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

Christopher Bergevin (University of Arizona)
Christopher Shera (Harvard Medical School)

Mathematical Physics Seminar
9/10/08
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

Amplitude

Phase

Group delay = −Phase slope

Normalized frequency $f / f_0$
\[ m\ddot{x} + b\dot{x} + kx = F_0 \cos(\omega t) \]  

eqn. of motion

\[ z(t) = A e^{i(\omega t + \delta)} \]  
sinusoidal steady-state

\[ \gamma = \frac{b}{m} \quad \omega_o = \sqrt{\frac{k}{m}} \]  
change of variables

\[ A(\omega) = \frac{F_0/m}{\left[(\omega_o^2 - \omega^2)^2 + (\gamma \omega)^2\right]^{1/2}} \]  
amplitude and phase relative to driving stimulus

\[ \delta(\omega) = \tan^{-1}\left(\frac{\gamma \omega}{\omega^2 - \omega_o^2}\right) \]
\[ \beta = \frac{\omega}{\omega_o} \quad Q = \frac{\omega_o}{\gamma} \]

one more change of variables

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

\[ \delta(\beta) = \tan^{-1} \left( \frac{1/Q}{\beta - 1/\beta} \right) \]
define the group delay:

\[ \tau_{HO} = -\frac{d\delta}{d\omega} \bigg|_{\omega_o} = -\frac{1}{\omega_o} \frac{d\delta}{d\beta} \bigg|_{\beta=1} \]

do some algebra.....

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

\[ \tau_{HO} = \frac{2Q}{\omega_o} \]
express group delay in periods: (i.e. dimension-less form)

\[ N_{HO} = \frac{Q}{\pi} \]

\[ N_{HO} = f_o \tau_{HO} = \frac{\omega_o}{2\pi} \tau_{HO} \]
Tuned Responses Take Time

Second Order System
(resonant frequency $\omega_o$)

$\Rightarrow$ External driving force at frequency $\omega$

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

$$\tau = \frac{Q}{\omega_o}$$
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
Gecko Inner Ear

Fig. 14.3. The auditory papilla of Rhaphidophorus musculifer. On the left is the basilar membrane in outline showing the row structures of the hair cells; and on the right are these cross-sectional views of the auditory papilla at three cochlear regions. Scale for outline, 100X; for cross-sectional views, 400X. From Wever, 1974a.
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)
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 scala.
- Papilla moves transversely as a rigid body (rotational modes are ignored).
- Consider hair cells grouped together via a sennet, 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 \( \omega \)).
- System is linear and passive.
- Small degree of irregularity is manifest in tuning along papilla length.

**Papilla**

\[ m_p \ddot{y}_p = -k_p y_p - r_p \dot{y}_p + \sum_n k_b^{(n)} (y_b^{(n)} - y_p) + A_p (p_v - P_t) \]

**Bundle**

\[ \ddot{y}_b^{(n)} = -\omega_b^{(n)} \left[ y_b^{(n)} - y_p \right] - \gamma_b^{(n)} \dot{y}_b^{(n)} \]

**Change of Variables**

\[ y_b^{(n)} = y_n = \text{bundle longitudinal location} \]

\[ \omega_n = \sqrt{\frac{k_n}{m_n}} = \omega_{\text{max}} e^{-x_n/l} \]

\[ \beta_n = \omega/\omega_n \]

\[ Q_n = \omega_n/\gamma_n \]

\[ A_p (P_v - P_t) \]

**Papilla:**

\[ Y_p \left[ -\omega^2 m_p + i \omega r_p + k_p + \sum_n k_n \right] = \sum_n k_n Y_n + A_p (P_v - P_t) \]

**Bundle:**

\[ Y_n = Y_p \frac{1}{1 - \beta_n^2 + i \beta_n/Q_n} \]
An Emission Defined

\[ Y_p \left[ -\omega^2 m_p + i\omega r_p + k_p + \sum_n k_n \frac{-\beta_n^2 + i\beta_n/Q_n}{1 - \beta_n^2 + i\beta_n/Q_n} \right] = A_p (P_v - P_t) \]

combine both eqns. of motion in frequency domain

Input Impedance

\[ i\omega Y_p A_p = U_{ow} \]

\[ Z \equiv \frac{P_v - P_t}{U_{ow}} = \frac{1}{i\omega A_p} \left[ Z_p + \sum_n k_n \frac{-\beta_n^2 + i\beta_n/Q_n}{1 - \beta_n^2 + i\beta_n/Q_n} \right] \]

Model impedance (Z) for ten different stimulus frequencies (thicker lines for higher crossing frequency). The plot shows contributions from the bundles, papilla terms are neglected. 150 bundles with CF's from 0.2-5 kHz; 10 stimulus frequencies linearly spaced from 0.5-4 kHz. Bundle stiffness (\( A_p \)) was assumed to vary exponentially.

Irregularity

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

\[ \Delta Z = \tilde{Z} - Z \]

\[ \Delta P \equiv \Delta Z U_{ow} \]

[SFOAE is complex difference between ‘smooth’ and ‘rough’ conditions]
Phase-Gradient Delay

\[ \tau_{\text{OAE}} = -\frac{1}{2\pi} \frac{\partial \phi}{\partial f} \quad \text{where} \quad \phi = \text{arg}(\Delta P) \]

\[ N_{\text{OAE}} = \int \tau_{\text{OAE}} \]

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.)

\[ \Delta P \approx \frac{U_{\text{ow}} k \ell}{\omega A^2} \int_{\beta_0}^{\beta_L} \frac{A^2}{Q} e^{2i\theta} d\beta \]

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

\[ x = \ell \ln \left( \frac{\beta}{\beta_0} \right) \]

\[ \frac{1}{1 - \beta^2 + i\beta/\ell} \equiv A(\beta)e^{i\theta(\beta)} \]

transfer function for the harmonic oscillator

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

\[ \sum_{\kappa} \varepsilon_{\kappa} e^{i\kappa \ell} \]

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

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

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

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

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....

\[
N_{\text{OAE}} \approx \frac{2Q}{\pi}
\]

thus, the phase gradient delay is directly proportional to the sharpness of tuning
Model and Data Comparison
A Step Further....

A better assumption as to the filter itself?

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

Gammatone filter of order \(m\)

\[ N \propto \frac{mQ}{\pi} \]
III - Traveling Waves (mammals) = Confounding factor
Lp=40 dB SPL

![Graph of Delay (ms) vs Emission Frequency [Hz]]

-cat and guinea pig data from Shera and Guinan, 2003-
Comparison of SFOAE Delays and ANF Tuning Across Species

**SFOAE Delay**

- Emission frequency (kHz)
- SFOAE delay, $N_{sFOAE}$ [periods]

**Sharpness of Tuning ($Q_{ERB}$)**

- Characteristic frequency (kHz)
- Sharpness of tuning, $Q_{ERB}$

Species included:
- Human
- Monkey
- Cat
- Guinea pig
Fini
Animals anesthetized to prevent movement

METHODS

OAE Measurement System

- System developed to give flexibility and allow for phase measurements

Animals *anesthetized* to prevent movement
Probe Alone
Probe + Suppressor
SFOAEs: Nonlinear suppression paradigm

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

FFT reveals magnitude and phase \textit{AT Probe Freq.}

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

FFT reveals magnitude and phase \textit{AT Probe freq.}

**Step 3.** Subtract phasors

SFOAE revealed!!