

RETROGRADE PROPAGATION OF COCHLEAR DISTORTION

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In 1992, Allen and Fahey suggested a method of estimating “cochlear amplifier” (CA) gain by employing simultaneous measurement of auditory nerve fibers and acoustic distortion products (DP). Their conclusion that CA gain must be less than 6 dB, based on their measurements in a cat, has been controversial. We have simulated the retrograde propagation of distortion in a nonlinear, active, one-dimensional model of cochlear mechanics. We conclude, based on results of this model, that the Allen-Fahey paradigm does not provide accurate estimates of CA gain.

1 Allen-Fahey Experiment

The experimental paradigm suggested Allen and Fahey [1] requires simultaneous measurement of (1) sound pressure level in the ear canal and (2) spike discharge of a single auditory nerve fiber (ANF). The primary frequencies of a two-tone stimulus are selected to produce intermodulation distortion ($2f_1-f_2$) at the characteristic frequency (CF) of the ANF. The two tones are equal in level and this level is adjusted so that the $2f_1-f_2$ distortion product (DP) produces threshold excitation of the ANF. If we assume (1) that the DP is generated near the f_2 place within the cochlea and (2) that the cochlear amplifier (CA) [2] achieves gain by means of a negative damping region (NDR), then the effective gain applied to the DP, as it travels toward its characteristic place (CP), will vary depending on the location of f_2 place relative to the NDR. If the forward component travels through less than the entire NDR, then its amplification will be less than the maximum possible CA gain. For the same reason, the DP-component generated at the f_2 place that travels back toward the stapes will also receive varying amounts of gain from the NDR. As f_2 is swept toward CF from one-octave above CF, the forward DP gain will decrease and the reverse DP gain will increase. Because the stimulus level must increase to compensate for reduced forward DP gain, the net increase in the backward DP gain is effectively doubled. As the f_2 place is swept through the NDR, the DP level observed in the ear canal should increase as much as twice the maximum forward DP gain.

The Allen-Fahey experiment has been replicated by Shera and Guinan [10] and has been extended by de Boer et al. [3] and Shera and Guinan [10] with similar results. In general, the DP level observed in the ear canal decreases as f_2 approaches CF, contrary to what would be expected if there were any CA gain. Shera [8] has suggested that beam-forming in DP generation may invalidate a key assumption of Allen-Fahey experiment, which assumes that the relative size of the forward and backward DP components does not change as f_2 is swept. Although beam-forming must certainly be a factor in DP generation and is consistent other DPOAE measurements, uncertainties in spatial

properties of DP generation make it difficult to quantify how the relative size of forward and reverse components change as a function of f_2 .

The importance of the Allen-Fahey experiments extends beyond estimates of CA gain. The Allen-Fahey experiment has been cited by Ren et al. [7] as evidence to support the existence of compression waves in the cochlea; however, this interpretation has been disputed by Shera et al. [11].

2 Cochlear Model

There are many ways to model the cochlea. The present model is based on physical variables and approximates Greenwood's frequency-place map [4], but the emphasis is on representing signal processing characteristics.

2.1 Macro-mechanics

Consider a model of cochlear macro-mechanics with one spatial dimension that consists of the following differential equations:

$$\partial_x P = -M_f \ddot{\xi}_f \quad (1)$$

$$\partial_x \dot{\xi}_f = w_p \dot{\xi}_r \quad (2)$$

In these equations, ∂_x represents a spatial derivative, the over-dot represents a time derivative, P represents the pressure difference across the basilar membrane (BM), $\dot{\xi}_f$ represents longitudinal volume-velocity of the scala fluid, ξ_r represents transverse displacement of the reticular lamina (RL), $M_f = 2\rho/A_s$ is the inertial component of the scala fluid impedance (per unit length), w_p is the effective width of the BM, and A_s is the cross-sectional area of the scala.

2.2 Micro-mechanics

To complete the cochlear model description, we represent cochlear *micro*-mechanics (at each point on the BM) by the following equations:

$$\xi_b = \xi_r + \xi_o \quad (3)$$

$$M_b \ddot{\xi}_b + R_b \dot{\xi}_b + K_b \xi_b = (-P/w_p) \quad (4)$$

$$M_o \ddot{\xi}_o + R_o \dot{\xi}_o + K_o \xi_o = \gamma \cdot (R_r \dot{\xi}_r + K_r \xi_r) \quad (5)$$

In these equations, ξ_b represents BM displacement and ξ_o represents outer hair cell (OHC) contraction, which reduces the separation between BM and RL. RL displacement ξ_r is assumed to provide the relevant input to the inner hair cell, which converts this

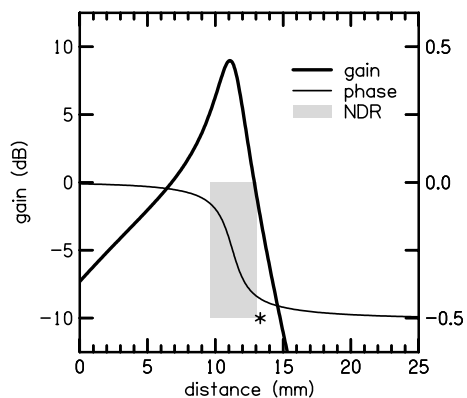


Figure 1. OHC contraction relative to RL displacement at 4 kHz as a function of distance from the stapes when $\gamma = 1$. The gray bar indicates the extent of the NDR produced when this OHC gain is included in the cochlear model. The asterisk indicates the characteristic place for a 4-kHz signal.

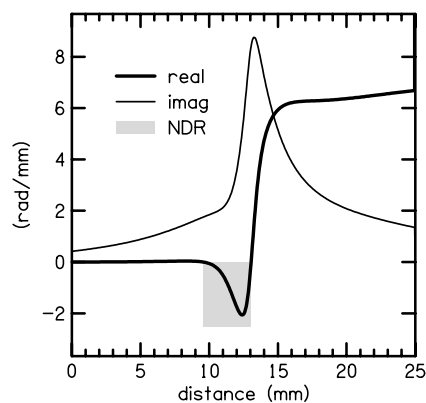


Figure 2. Propagation function at 4 kHz as a function of distance from the stapes. The real part (thick line) determines the slope of the pressure log-magnitude, while the imaginary part (thin line) determines the slope of the pressure phase. The gray bar indicates the extent of the NDR.

mechanical signal into a neural signal. Simultaneous solution of Eqs. 1-5, with appropriate boundary conditions, quantifies RL displacement for a stimulus specified in terms of stapes displacement.

2.3 Outer hair cell

The ability of an OHC to change its length in response to changes in membrane potential gives the OHC the role of a controlled source of mechanical energy in a model of cochlear mechanics. For simplicity, OHC motility is represented in the present model only in terms of its input and output, which hides the details of mechano-electric and electro-mechanic transductions.

The OHC is tuned in this model by its mechanical load. This tuning is independent of basilar membrane tuning and may be demonstrated by looking at the transfer function between OHC input, which is hair-bundle (HB) displacement, and output, which is contraction of the length of the cell body. In the frequency domain, OHC contraction relative to RL displacement is a low-pass filter:

$$H_o \equiv \left(\frac{\xi_o}{\xi_r} \right) = \gamma \cdot \left(\frac{R_r + K_r/s}{sM_o + R_o + K_o/s} \right). \quad (6)$$

In this equation s is the Laplace transform frequency variable. The parameter γ allows the model to represent a transition from completely passive ($\gamma = 0$) to fully active ($\gamma = 1$).

The OHC transfer function H_o is shown in Fig. 1 at 1, 4, and 16 kHz for model parameters selected to represent a cat cochlea (in particular, $R_r = 0$). When OHC gain at 4 kHz is maximum, the OHC contraction is about 2.8 times the RL displacement. OHC

contraction is in-phase with RL displacement at low frequencies, lags RL displacement by $\frac{1}{4}$ cycle when OHC gain is maximum, and lags RL displacement by $\frac{1}{2}$ cycle at high frequencies.

2.4 Propagation function

In the frequency-domain, the propagation function $\kappa \equiv \sqrt{Z_f Y_p}$ describes wave propagation in the cochlea, where Z_f is the impedance (per unit length) of the scala fluid and Y_p is the admittance (per unit length) of the cochlear partition:

$$Z_f \equiv \begin{pmatrix} \frac{\partial_x P}{-\dot{\xi}_f} \end{pmatrix} = sM_f \quad (7)$$

$$Y_p \equiv \begin{pmatrix} \frac{\partial_x \dot{\xi}_f}{-P} \end{pmatrix} = \frac{1}{(sM_b + R_b + K_b/s) \cdot (1 + H_o)}. \quad (8)$$

The propagation function is shown in Fig. 2 at 1, 4, and 16 kHz for model parameters selected to represent a cat cochlea. The propagation functions shown in Fig. 2 are similar in shape and amplitude to the propagation functions and wave numbers derived from cat and chinchilla tuning-curve data by Shera [9].

3 Model Results

Iso-displacement tuning curves are shown in Fig. 3 for model parameters selected to represent a cat cochlea. These tuning curves were derived from impulse responses in a linear version of the model. The entire length of the BM is represented in this model by 500 points, which is 20 points/mm for the typical 25-mm length of a cat cochlea.

Cochlear nonlinearity is introduced by γ a function of RL displacement:

$$\gamma(\xi_r) \equiv \frac{1}{1 + |\xi_r / \xi_h|^{0.2}}, \quad (9)$$

where the parameter ξ_h specifies the RL displacement at which $\gamma = 1$. For smaller displacements, γ approaches one and CA gain is maximum. For larger displacements, γ approaches zero and CA gain is eliminated.

To simulate the Allen-Fahey experiment, the 4-kHz place in the cochlea was selected to represent the location at which excitation was kept constant under all stimulus conditions. Prior to generating DPOAEs, a threshold-tuning curve (TTC) was obtained by presenting single-tone stimuli over the range of frequencies from 2 to 8 kHz and varying the level of these tones to maintain constant displacement at the 4-kHz place. The single-tone stimulus levels determined by this procedure are shown in Fig. 4 as a thick-solid (blue) line.

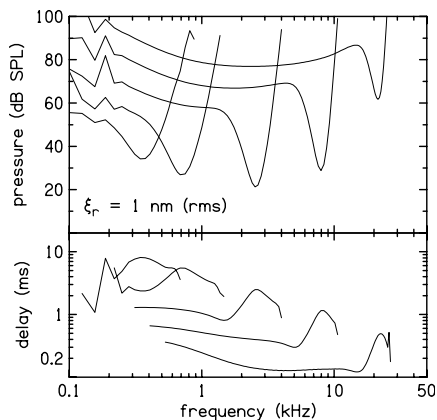


Figure 3. Iso-displacement curves at locations 20, 40, 60, 80, and 90% of the distance from the stapes. These transfer functions were obtained from impulse responses in a linear version of the time-domain model.

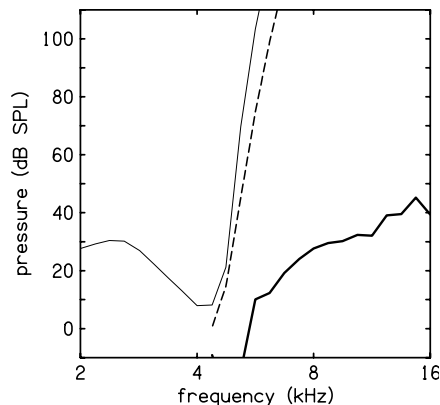


Figure 4. DPOAE level (thick line) as a function of f_1 . For comparison, the two-tone stimulus level (dashed line) and single-tone threshold level (thin line) are also shown. The DPOAE level shows no indication of the CA gain present in the model.

DPOAEs were generated in the model by presenting two-tone stimuli with f_1 decreasing over the range from 16 to 4 kHz and f_2 selected to make the $2f_1-f_2$ distortion product always at 4 kHz. The stimulus tones always had the same level $L_1=L_2$, which was adjusted to maintain the same displacement at the 4 kHz place in the cochlea that was used to produce the TTC. The two-tone stimulus level is shown in Fig. 4 at the f_1 frequency as a dashed line. The thick line in Fig 4 indicates the corresponding DPOAE level at the eardrum in response to this two-tone stimulus. Although there is fine-structure in the DPOAE level across frequency that suggests partial cancellation due to multiple sources, there is no evidence of amplification as f_1 approaches 4 kHz. Thus, the model results are consistent with results observed by Allen and Fahey in that the DPOAE shows no evidence of cochlear amplifier gain. However, examination of RL displacement and power flow reveals that the model provides 12 dB of power gain to a 4-kHz tone at 20 dB SPL and 47 dB of tip-to-tail displacement gain at 0 dB SPL. We must conclude that the Allen-Fahey paradigm does not provide an accurate indication of CA gain in this model.

4 Discussion

The Allen-Fahey paradigm reveals important information about cochlear mechanics; however, due to the inherent limitations of this paradigm, estimates of cochlear amplifier gain obtained by this method may underestimate both displacement gain and power gain present within the cochlea. Two-tone neural responses, recorded from hundreds of single auditory-nerve fibers [6] suggest a spatial distribution of distortion generation that is less localized than assumed by Allen and Fahey [1]. Our time-domain model results are consistent with the quasi-linear examination of the Allen-Fahey paradigm in frequency-

domain model by Kanis and de Boer [5], which also found DPOAE level to be an inaccurate indication of CA gain.

Acknowledgments

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