Long Delays Without Basilar-Membrane Traveling Waves: Correlations Between Tuning Bandwidth and Emission Delay in a Model of the Gecko Inner Ear

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Motivation

- Stimulus-frequency otoacoustic emissions (SFOAEs) demonstrate significant phase-gradient delays on the order of a millisecond or longer in a wide array of species [Bergevin et al. 2008].

- Phase-gradient delays, defined as the slope of the emission phase with respect to stimulus frequency, are similar to delays measured in the time domain in both mammals and non-mammals [Schoonhoven et al. 2001; Withnell et al. 2005; Meenderink and Narins, 2005; Sisto et al. 2007].

- These delays are not due to the middle ear, whose contribution is on the order of tens of microseconds [Rosowski et al. 1985].

- The source of these delays is not well understood, particularly in species that lack a propagating traveling wave along the basilar membrane (BM) [Figure 1].

QUESTION: *What is the mechanism that gives rise to significant delays observed in OAEs?*

FIGURE 1 Comparison of SFOAE phase-gradient delays systematically measured across a wide range of vertebrate species. In spite of gross morphological differences (size, a BM that supports traveling waves, etc.), delays are comparable between common laboratory mammals and non-mammals such as birds and lizards [Bergevin et al. 2008].

Lizards Ears as a Model

HYPOTHESIS: *Delays arise from mechanical tuning in the inner ear*

- To address this question/hypothesis, we develop a model for a relatively simple ear where delays are significant (~1 ms) and BM traveling waves are not present, the idea being that 'travel time' is minimized as a confounding factor.

- We focus here on the inner ear of the gecko, a lizard that exhibits low thresholds and robust emissions. There is also a significant body of literature on various aspects of gecko auditory anatomy and physiology (e.g., auditory nerve fiber responses) [Wever, 1978; Manley et al. 1999].

- The gecko inner ear consists of ~1000 hair cells sitting atop the relatively rigid basilar papilla, with regions of both a continuous and discretized overlying tectorial membrane coupling nearby cells together [Wever, 1978]

- The general approach taken here is to model the ear as a series of coupled oscillators based upon the assumption that low-level SFOAE generation is essentially a linear process. Additionally, the following assumptions are made:

  o Papilla moves as a rigid body with one degree of freedom (rotational modes are ignored)
  o Hair cell groups coupled via sallets act as resonant elements [Authier and Manley, 1995; Aranyosi and Freeman, 2004]
  o Coupling among elements comes via the papilla only (no fluid or elastic coupling)
  o Each resonant element as well is the papilla is considered to be both linear and passive
  o Small degree of irregularity is manifest (i.e., perturbations) in the tuning of each resonant element

FIGURE 2 *Left*: Simplified transverse-radial cross-sectional schematic of the gecko inner-ear anatomy showing hair cells embedded in the papilla. Papilla has an effective area A_p and length $L = 0.1$ cm. The gecko is one of many lizard species that has sallets, discretized sections of tectorium that are thought to behave as resonant filters. White regions are fluid-filled, gray region represent the overlying tectorium, gray striped areas represent bone, and stippled areas are supporting cellular structures. Abbreviations: BM - basilar membrane, TM - tectorial membrane, SA - sallet. *Right*: Longitudinal-transverse cross-section of the model, consisting of a collection of linear oscillators coupled by the motion of the basilar papilla.

Estimating Model Parameters from Gecko ANFs

- A starting point is to assume that the underlying filters are second order (i.e., harmonic oscillators; $m=1$), each with a unique characteristic frequency (β) and tuning bandwidth (Q). Analysis of this case has been previously described [Bergevin and Shera, 2008].

- However, 2nd order filters do not capture many of the features observed in the ANF data (e.g., significantly longer phase delays) and a more suitable underlying filter assumption is needed.

$$H(\beta) = \frac{1}{(1 - \beta^2 + i\beta/Q)^m}$$

Equation 1: Transfer function for the m'th order gammatone filter. β is the normalized frequency (i.e., $\beta = f/f_o$ where f is the driving frequency and f_o is the filter center frequency, or CF) and Q is the filter bandwidth

- Gammatone filters (Eqn.1) have been proposed to account for many of the features observed in the linear behavior of ANFs [e.g., de Boer 1975; Carney and Yin, 1988] and are better able to handle the asymmetry in the magnitude response. Gammatone filters have also been used to estimate tuning bandwidths based upon DPOAE delays [Bowman et al. 1998].

- The gammatone filters (Eqn.1) can readily be incorporated into the model impedance (Eqn.2) as shown in Figure 3. The resulting SFOAE is defined as the complex difference in the impedance between the perturbed and unperturbed case (analogous to a nonlinear suppression paradigm) as given in Eqn.3. Subsequently, the phase-gradient delay is defined by Eqn.4.

$$\mathbf{Z} \equiv \frac{\mathbf{P_v} - \mathbf{P_t}}{\mathbf{U_{ow}}} = \frac{1}{i\omega A_p^2}\left[Z_p + \sum_n^{150} k_n \frac{1 - [1 - \beta_n^2 + i\beta_n/Q_n]^m}{[1 - \beta_n^2 + i\beta_n/Q_n]^m}\right]$$

Equation 2: Input impedance to lizard inner ear model assuming m'th order gammatone filters. Subscript p indicates papilla parameters (e.g., A_p is the papilla area) while n indicates an individual bundle (e.g., k_n is the stiffness of the n'th bundle). Sum represents inclusion of contributions from all bundles along papilla

FIGURE 3: Model impedance (**Z**) for twelve different stimulus frequencies (thicker lines for higher driving frequency). The plot shows contributions from the bundles, papilla terms are neglected. Both the perturbed (red) and unperturbed (blue) cases are shown. Bundle stiffness (k_n) was assumed to vary exponentially. Filter order varied as m(CF)=4.5 CF$^{0.12}$ [150 bundles with CFs from 0.3-5 kHz; 12 stimulus frequencies linearly spaced from 0.4-3 kHz]

$$\Delta\mathbf{P} \equiv (\tilde{\mathbf{Z}} - \mathbf{Z})\mathbf{U_{ow}}$$

Equation 3: Model SFOAE defined. The tilde (~) specifies the inclusion of small degree of normally distributed irregularity (along papilla) in Q

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

Equation 4: Definition of the phase-gradient delay for the model

- Model parameters can be estimated by fitting a gammatone filter response to ANF tuning curves. As shown in Figure 4, fits were computed to estimate how Q and m vary with frequency. Furthermore, ANF tracing experiments (Manley et al. 1999) provide the tonotopic map for the papilla. The following equation provides an explicit connection between Q_{10} and Q for the m'th order gammatone filter [Hartmann, 1998]: $Q = Q_{10dB}\sqrt{10^{1/m} - 1}$

- The match to the ANF tuning curves was improved by fitting the data to the gammatone velocity response curve, $i\beta H(\beta)$ rather than $H(\beta)$ itself. This observation suggests that when modeling the underlying resonant element with a gammatone filter, its behavior appears consistent with a velocity sensor (as opposed to displacement).

FIGURE 4 Gecko ANF tuning curves [Manley et al. 1999] for six different fibers. Solid curves show estimated best fit for a gammatone filter evaluated via nonlinear regression. A Gaussian weighting function was used that was centered about the tip. Q_{10} was estimated directly from the data and used to help constrain the parameter space. *Inset*: Estimated variation in gammatone filter order (m) with respect to fiber CF

Model Results & Comparison to SFOAE Data

FIGURE 5 *Left*: Representative SFOAE data using a 20 dB SPL probe level in two geckos. SFOAEs measured using a off-frequency suppression paradigm. The dashed line indicates the noise floor. *Right*: Model SFOAE for three different ears (i.e., roughness patterns). Bundle stiffness (k_n) was assumed constant and filter order varied as the power law m(CF)=4.5 CF$^{0.35}$ [150 bundles with CFs from 0.3-5 kHz; 512 stimulus frequencies linearly spaced from 0.3-6 kHz].

- As shown in Figure 5, the model captures many of the qualitative features observed in the SFOAE data. There are characteristic peaks and valleys in the magnitude that are unique to a given 'ear'. Also, there is a sharp roll-off for stimulus frequencies above the maximum CF. The overall amount of phase accumulation is also similar.

- Model phase-gradient delay dependence upon stimulus frequency is shown in Figure 6. The model predicts that the trend in N_{OAE} is proportional Q. The physical intuition is that the long delays associated with the underlying filters (as they store energy approaching steady-state) account for the long delays observed in the SFOAE phase-gradients.

- Figure 6 also shows a comparison of model delays to those measured from SFOAEs evoked using a moderate stimulus level. Though the model appears to overestimate delays slightly, there is good agreement in the frequency dependence above 1 kHz. Below that frequency, SFOAE delays become significantly shorter than those predicted, in similarity to observations in mammalian OAEs.

- We made our assumption for how m varies with respect to CF based upon parameter estimates from the ANF data. However, the observation of proportionality between N_{OAE} and Q is maintained even upon very different filter assumptions.

FIGURE 6 Comparison of N_{OAE} from model and gecko SFOAEs (Lp=40 dB SPL, 18 ears). Model results from 12 different ears. **Note proportionality between N_{OAE} and Q.** Model parameters similar to those used in Figure 5.

$$N_{OAE} \approx \frac{mQ}{\pi}$$

Equation 5: Approximate SFOAE phase-gradient delay (expressed in periods) for model comprised of gammatone filters. Approximation good for filter order m in the range of 2-8

CONCLUSIONS

1. A model for an ear lacking BM waves suggests that tuned filters can account for long delays observed in SFOAEs
2. The model predicts that emission delays are proportional to the underlying auditory filter bandwidths
3. These results lend further support that SFOAE delays can provide an objective estimate of cochlear tuning