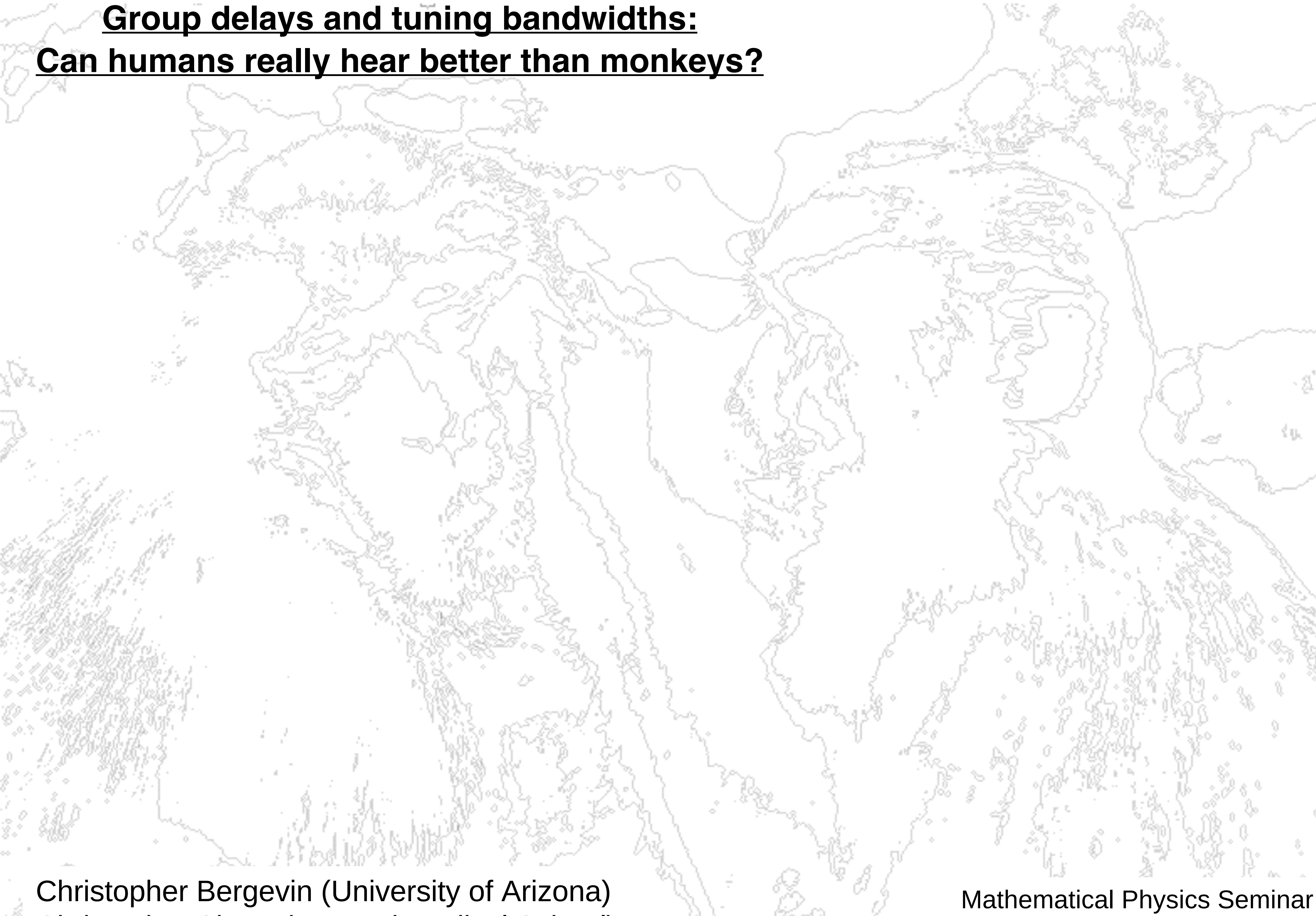
Group delays and tuning bandwidths: Can humans really hear better than monkeys?



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Christopher Shera (Harvard Medical School)

Mathematical Physics Seminar
9/10/08


National Geographic

Big Picture:

Establish a connection between OAE group delays and tuning bandwidth for a series of cascaded filters (i.e., the inner ear)

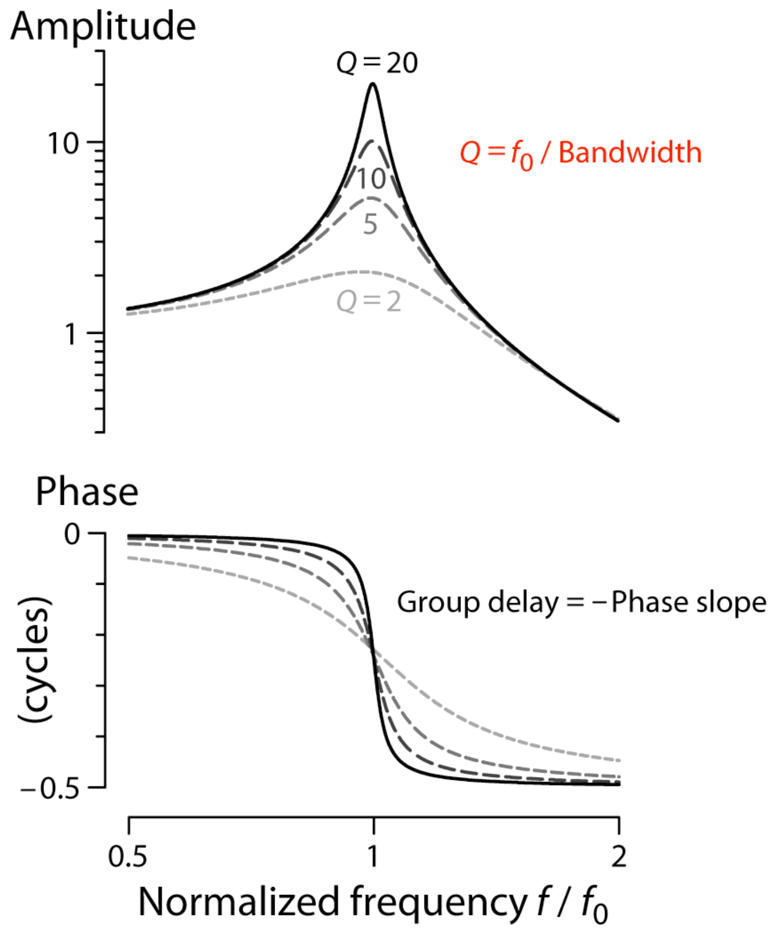
Outline

I - Harmonic Oscillator

II - OAEs, Lizard Ears and Coupled Oscillators

III - Moving Up the Phylogentic Tree

I - Harmonic Oscillator Group Delay



$$m\ddot{x} + b\dot{x} + kx = F_o \cos(\omega t)$$

eqn. of motion

$$z(t) = A\, e^{i(\omega t + \delta)}$$

sinusoidal steady-state

$$\gamma = \frac{b}{m} \qquad \omega_o = \sqrt{k/m}$$

change of variables

$$A(\omega) = \frac{F_o/m}{\left[(\omega_o^2 - \omega^2)^2 + (\gamma\omega)^2\right]^{1/2}}$$

$$\delta(\omega) = \tan^{-1}\left(\frac{\gamma\omega}{\omega^2 - \omega_o^2}\right)$$

amplitude and phase relative to driving stimulus

$$\beta = \frac{\omega}{\omega_o} \qquad Q = \frac{\omega_o}{\gamma}$$

one more change of variables

$$A(\beta) = \frac{F_o}{k} \frac{1/\beta}{\left[\left(\frac{1}{\beta} - \beta\right)^2 + \left(\frac{1}{Q^2}\right)^2\right]^{1/2}}$$

$$\delta(\beta) = \tan^{-1}\left(\frac{1/Q}{\beta - \frac{1}{\beta}}\right)$$

define the group delay:

$$\tau_{\mathrm{HO}} = -\frac{d\delta}{d\omega}\bigg|_{\omega_o} = -\frac{1}{\omega_o}\,\frac{d\delta}{d\beta}\bigg|_{\beta=1}$$

do some algebra.....

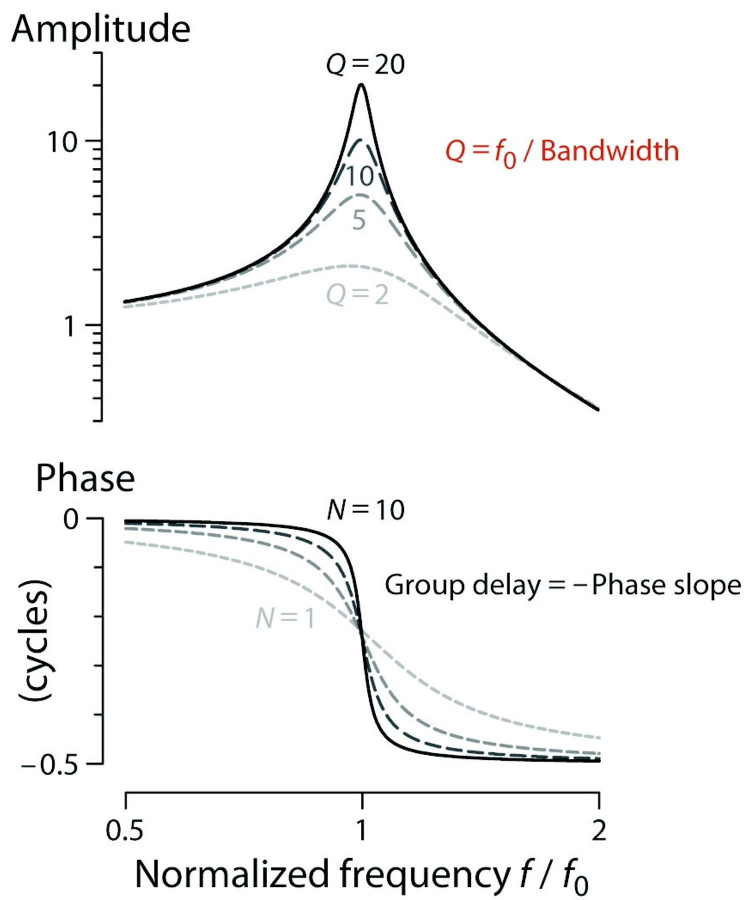
$$\frac{d\delta}{d\beta} = -\frac{1+1/\beta^2}{Q\left[\left(\beta-\frac{1}{\beta}\right)^2+\left(\frac{1}{Q}\right)^2\right]}$$

$$\tau_{\mathrm{HO}} = \frac{2Q}{\omega_o}$$

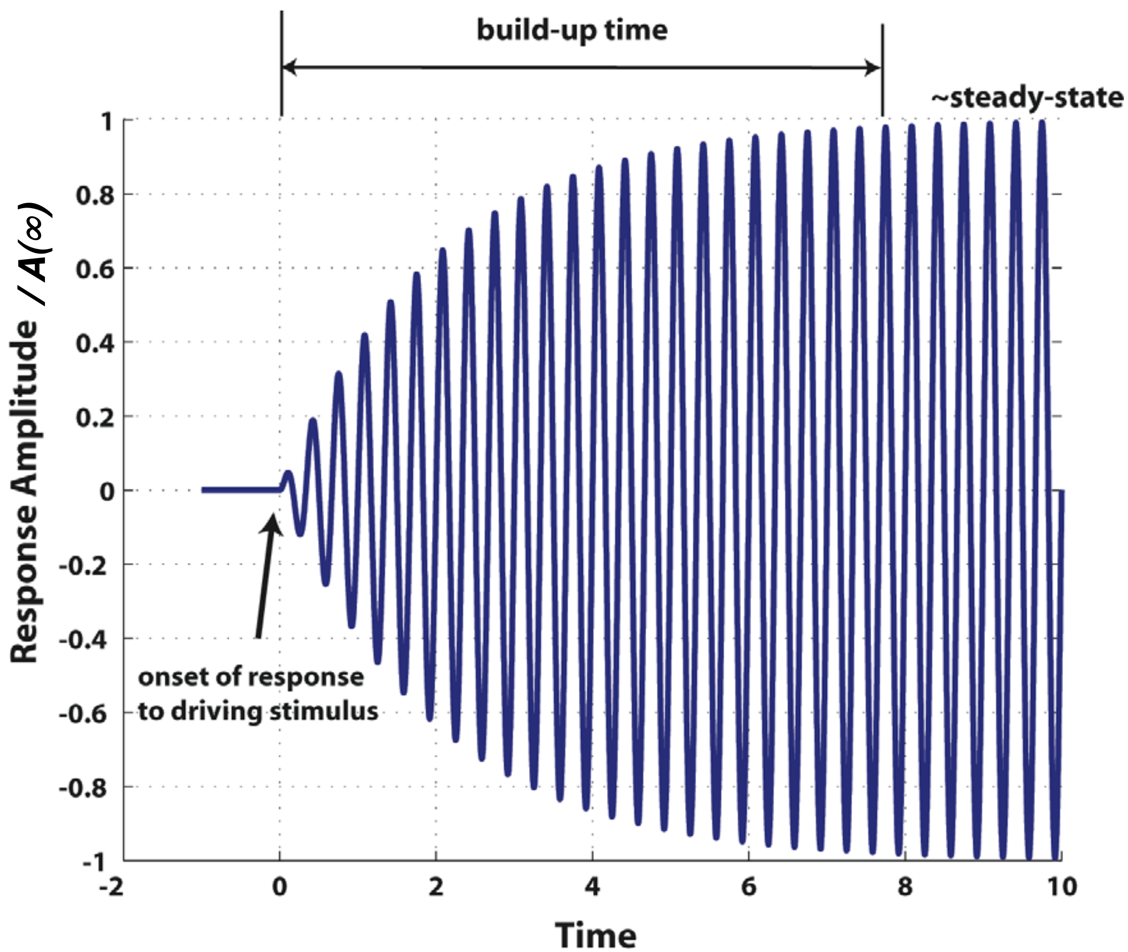
express group delay in periods:
(i.e. dimension-less form)

$$N_{\mathrm{HO}} = f_o \tau_{\mathrm{HO}} = \frac{\omega_o}{2\pi} \tau_{\mathrm{HO}}$$

$$N_{\mathrm{HO}} = \frac{Q}{\pi}$$



Tuned Responses Take Time

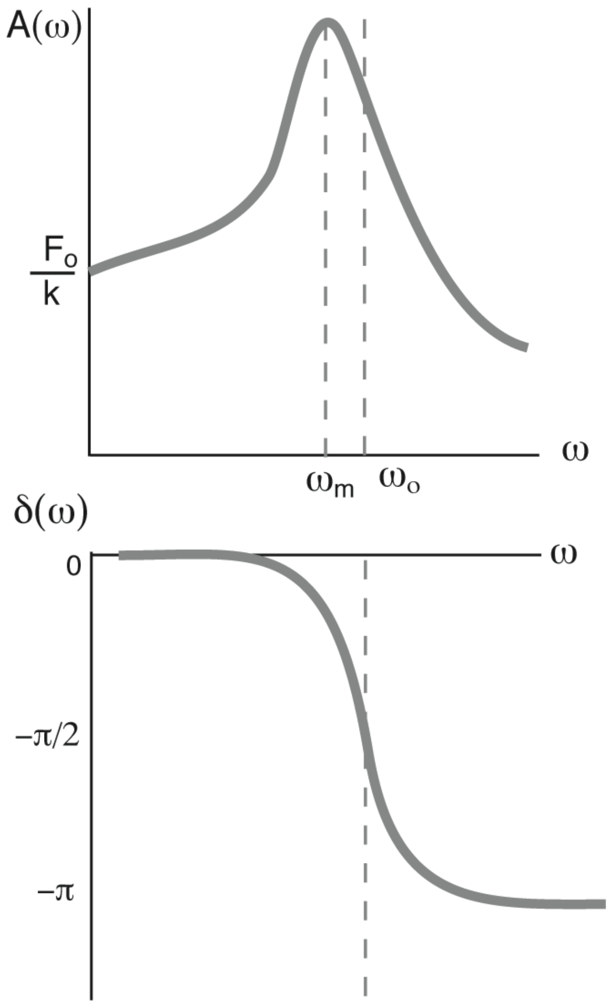


Second Order System
(resonant frequency ω_o)

$\Rightarrow$ **External driving force at frequency ω**

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

$$\tau = Q / \omega_o$$



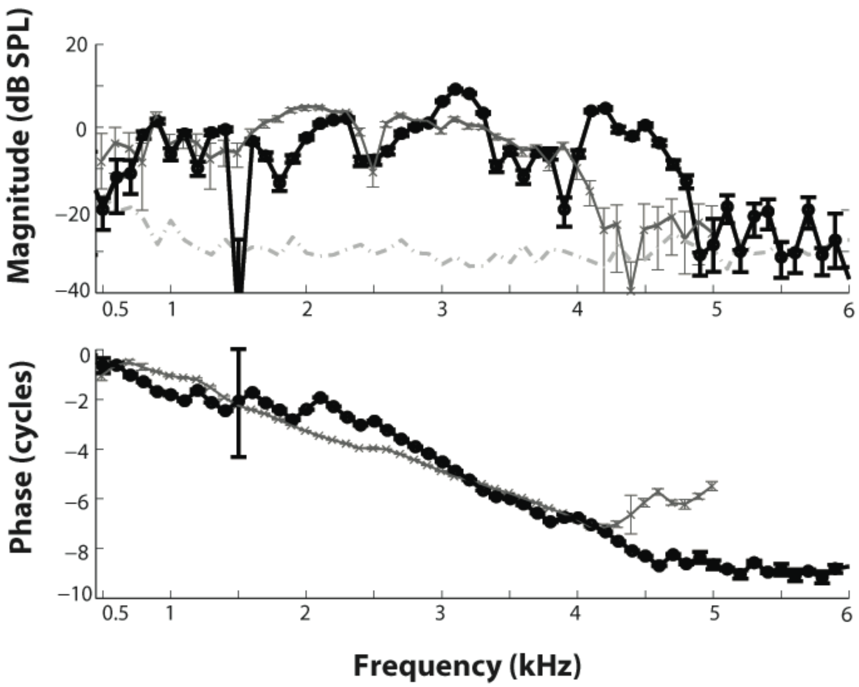
Unresolved: Physical basis for frequency difference between peak in magnitude and largest phase gradient

II - Otoacoustic Emission (OAE) Delays

- An OAE is a sound emitted by the ear, either spontaneously or in response to an external stimulus

- When a single *stimulus frequency* is presented, an SFOAE is evoked (at that same frequency)

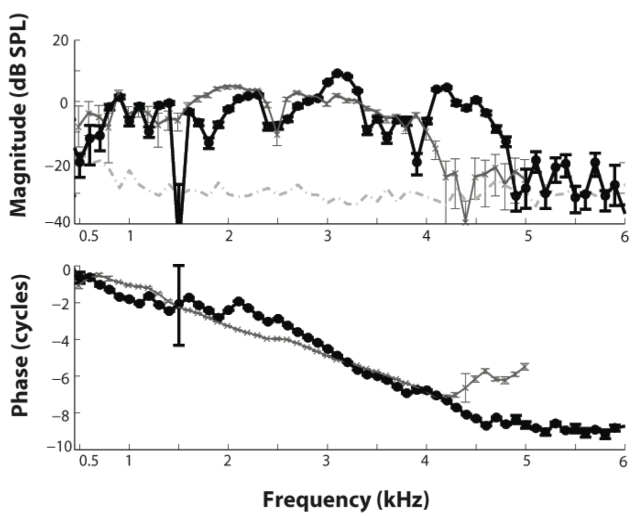
- SFOAEs can be observed in a wide range of species with differing morphologies



⇒ SFOAE data (*from a gecko ear shown here*) has peaks and valleys in the magnitude and large group delays across frequency

Hypothesis:

SFOAE group delays* reflect tuning mechanisms in the inner ear



* group delay ≡ phase-gradient delay

<u>Gecko Inner Ear</u>

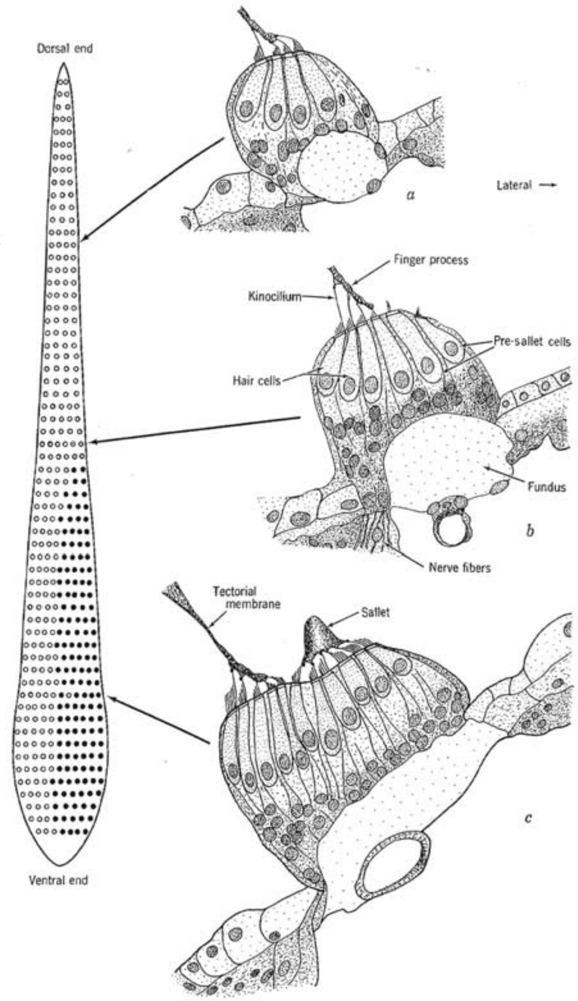
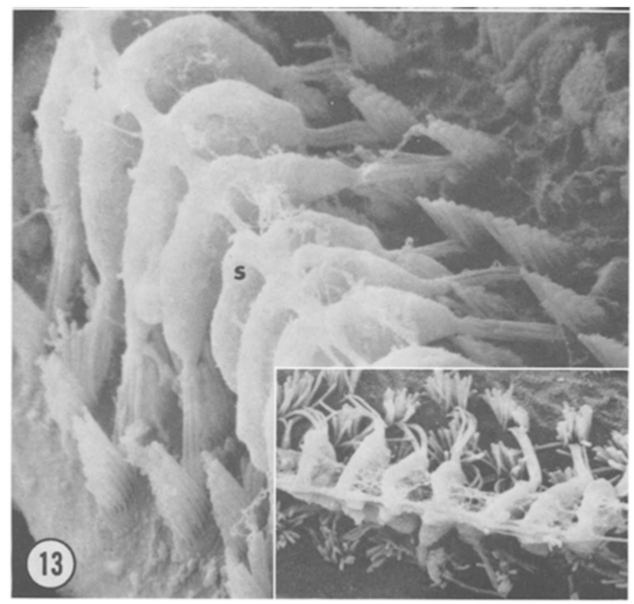


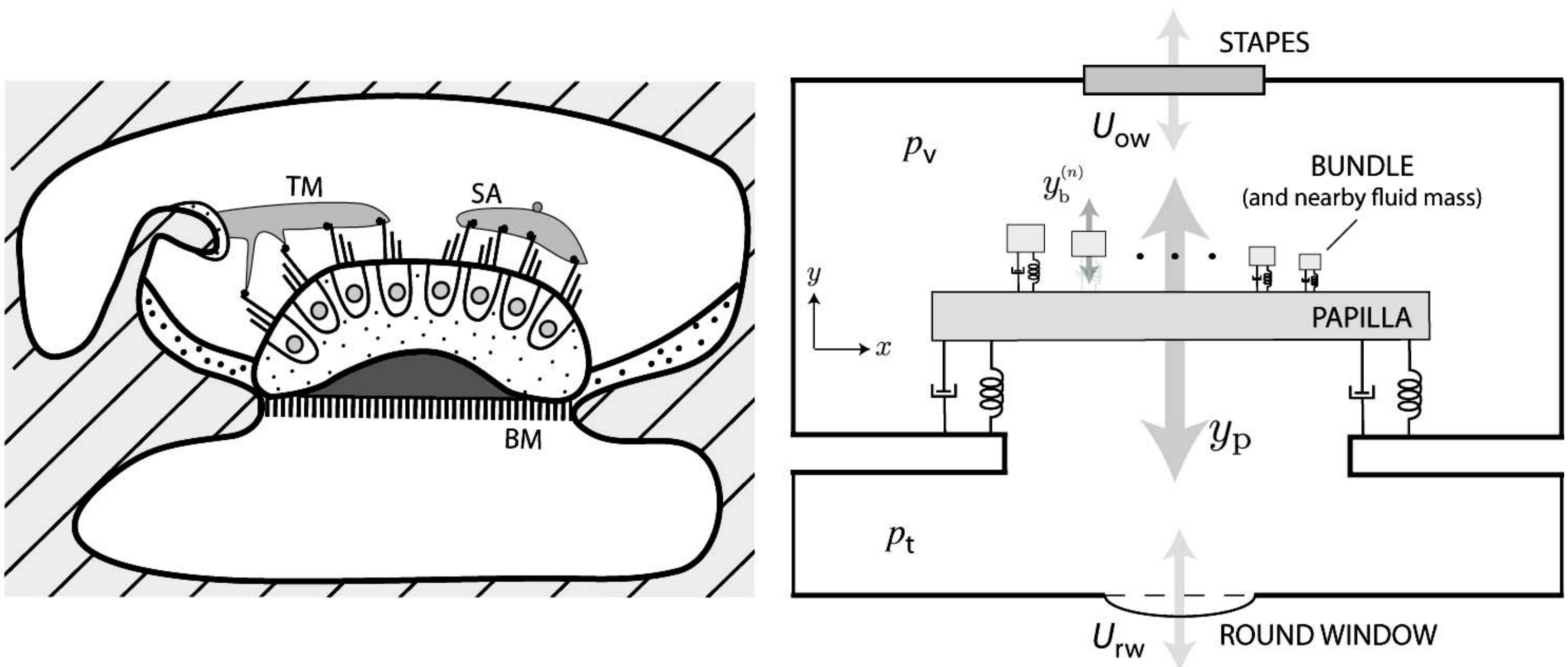
FIG. 14-3. The auditory papilla of *Eublepharis macularius*. On the left is the basilar membrane in outline showing the row structures of the hair cells; and on the right are three cross-sectional views of the auditory papilla at three cochlear regions. Scale for outline, 100×; for cross-sectional views, 400×. From Wever, 1974b.

Wever (1978)



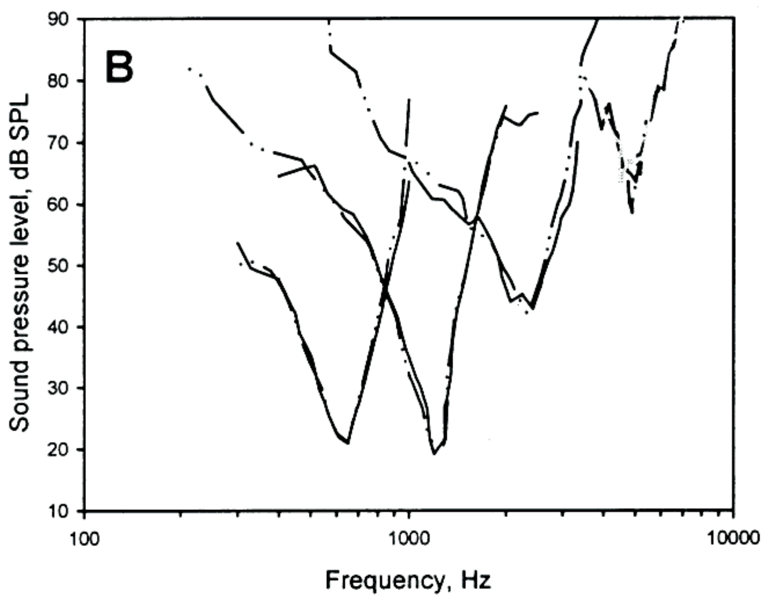
Miller (1973)

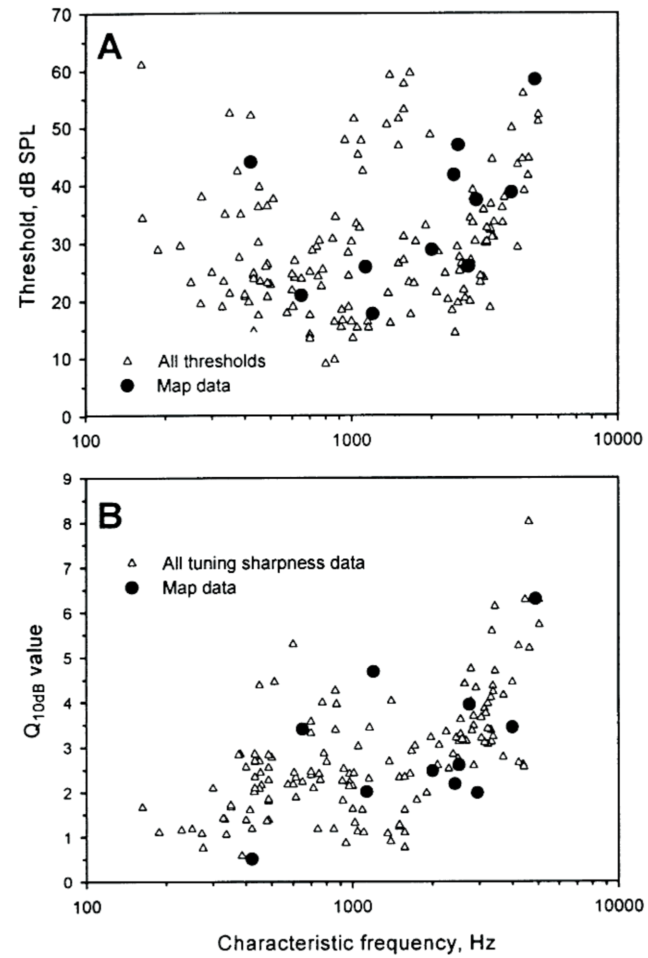
Coupled resonators (2nd order filters)



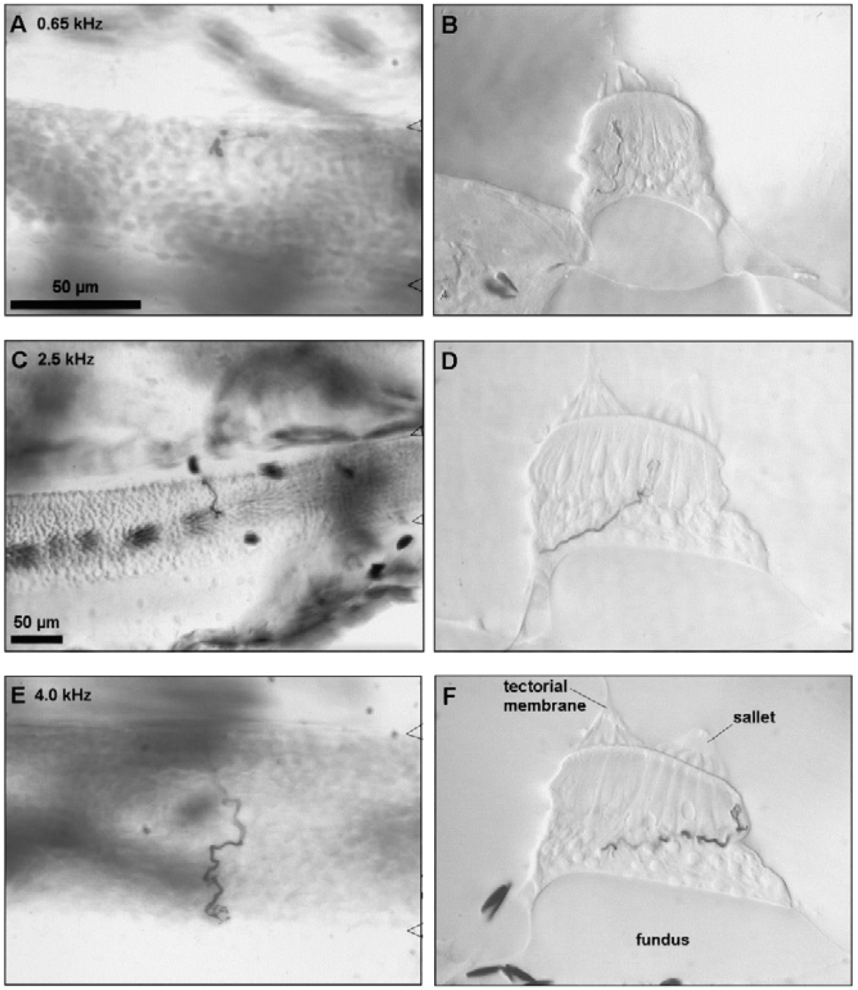
⇒ Each resonator has a unique tuning bandwidth [$Q(x)$] and spatially-defined characteristic frequency [$\beta(x)$]

Tokay Gecko Auditory Nerve Fiber Responses

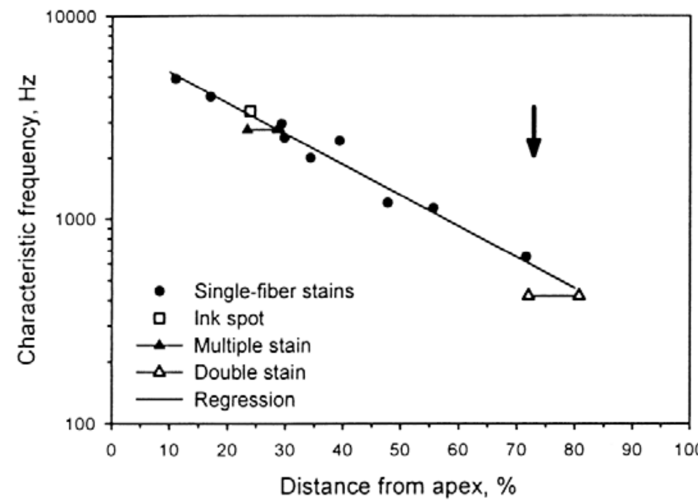




Manley et al. (1999)



Manley et al. (Hearing Research 1999)

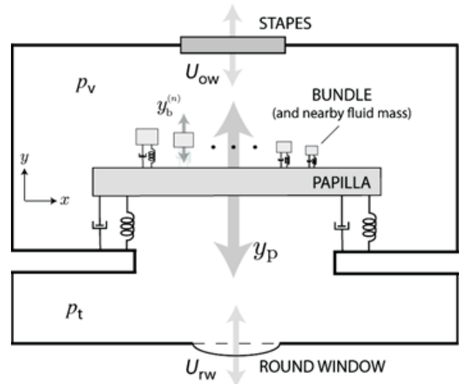


Physiological data quantifies both sharpness of tuning [$Q(x)$] and frequency map [$\beta(x)$]

Equation of Motion

Assumptions

- inner fluids are incompressible and the pressure is uniform within each scalae
- papilla moves transversely as a rigid body (rotational modes are ignored)
- consider hair cells grouped together via a sallet, each as a resonant element (referred to as a bundle from here on out)
- bundles are coupled only by motion of papilla (fluid coupling ignored)
- papilla is driven by a sinusoidal force (at angular frequency ω)
- system is **linear** and **passive**
- small degree of irregularity is manifest in tuning along papilla length



Change of Variables

$y_{\mathrm{b}}^{(n)} = y(x_n) = y_n$ *bundle longitudinal location* *(and similar notation for other parameters)*

$$\omega_n = \sqrt{\frac{k_n}{m_n}} = \omega_{\max} e^{-x_n/\ell}$$

n'th bundle characteristic frequency (CF)

$\beta_n = \omega/\omega_n$ *ratio of bundle resonant and stimulus frequencies*

$Q_n = \omega_n/\gamma_n$ *bundle bandwidth*

$A_{\mathrm{p}}(\mathbf{P}_{\mathrm{v}} - \mathbf{P}_{\mathrm{t}})$ *pressure difference across papilla is driving stimulus*

Papilla

$$m_{\mathrm{p}}\ddot{y}_{\mathrm{p}} = -k_{\mathrm{p}}y_{\mathrm{p}} - r_{\mathrm{p}}\dot{y}_{\mathrm{p}} + \sum_n k_{\mathrm{b}}^{(n)}(y_{\mathrm{b}}^{(n)} - y_{\mathrm{p}}) + A_{\mathrm{p}}(p_{\mathrm{v}} - p_{\mathrm{t}})$$

Bundle

(*n*'th bundle along papilla length)

$$\ddot{y}_{\mathrm{b}}^{(n)} = -\omega_{\mathrm{b}}^{(n)\,2}\left[y_{\mathrm{b}}^{(n)} - y_{\mathrm{p}}\right] - \gamma_{\mathrm{b}}^{(n)}\dot{y}_{\mathrm{b}}^{(n)}$$

time domain

$$y(t) = \mathbf{Y}(\omega)e^{i\omega t}$$

frequency domain

Papilla:

$$\mathbf{Y}_{\mathrm{p}}\left[-\omega^2 m_{\mathrm{p}} + i\omega r_{\mathrm{p}} + k_{\mathrm{p}} + \sum_n k_n\right] = \sum_n k_n \mathbf{Y}_n + A_{\mathrm{p}}(\mathbf{P}_{\mathrm{v}} - \mathbf{P}_{\mathrm{t}})$$

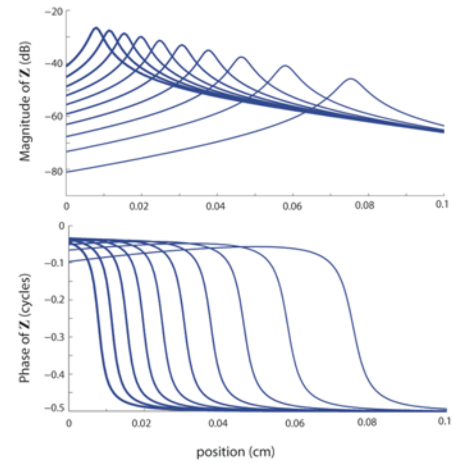
Bundle:

$$\mathbf{Y}_n = \mathbf{Y}_p \frac{1}{1 - \beta_n{}^2 + i\beta_n/Q_n}$$

An Emission Defined

$$\mathbf{Y}_\mathrm{p}\left[-\omega^2 m_\mathrm{p} + i\omega r_\mathrm{p} + k_\mathrm{p} + \sum_n k_n \frac{-\beta_n^2 + i\beta_n/Q_n}{1-\beta_n^2 + i\beta_n/Q_n}\right] = A_\mathrm{p}(\mathbf{P}_\mathrm{v} - \mathbf{P}_\mathrm{t})$$

combine both eqns. of motion in frequency domain



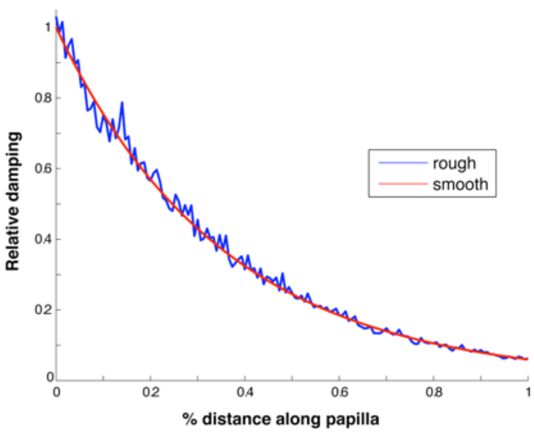
Model impedance (**Z**) for ten different stimulus frequencies (thicker lines for higher driving frequency). The plot shows contributions from the bundles, papilla terms are neglected. [150 bundles with CFs from 0.2-5 kHz; 10 stimulus frequencies linearly spaced from 0.6-4 kHz]. Bundle stiffness (k_n) was assumed to vary exponentially.

Input Impedance

$$i\omega \mathbf{Y}_\mathrm{p} A_\mathrm{p} = \mathbf{U}_\mathrm{ow}$$

conservation of mass

$$\mathbf{Z} \equiv \frac{\mathbf{P}_\mathrm{v} - \mathbf{P}_\mathrm{t}}{\mathbf{U}_\mathrm{ow}} = \frac{1}{i\omega A_\mathrm{p}^2}\left[Z_\mathrm{p} + \sum_n k_n \frac{-\beta_n^2 + i\beta_n/Q_n}{1-\beta_n^2 + i\beta_n/Q_n}\right]$$



Irregularity

$$\tilde{Q}_n = Q_n(1+\epsilon_n)$$

ϵ_n is a small perturbation term

$$\Delta\mathbf{Z} = \tilde{\mathbf{Z}} - \mathbf{Z}$$

impedance difference between irregular and smooth conditions

$$\boxed{\Delta\mathbf{P} \equiv \Delta\mathbf{Z}\ \mathbf{U}_\mathrm{ow}}$$

papilla contributions cancel out

[SFOAE is complex difference between ‘smooth’ and ‘rough’ conditions]

Phase-Gradient Delay

$$\tau_{\rm OAE} = -\frac{1}{2\pi}\frac{\partial \phi}{\partial f} \quad \text{where } \phi = \arg(\Delta P) \longrightarrow \boxed{N_{\rm OAE} = f\tau_{\rm OAE}}$$

Analytic Approximation

-To derive an approximate expression for the model phase-gradient delay, we make several simplifying assumptions (e.g., convert sum to integral, assuming bundle stiffness term is approximately constant, etc.)

$$\Delta P \approx \frac{U_{\rm ow} k_{\rm o} \ell}{\omega A^2} \int_{\beta_0}^{\beta_L} \epsilon(x) \frac{A^2}{Q} e^{2i\theta} d\beta$$

rewrite expression for emission in continuous limit with suitable change of variables

$$\beta_L \equiv \omega/\omega_{\rm min} \qquad \beta_0 \equiv \omega/\omega_{\rm max} \qquad x = \ell \ln\left(\frac{\beta}{\beta_0}\right)$$

$$\frac{1}{1-\beta^2+i\beta/Q} \equiv A(\beta)e^{i\theta(\beta)}$$

transfer function for the harmonic oscillator

express irregularity as composed of distinct spatial frequencies along length of papilla

$$\epsilon(x) = \sum_\kappa \epsilon_\kappa e^{i\kappa x}$$

frequency dependence of emission phase (ϕ) comes primarily from this term, requiring us to determine $\kappa_{\rm opt}$

the amplitude is a sharply peaked function (Fig.3), indicating the value of the integral is relatively constant with respect to stimulus frequency (ω)

given the strongly peaked nature of the integrand and by analogy to coherent reflection theory, we expect that only spatial frequencies close to some optimal value will contribute

$$\Delta P \approx \frac{U_{\rm ow} k_{\rm o} \ell \epsilon_{\kappa_{\rm opt}}}{\omega A^2} e^{-i\kappa_{\rm opt}\ell \ln \beta_0} \int_{\beta_0}^{\beta_L} \frac{A^2(\beta)}{Q(\beta)} e^{i[\kappa_{\rm opt}\ell \ln\beta + 2\theta(\beta)]} d\beta$$

Analytic Approximation (cont.)

for the integral to be maximal, we require the phase be stationary about the magnitude peak (i.e., $\beta = 1$), allowing us to solve for the optimal spatial frequency

$$\frac{\partial}{\partial\beta}\left[\kappa_{\text{opt}}\ell\ln\beta + 2\theta(\beta)\right]\big|_{\beta=1} = 0 \quad \longrightarrow \quad \kappa_{\text{opt}} = -\frac{2}{\ell}\frac{\partial\theta}{\partial\beta}\bigg|_{\beta=1} = -\frac{2\omega}{\ell}\frac{\partial\theta}{\partial\omega}$$

as shown previously for the harmonic oscillator

$$\frac{\partial\theta}{\partial\omega}\bigg|_{\omega_o} = -\frac{Q}{f\pi}$$

from above, our expression for the model phase-gradient delay will be

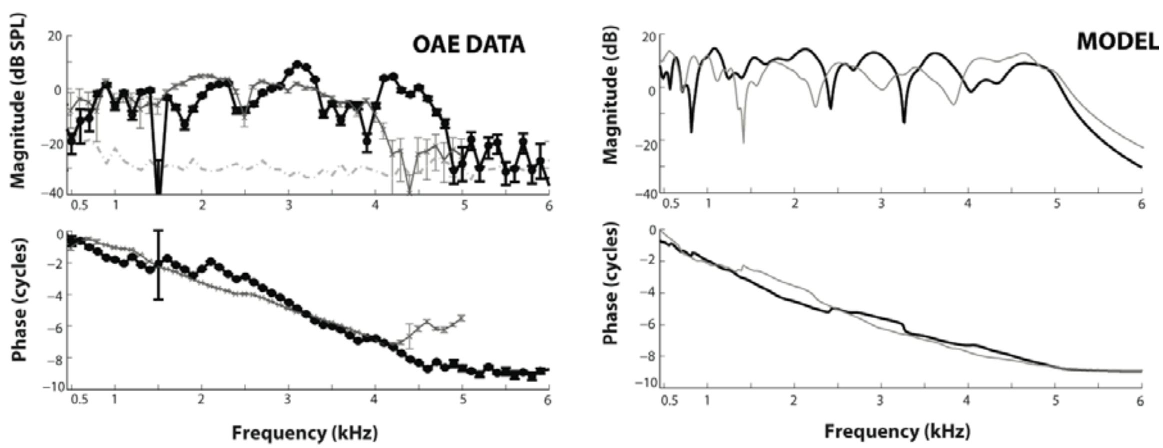
$$N_{\text{OAE}} = \frac{\kappa_{\text{opt}}\ell}{2\pi}$$

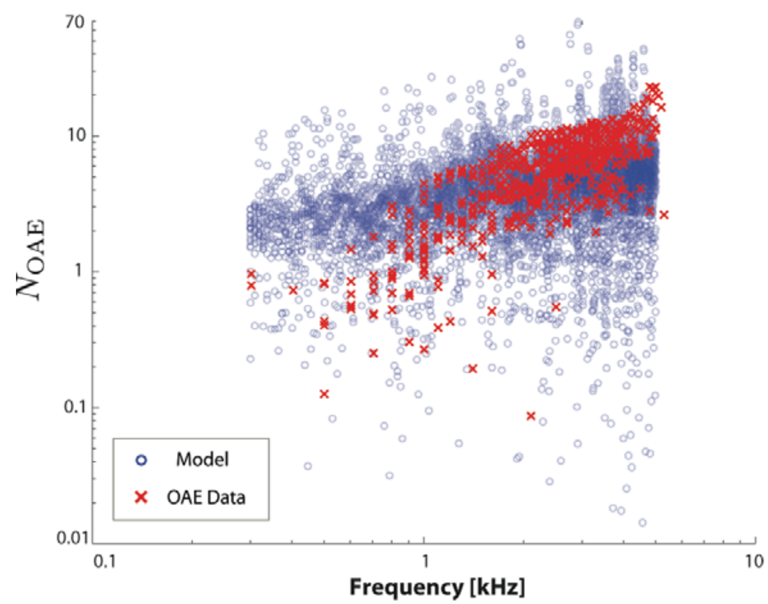
combining all our expressions we finally have....

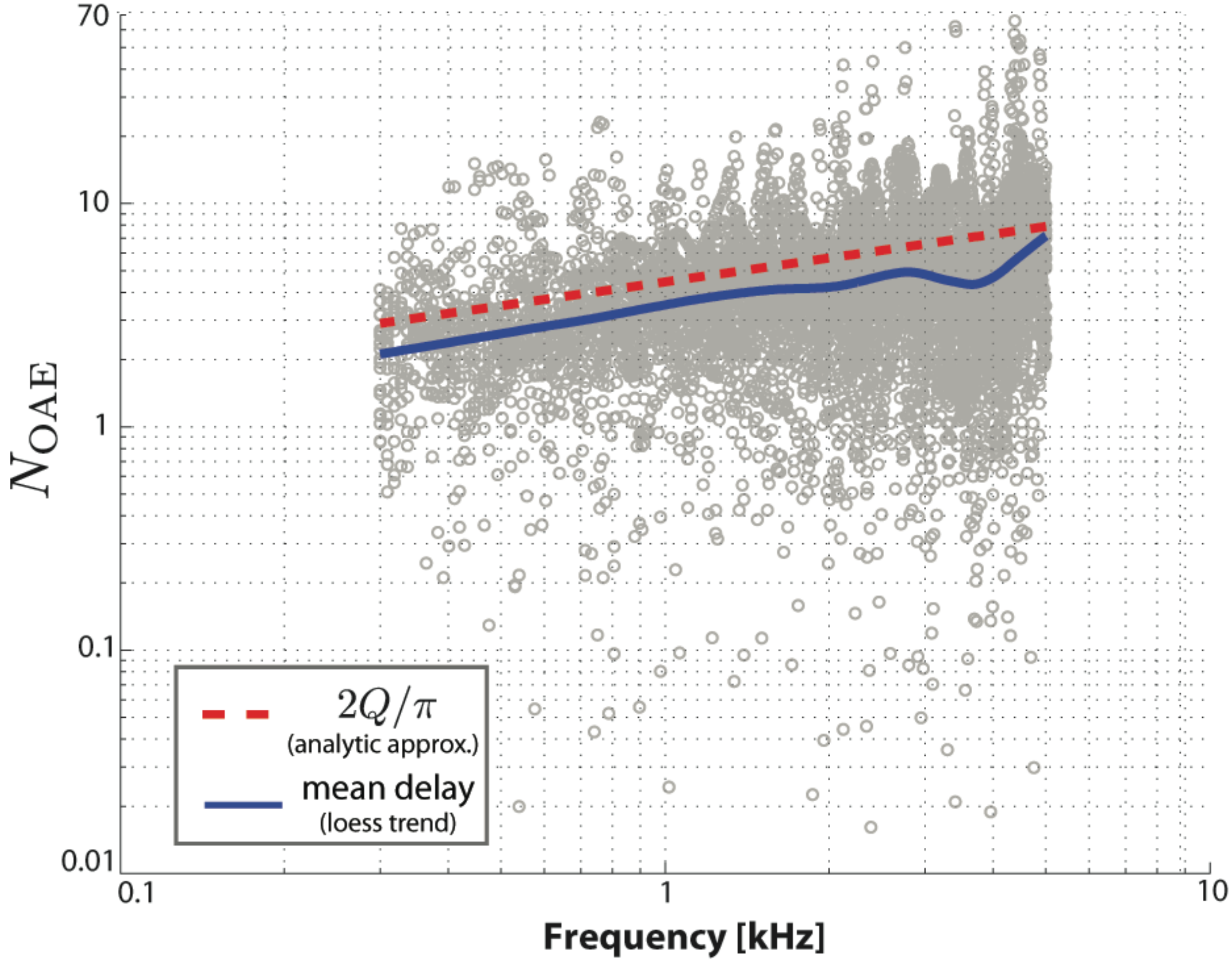
$$\boxed{N_{\text{OAE}} \approx \frac{2Q}{\pi}}$$

thus, the phase gradient delay is directly proportional to the sharpness of tuning

Model and Data Comparison



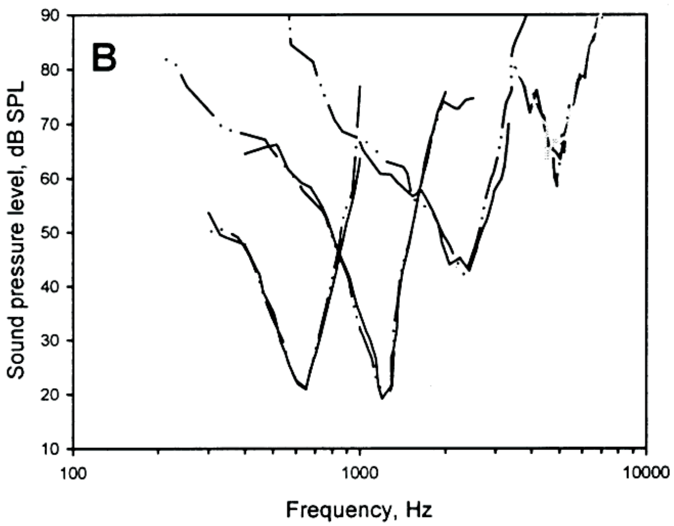




70
10
1
0.1
0.01
0.1
1
10
N_{OAE}
Frequency [kHz]
$2Q/\pi$
(analytic approx.)
mean delay
(loess trend)

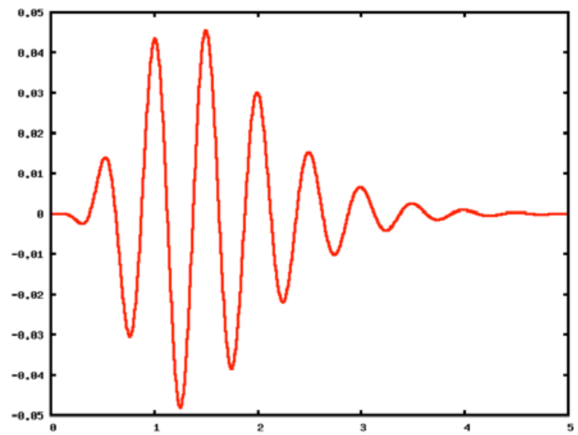
A Step Further....

A better assumption as to the filter itself?



$$\frac{1}{[1-\beta^2+i\beta/Q]^m}$$

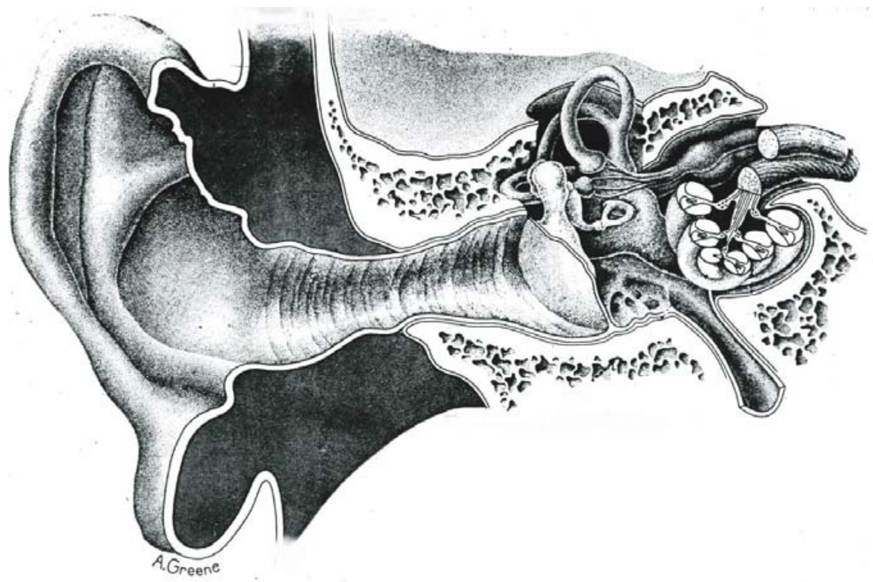
Gammatone filter of order m

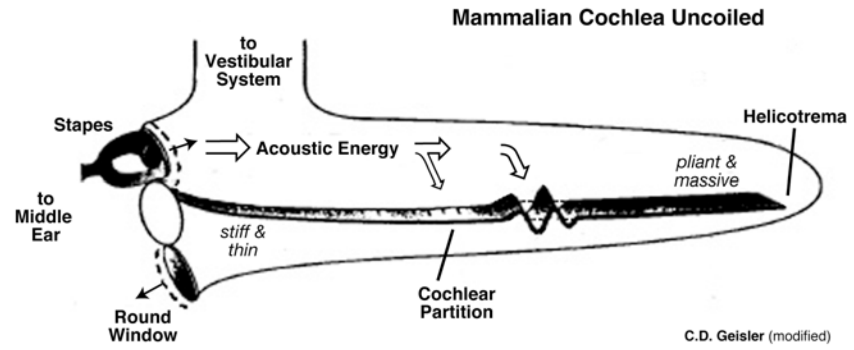


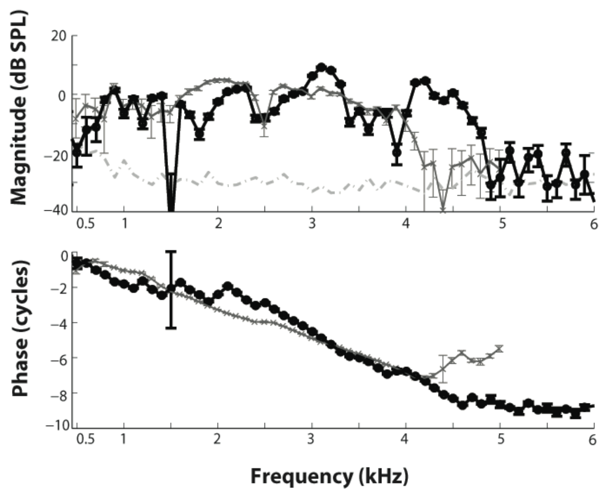
http://en.wikipedia.org/wiki/Image:Sample_gammatone.png

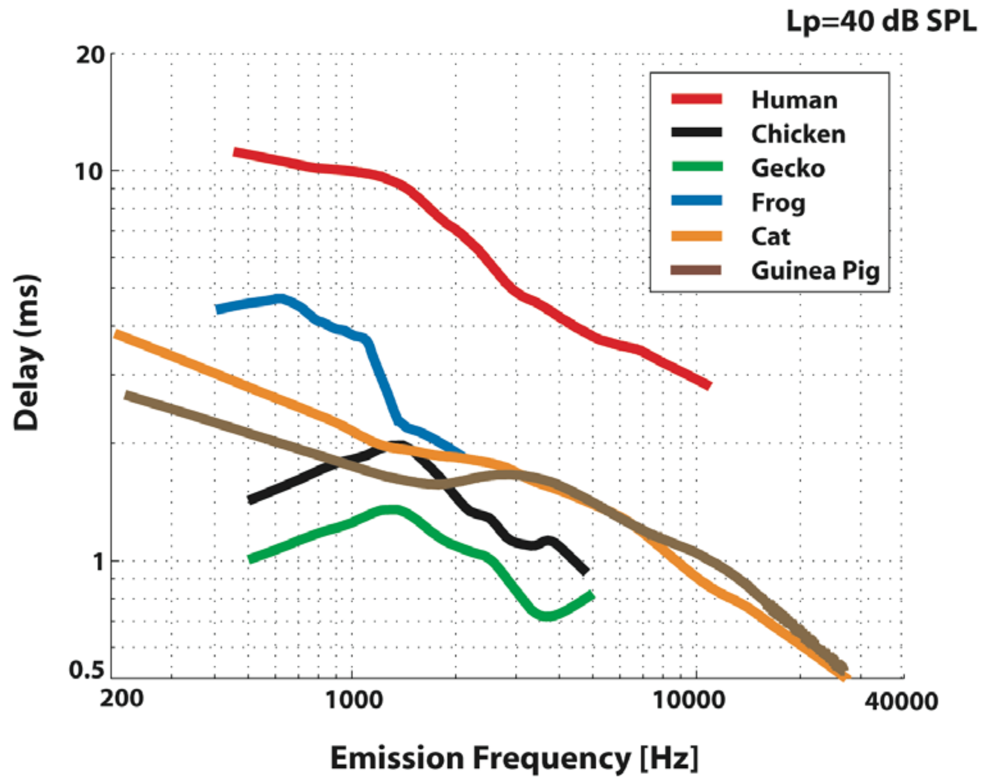
$$N \propto \frac{mQ}{\pi}$$

III - Traveling Waves (mammals) = Confounding factor



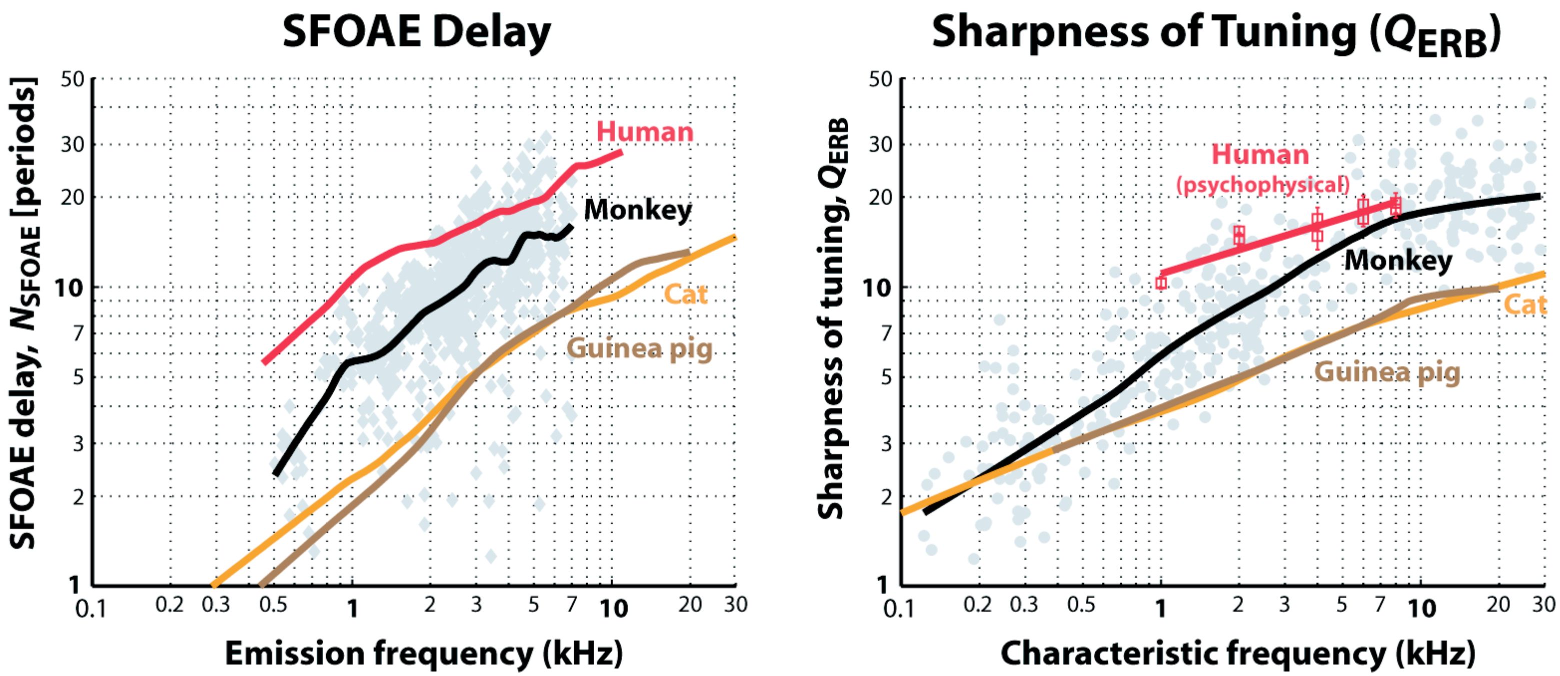






[cat and guinea pig data from Shera and Guinan, 2003]

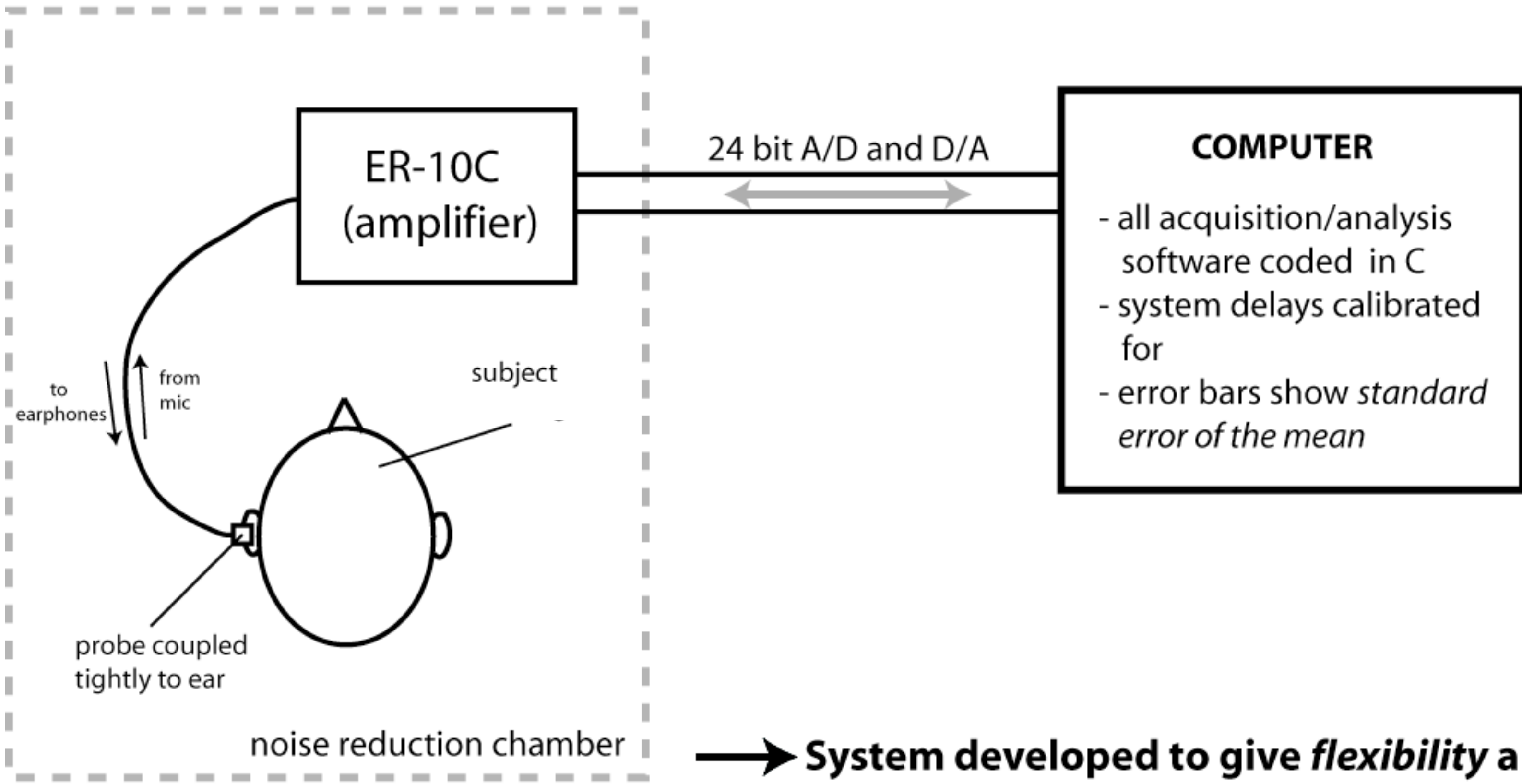
Comparison of SFOAE Delays and ANF Tuning Across Species



Fini

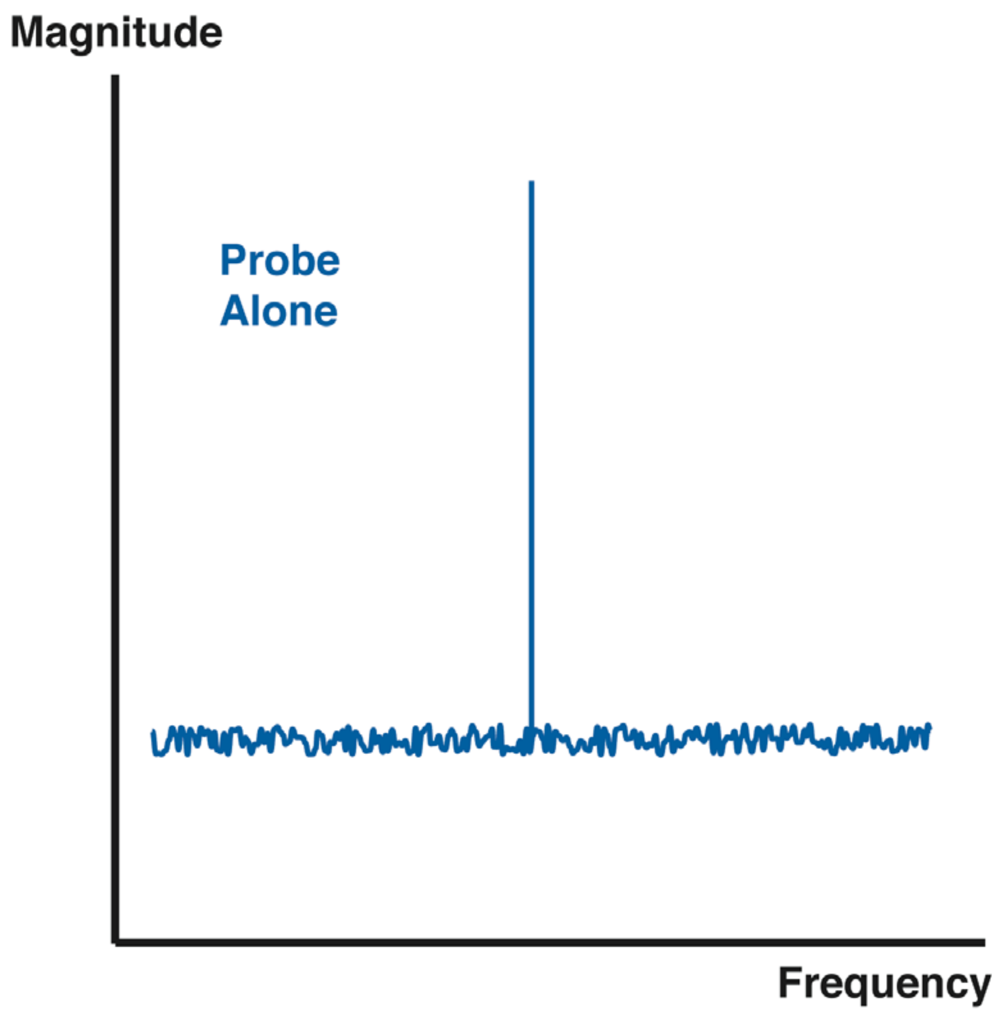
METHODS

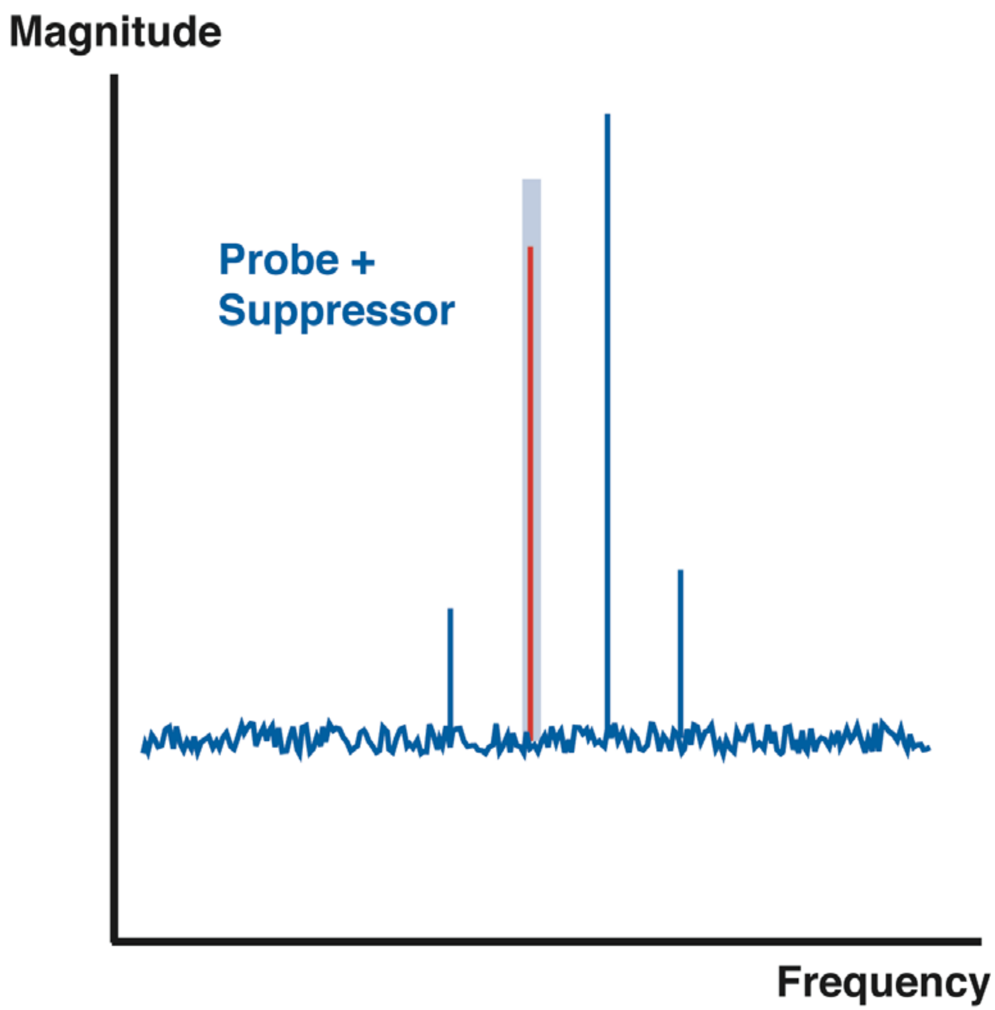
OAE Measurement System



→ **System developed to give *flexibility* and allow for *phase* measurements**

Animals *anesthetized* to prevent movement


Magnitude
Probe
Alone
Frequency

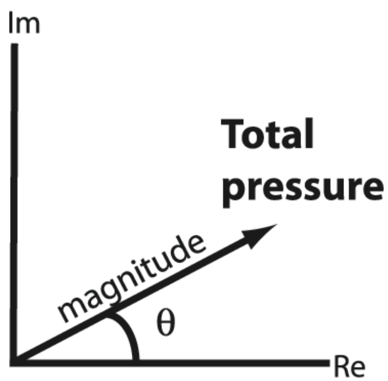


Magnitude
Probe +
Suppressor
Frequency

SFOAEs: Nonlinear suppression paradigm

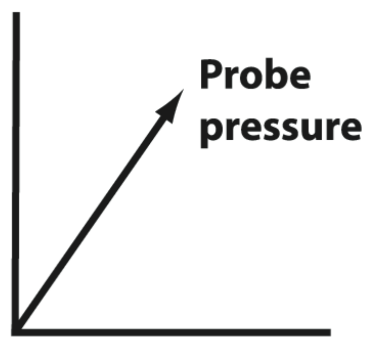
Step 1.
Present Probe Alone
(**emission is present**)

FFT reveals magnitude
and phase **AT Probe Freq.**



Step 2.
Present both Probe &
Suppressor tones
(**emission not present**)

FFT reveals magnitude
and phase **AT Probe freq.**



Step 3.
Subtract phasors