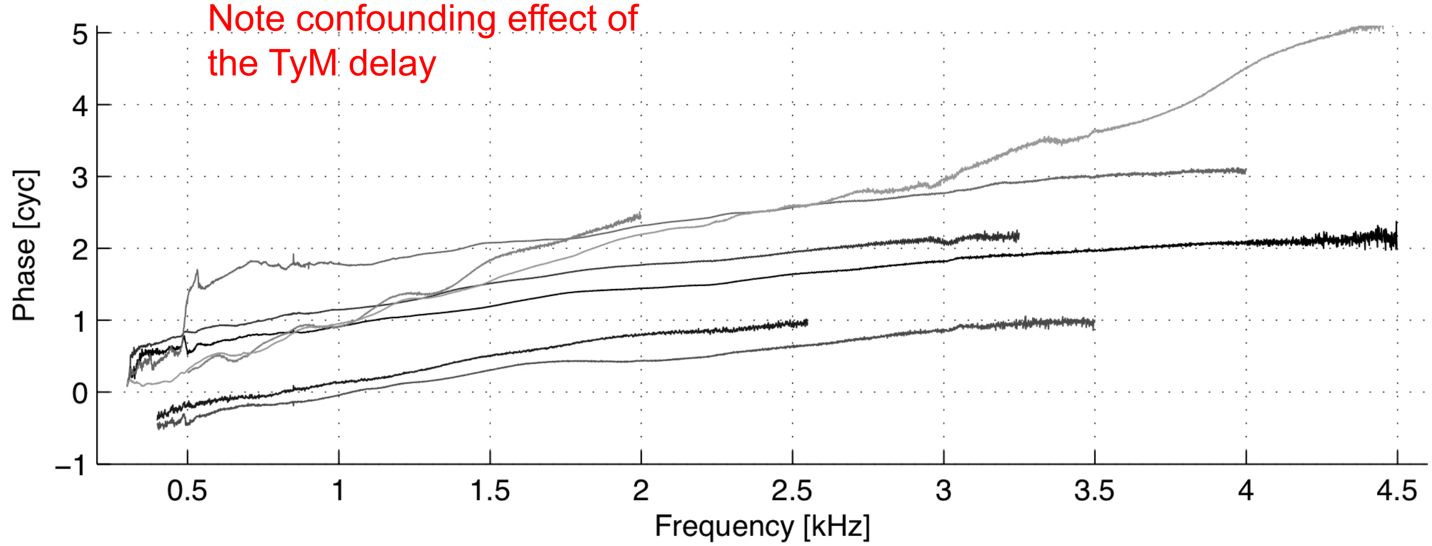


Results → Input impedance

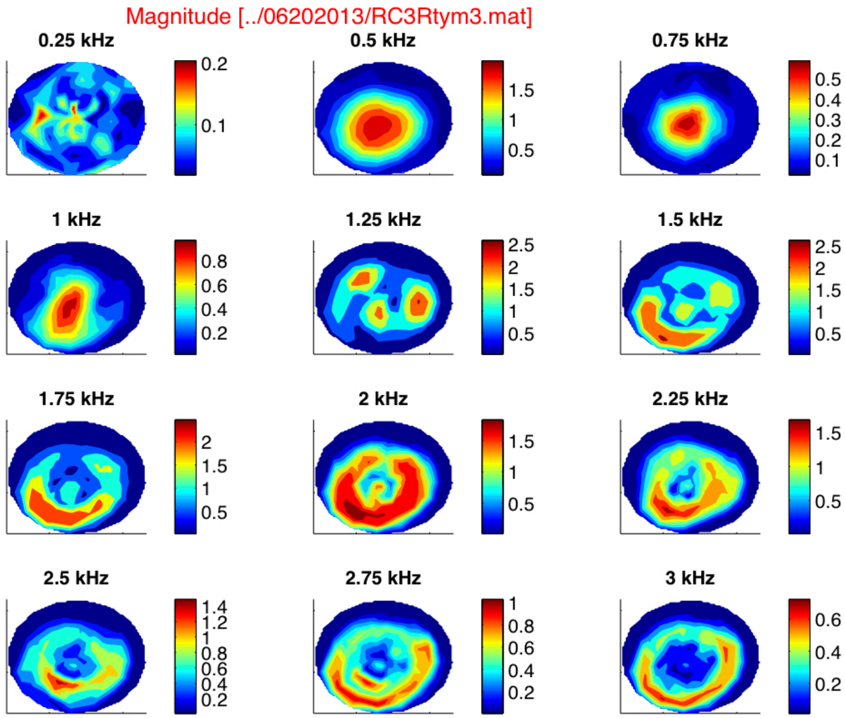
Data compiled from all ears measured

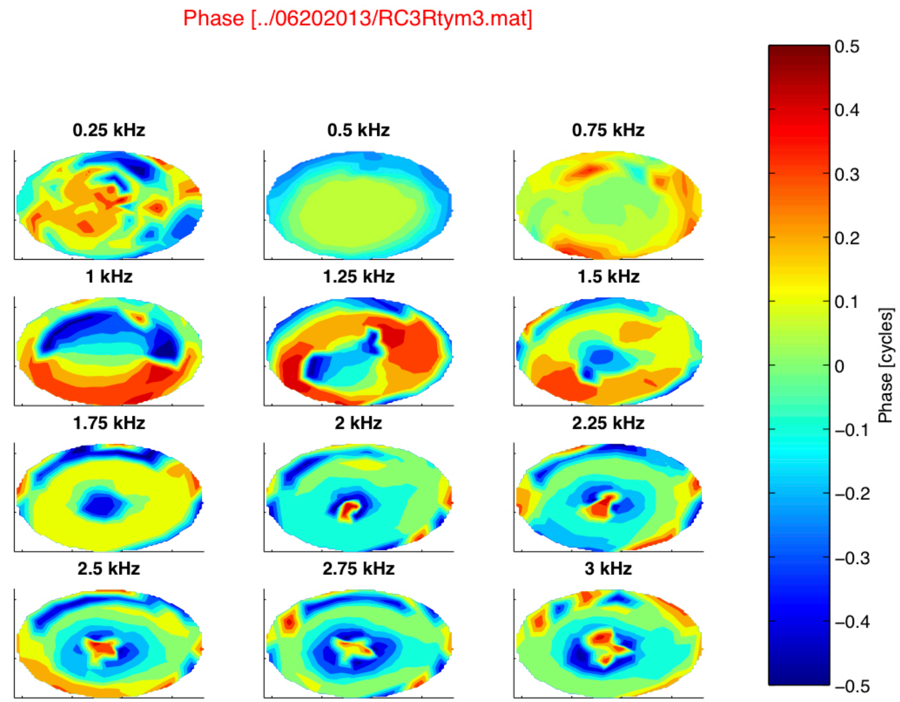


Note confounding effect of the TyM delay



Results → Misc. contour maps



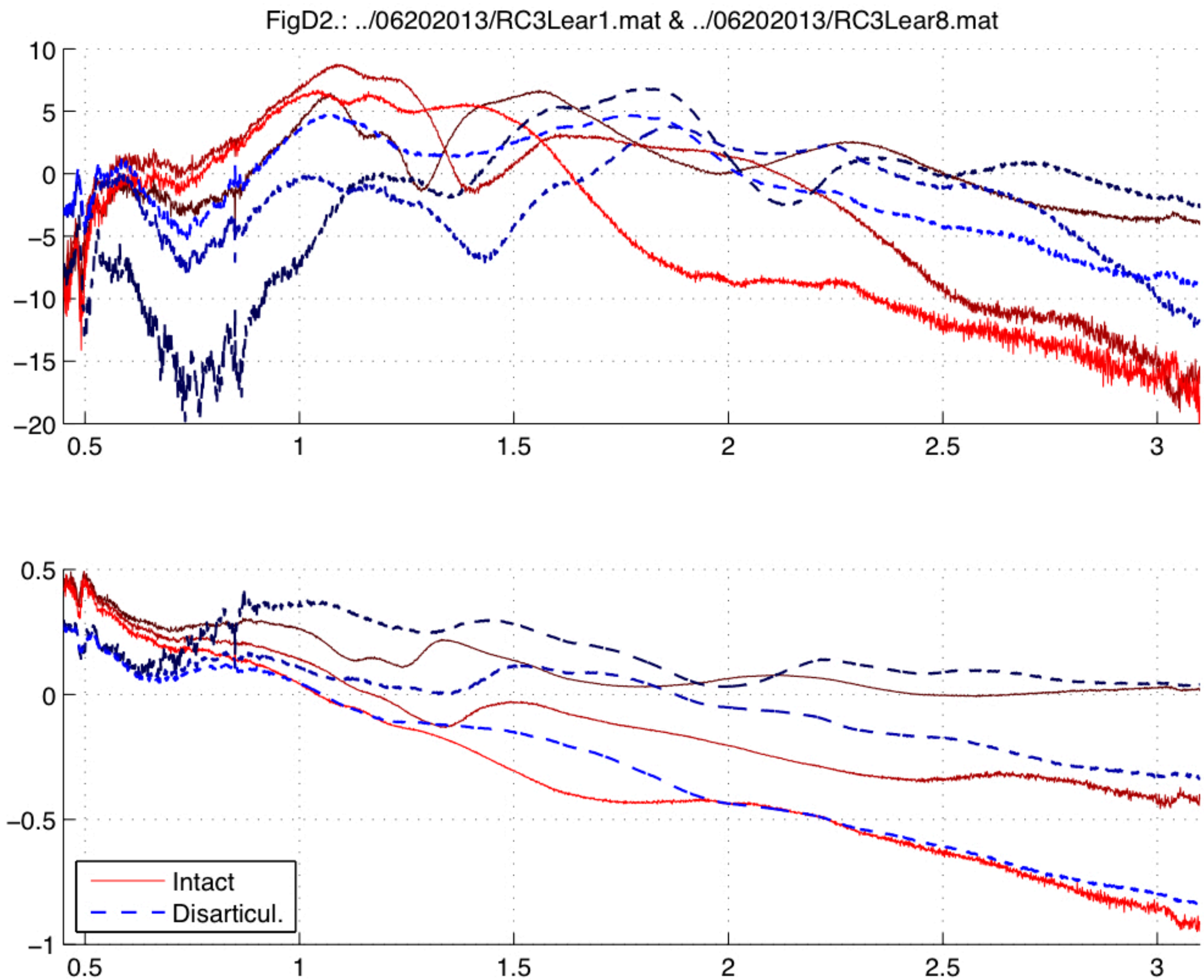


Magnitude

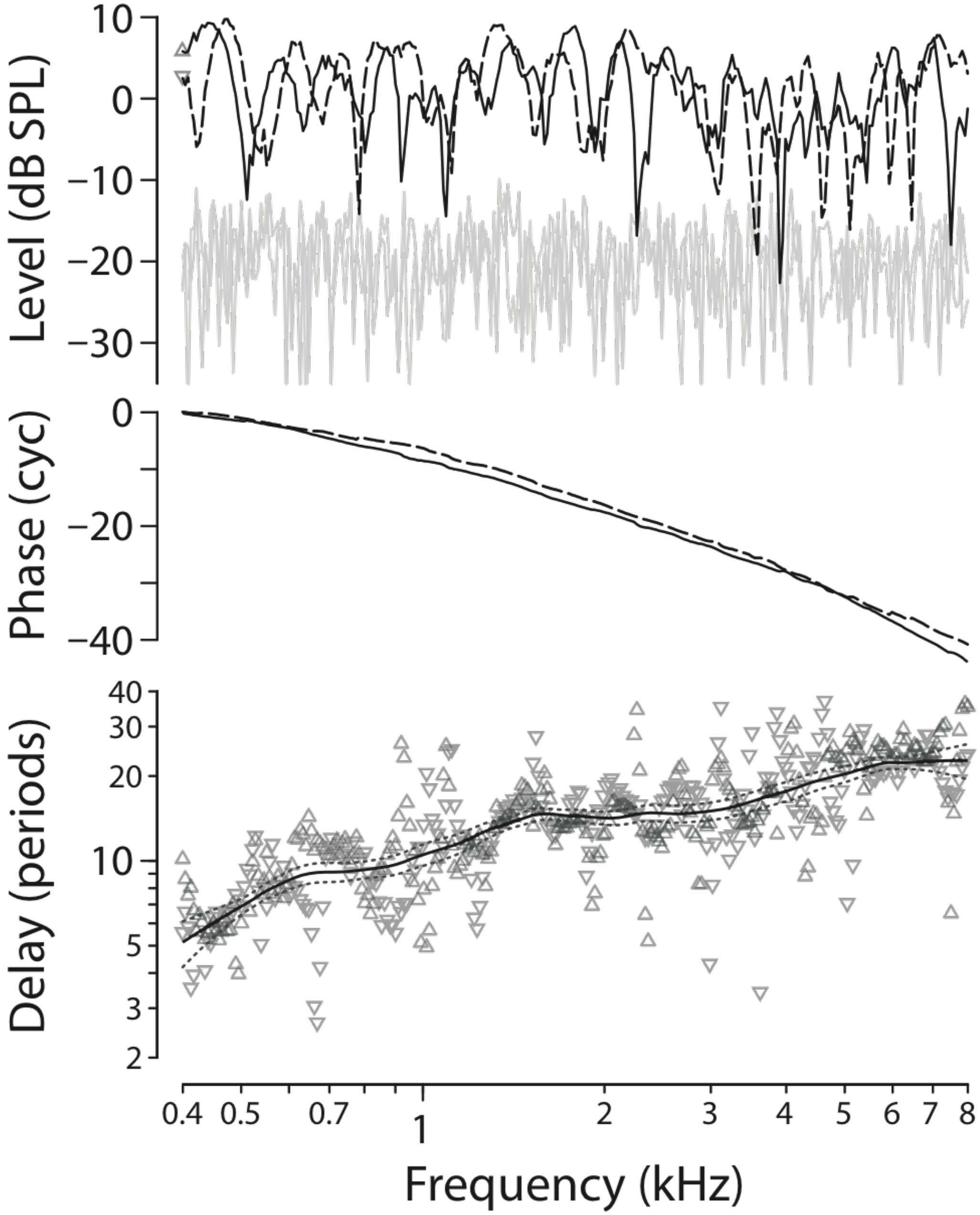
Phase

Results → Misc. contour maps

Data here are from one individual

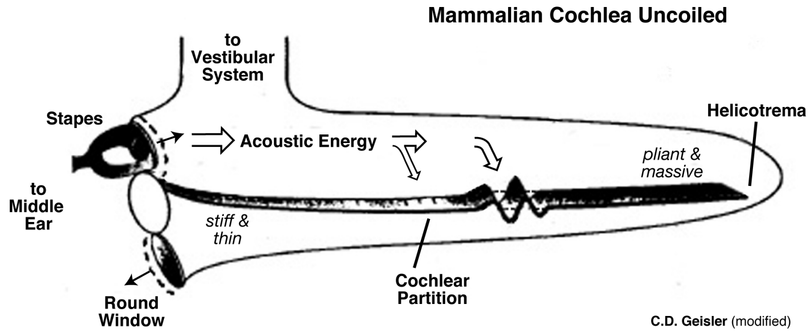


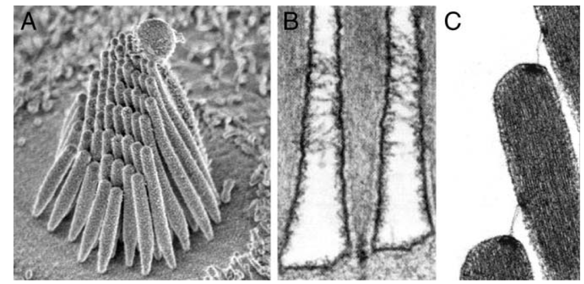
SFOAE overview



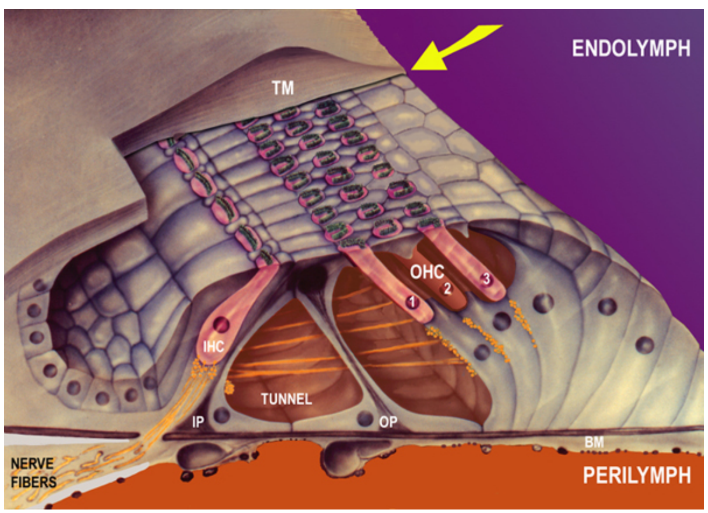
Shera & Bergevin (JASA 2012)

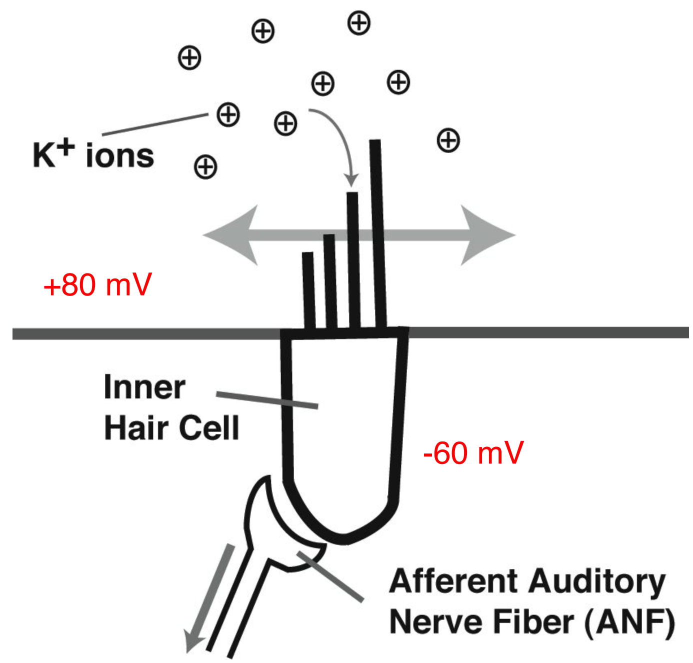
Hair cell = '*mechano-electro'* transducer





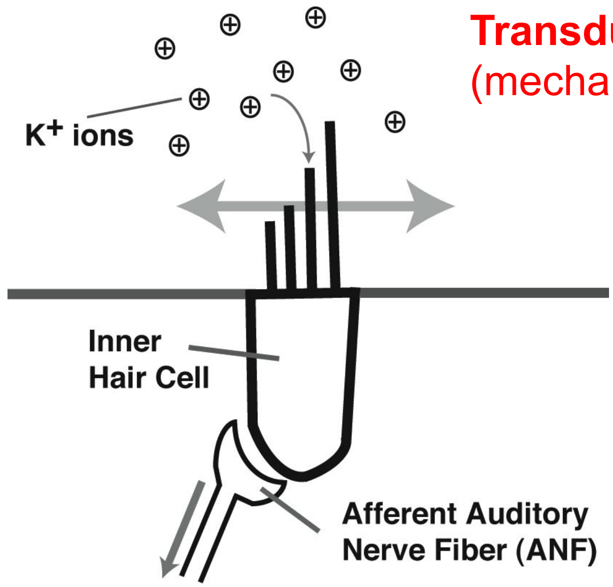
Martin (2008)



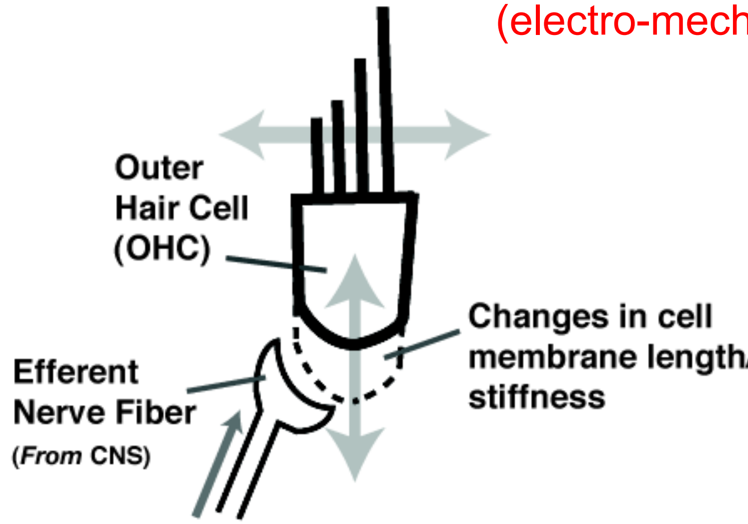


Hair cell = amplifier?

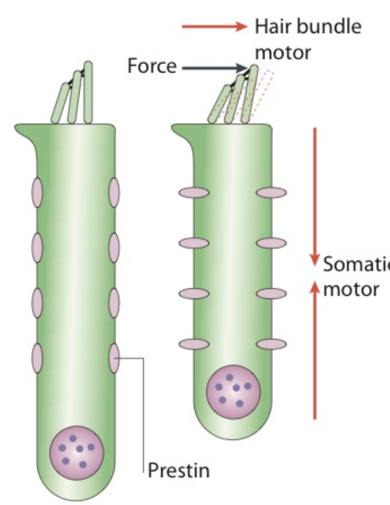
Forward Transduction
(mechano-electro)



Reverse Transduction
(electro-mechano)



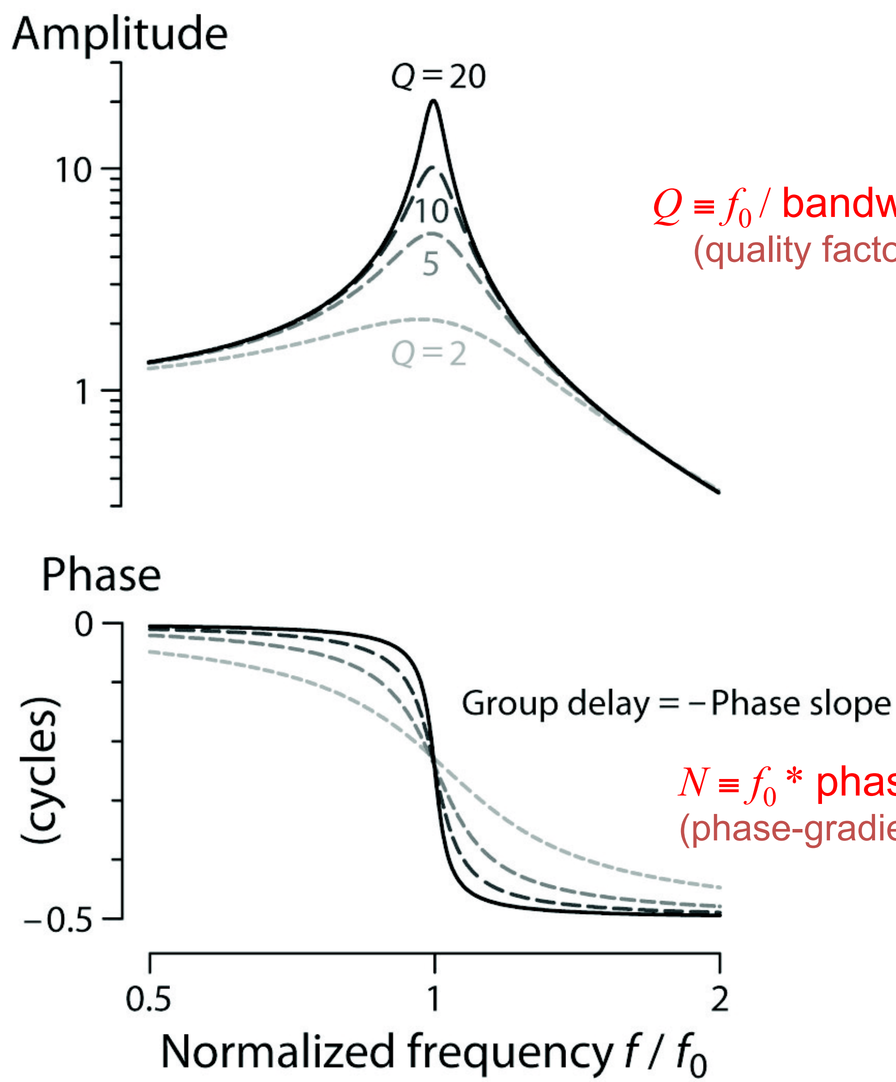
→ Hair cells also amplify (forming basis for OAEs)



Fettiplace & Hackney (2006)

Phase-Gradient Delay ⇔ Sharpness of Tuning

First consider a single 2nd order filter



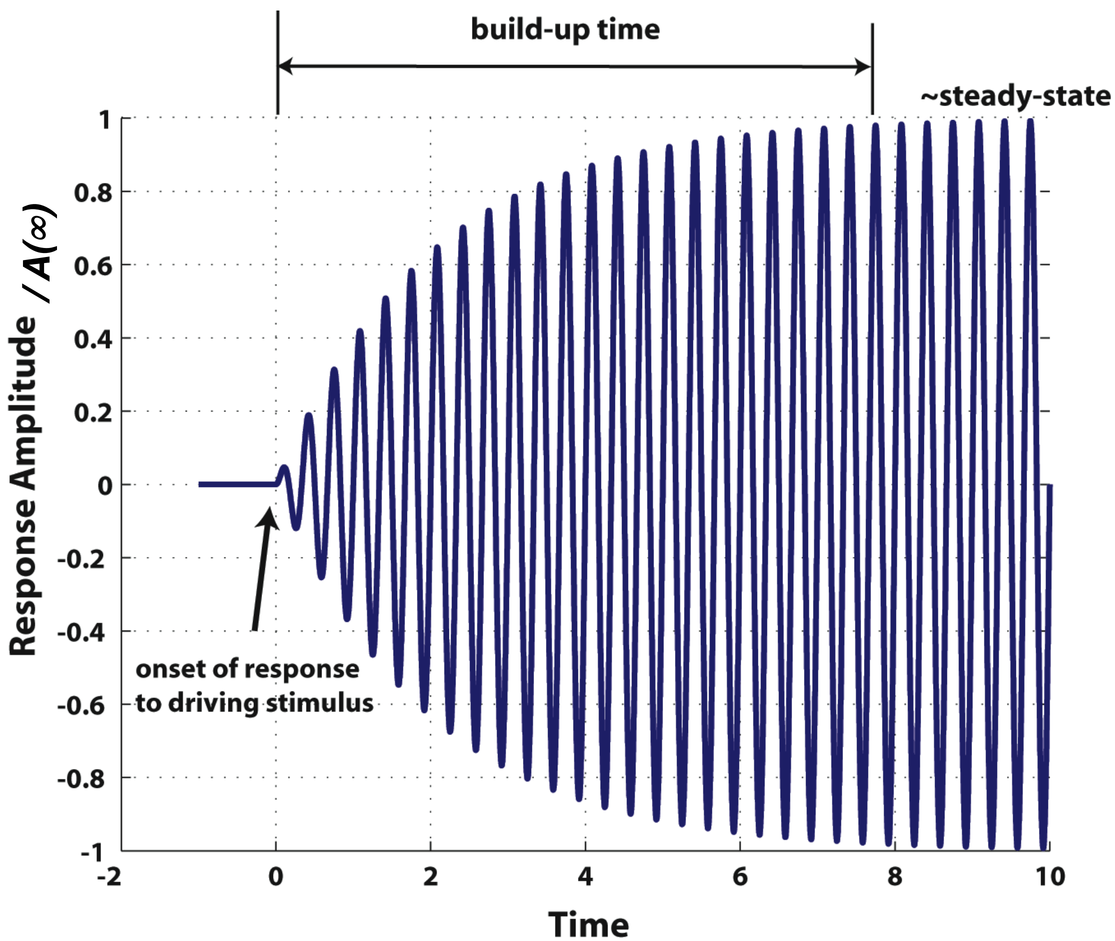
$Q \equiv f_0$ / bandwidth
(quality factor)

$N \equiv f_0$ * phase slope
(phase-gradient delay)

$Q \propto N$

Shera et al. (JARO, 2010)
Bergevin & Shera (JASA, 2010)

Basic Idea: Tuned Responses Take Time



Second Order System
(resonant frequency ω_o)

⇒ **External driving force at frequency** ω

$$x(t) = A(\infty)\,[1 - e^{(-t/\tau)}]$$

$$\tau = Q / \omega_o$$