Otoacoustic emissions from a nonlinear, active model of cochlear mechanics

S. T. Neely and L. J. Stover

Boys Town National Research Hospital
555 North 30th Street, Omaha, Nebraska 68131, U.S.A.

1 Introduction

One of the challenges of putting nonlinear and active elements into a model of cochlear mechanics is to place them in a way that makes sense both in terms of (1) the anatomy of the cochlear partition and (2) the physical influence of these elements on measurable responses. The recent observation that distortion-product otoacoustic emissions (DPOAE) are band-pass filtered with a center frequency related to the place of generation within the cochlea (Brown, Gaskill, and Williams, 1992) provides an important clue about the details of cochlear micromechanics.

We will describe a model of cochlear mechanics in which the outer hair cell (OHC) is represented explicitly in each radial cross-section by a force applied between the basilar membrane and reticular lamina. The OHC force is (1) controlled by displacement of the hair bundle (HB) at the top of the OHC, (2) saturates for large HB displacements, and (3) lags HB displacement by nearly 90 degrees in phase at high frequencies due the electrical capacitance of OHC membrane (thereby producing negative-damping forces). The same nonlinearity that causes OHC forces to saturate for large HB displacements also generates distortion products for smaller HB displacements. DPOAEs in this nonlinear, active model are filtered by a place-dependent, band-pass filter.

2 Description of the model

The usual one-dimensional (transmission-line) equations have been used to model cochlear macromechanics. The micromechanics of each radial cross-section (RCS) are modeled independently, with no longitudinal coupling except through the fluid. This time-domain model is similar to the frequency-domain model described by Neely (1993).

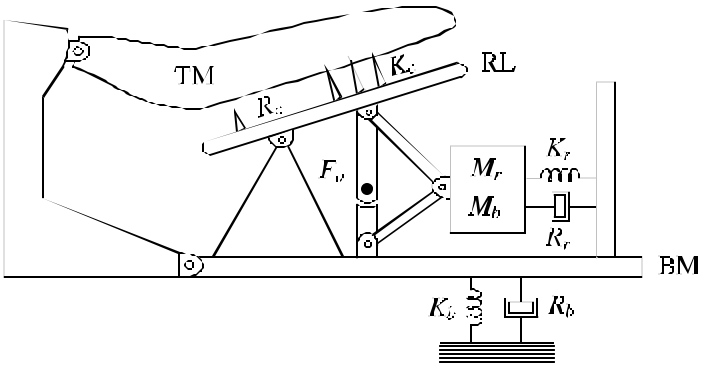

Figure 1. Micromechanics of a radial cross-section (RCS). The OHC is assumed to exert a force F_o between BM and RL which is controlled by the RL-TM shear displacement. Motion of the RL relative to the BM is opposed by inertial, damping and stiffness forces.

2.1 Micromechanics

We represent the micromechanics with two mechanical degrees of freedom (DOF) as illustrated in Fig. 1. Fluid pressure differences across the cochlear partition (CP) create forces acting on the basilar membrane (BM) and provide the signal input to the micromechanics. Displacement of the BM results in shear displacement between the reticular lamina (RL) and the tectorial membrane (TM) which is detected by the inner hair cell (IHC). The IHC receptor potential provides the output signal from the micromechanics. The TM is assumed to have a high impedance relative to the RL-TM shear and will not be represented explicitly in this model.

If we let x_b represent BM displacement and x_c represent the RL-TM shear displacement, then one equation of motion can be written as

$$M_b\ddot{x}_b + R_b\dot{x}_b + K_b x_b + R_c\dot{x}_c + K_c x_c = -A_p P_d \tag{1}$$

where M_b, R_b, and K_b are the mass, stiffness, and damping associated with BM displacement; R_c, and K_c are the stiffness and damping associated with RL-TM shear displacement; P_d is the fluid pressure difference across the CP; and A_p is the area of the CP in a single RCS. The displacement of the RL relative to the BM is assumed to cause the surrounding cells to move from side to side, and, consequently, this motion will be opposed by inertial, damping and stiffness forces, in the same manner as the BM. If we represent the RL displacement relative to the BM by x_r, then the second equation of motion becomes

$$M_r\ddot{x}_r + R_r\dot{x}_r + K_r x_r - R_c\dot{x}_c - K_c x_c = F_o \tag{2}$$

where M_r, R_r, and K_r are the mass, stiffness, and damping associated with RL displacement and F_o is the force exerted by the OHC between the RL and the BM. We assume that this

force is proportional to the voltage V_o across the lateral membrane of the OHC and that the electrical current through the cell is proportional to the HB displacement. In this model, we compute the OHC force by the following equations

$$\tau_o \dot{V}_o + V_o = \gamma g_f x_c \tag{3}$$

$$F_o = K_o g_r V_o \tag{4}$$

where τ_o is the electrical time-constant of the OHC membrane, g_f and g_r are forward and reverse displacement-to-voltage transduction coefficients, K_o is the internal stiffness of the OHC, and γ is a dimensionless multiplier which we will use to introduce a saturating nonlinearity into the system. In a time-domain model we can make γ depend on the HB displacement

$$\gamma = \frac{d_o}{d_o + |x_c|} \tag{5}$$

For small displacements γ is close to one and for large displacements γ is close to zero. The displacement at which $\gamma = 0.5$ is determined by the parameter d_o.

Since the TM is assumed not to have an independent motion

$$x_c = x_b - x_r \tag{6}$$

If desired, this model could easily be extended to include a separate TM motion.

2.2 Impedance and transfer functions

This model provides additional filtering between the BM and the IHC response functions. In the frequency domain, the transfer function can be written as

$$H_c(\omega) = \frac{\left(K_r - \omega^2 M_r\right) + i\omega R_r}{\left(K_r + K_c + \dfrac{\gamma g_f g_r K_c}{1+\omega^2 \tau_o^2} - \omega^2 M_r\right) + i\omega\left(R_r + R_c - \dfrac{\gamma g_f g_r K_c \tau_o}{1+\omega^2 \tau_o^2}\right)} \tag{7}$$

and is shown in Fig (2). This transfer function has similar characteristics to those attributed to the TM by Allen (1980). The "spectral zero" of this transfer function (illustrated in Fig. 2) is often evident in neural response functions.

It is interesting to see the effect of the OHC force on the driving-point impedance of the CP. This impedance can be written as

$$Z_p(\omega) = i\omega M_b + R_b + K_b / i\omega + \left(R_c + K_c / i\omega\right) H_c(\omega) \tag{8}$$

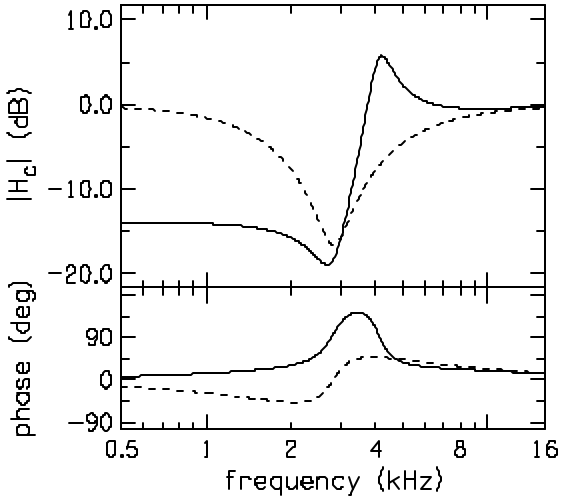

Figure 2. Transfer function between the BM and the RL-TM shear displacement at the 4 kHz place. The magnitude (upper panel) and phase (lower panel) are shown for $g = 1$ *(solid line) and* $g = 0$ *(dashed line). Note the dip in magnitude (and increase in phase) at about 2.8 kHz due to the "spectral zero" in this transfer function.*

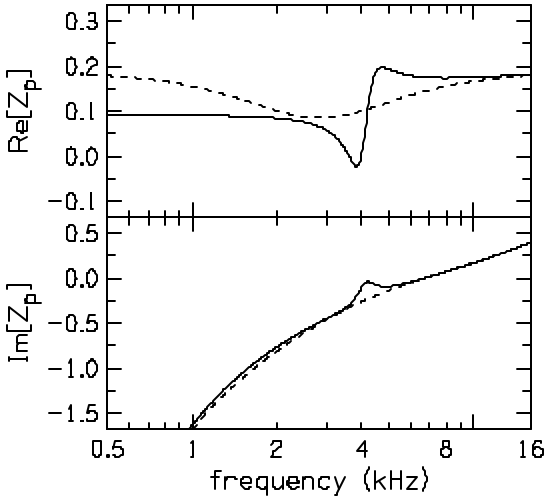

Figure 3. Cochlear partition impedance at the 4 kHz place. The real (upper panel) and imaginary (lower panel) parts are shown for $g = 1$ *(solid line) and* $g = 0$ *(dashed line). Note the reduction in the reactive component (lower panel) near the CF and the region of negative damping (upper panel) below CF due to the OHC force.*

The real and imaginary parts of Z_p are shown in Fig. 3 for the 4 kHz place with $g = 1$ and $g = 0$. The effect of the OHC force on the impedance function is to (1) reduce the reactive component (imaginary part) at the characteristic frequency (CF), (2) reduce the resistive component (real part) below CF, and (3) increase the resistive component above CF. The small region of negative resistance (damping) just below CF will enhance the sensitivity and sharpness of tuning of the BM responses, as well as the IHC responses.

3 Model results

The isodisplacement tuning curves shown in Fig. 4 were inferred from model results using a very low-level (sub-threshold) click. The model is essentially linear for very low-level stimuli. The model parameters were chosen to provide a frequency-place map similar to that of the human cochlea. The group delay in the lower panel of Fig. 4 is computed as minus the slope of the phase with respect to frequency.

The growth of the IHC response with increasing stimulus level is illustrated in Fig. 5 for a 4 kHz tone. The parameter d_o was set to 10 nm, which is equivalent to 80 dB on the ordinate of

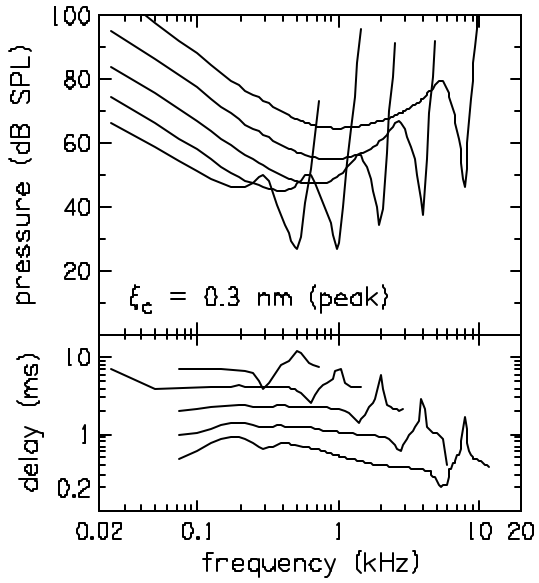

Figure 4. Isodisplacement tuning curves at the 0.5, 1, 2, 4, and 8 kHz places. These tuning curves were inferred from the model response to a very low-level click.

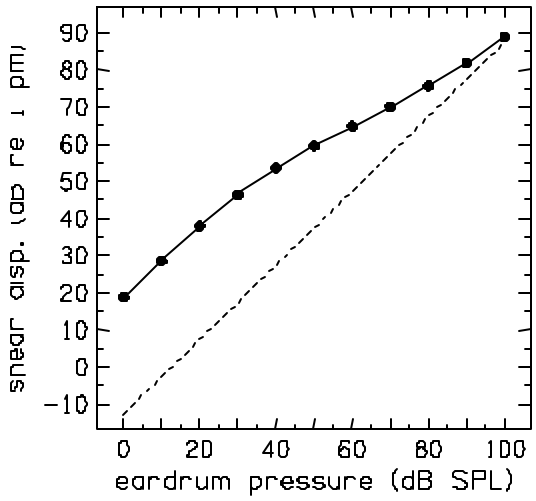

Figure 5. Growth of RL-TM shear displacement at the 4 kHz place with increasing stimulus level. The stimulus was a 4 kHz tone. The dashed line represents the corresponding growth function for a passive, linear version of the model.

Fig. 5. The total compression provided by the micromechanics is about 30 dB over this 100 dB range of stimulus levels. The maximum compression is around 60 dB SPL where the slope of the growth function is about 0.5. For comparison, the dashed line shows the growth function for the passive case (obtained by setting $d_o = 10^{-18}$ m).

The model results for amplitude of distortion-product otoacoustic emissions (DPOAE) measured at the eardrum are shown in the right panel of Fig. 6. These DPOAEs were generated at fixed place along the CP by holding the higher-frequency (F_2) tone fixed and varying the lower-frequency tone (F_1) to obtain a range of distortion-product (DP) frequencies (F_d). The model results show that the DP frequencies are band-pass filtered with a center frequency about one-half octave below the F_2 frequency. This is the same as the frequency of the "spectral zero" in the transfer function shown in Fig. 2.

4 Discussion

The generation of DPOAEs is closely linked to the normal function of cochlear outer hair cells (OHC). The amplitude of DPOAEs has been observed to decrease in a predictable manner with decreases in endocochlear potential (EP) (Mills, Norton, and Rubel, 1993). The most obvious interpretation is that the motile forces exerted by the OHC are responsible for the generation of DPOAEs. The EP drives the electrical current through the OHC which is modulated by displacement of the HB. This current influences the voltage across the lateral

membrane of the OHC which controls the force exerted by the OHC. Since the transduction from HB displacement to electrical current is inherently nonlinear, the forces generated by the OHC will contain relatively large distortion products.

One of the significant features of the model presented here is that nonlinear forces are introduced in an appropriate way: a saturation of the voltage that controls the OHC force exerted between the BM and the RL. Distortion products generated by nonlinear forces introduced in this way are band-pass filtered due to the "spectral zero" frequency of the RL resonance. If DPs are due to forces between RL and BM, they will not be band-pass filtered by a TM resonance, as suggested by Brown, Gaskill, and Williams (1992) and by Allen and Fahey (1993).

Allen and Fahey (1993) argue that DPs are generated by a nonlinearity in the stiffness of the BM and are band-pass filtered by a TM resonance. This would place the source of the nonlinear force in parallel with the stiffness element K_b in Fig. 1, between the BM and the inertial reference. This placement seems unlikely considering the intimate link between OHC motility and DP generation.

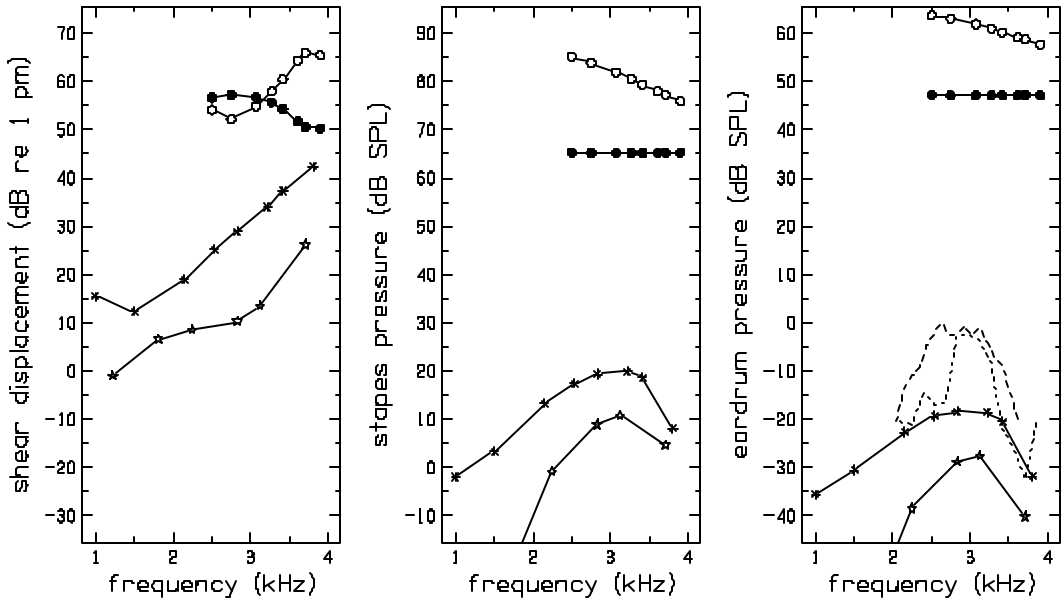

Figure 6. DP amplitude as a function of DP frequency for a fixed DP generation site. The DP generation site was held fixed by keeping the F_2 frequency constant at 4 kHz. Model results are shown for the RL-TM shear displacement at the 4 kHz place (left panel), the pressure at the stapes (center panel), and the pressure at the eardrum (right panel). The amplitudes of both stimulus components F_1 (open circles) and F_2 (closed circles) are plotted at the F_1 frequency. The amplitude of the DP components $2F_1$-F_2 (asterisks) and $3F_1$-$2F_2$ (stars) are plotted at the DP frequency. At the stapes and at the eardrum, the amplitude of both DP components appear to be band-pass filtered with a center frequency about one-half octave below F_2. The band-pass filter is due to the same RL resonance that produces the "spectral zero" shown in Fig. 2. The dashed lines (right panel) show data from a human subject for comparison.

The gain of the cochlear amplifier[1] (CA) can be measured in terms of either (1) the total power absorbed by the CP or (2) the displacement sensitivity of the IHC. Since the OHC forces reduce the reactive component of the CP impedance (in addition to creating a negative damping region) the gain in displacement sensitivity can be much larger than the power gain. For example, the CA in the model presented here increases displacement sensitivity by 30 dB at the 4 kHz place, while the total power gain is less than 1 dB. Using the CA to reduce the reactive component of the partition impedance with minimal power gain was suggested by Kolston, *et al*. (1990). The lower power gain of the present model is consistent with the CA gain measurements of Allen and Fahey (1992).

[1]The term cochlear amplifier refers to the improvement in low-level sensitivity and frequency selectivity that result from the presence of active elements in the cochlear partition.

A physical model of transduction," J. Acoust. Soc. Am. **68**, 1660-1670.

Allen, J. B. and Fahey, P. F. (1992). "Using distortion products to measure the cochlear amplifier gain on the basilar membrane," J. Acoust. Soc. Am. **92**, 178-188.

Allen, J. B. and Fahey, P. F. (1993). "A second cochlear-frequency map that correlates distortion product and neural tuning measurements," J. Acoust. Soc. Am. (submitted).

Brown, A. M., Gaskill, S. A., and Williams, D. M. (1992). "Mechanical filtering of sound in the **250**, 29-34.

Kolston, P. J., de Boer, E., Viergever, M. A., Smoorenburg, G. F. (1990). "What type of force does the cochlear amplifier produce?," J. Acoust. Soc. Am. **88**, 1794-1801.

Mills, D. M., Norton, S. J., and Rubel, E. W. (1993). "Vulnerability and adaptation of distortion product otoacoustic emissions to endocochlear potential variation," J. Acoust. Soc. Am. **94**, 2108-2122.

Neely, S. T. (1993). "A model of cochlear mechanics with outer hair cell motility," J. Acoust. Am. **94**, 137-146.