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MODELING THE NOISE DAMAGED COCHLEA

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Introduction

The purpose of this paper is to present a specific model (Allen, 1980) of the cochlea which replicates normal cat threshold neural tuning curves. This model is first introduced as a linear passive model. In the process of fitting the model to the neural data, it was discovered that changes in the basilar membrane stiffness could modify the model cilia frequency response in a manner similar to the noise damaged neural tuning curves of Liberman and Dodds (1984). Liberman and Dodds found that the tips of the tuning curves become elevated by more than 40 dB, and the tails become hypersensitive by about 10 dB, after a noise trauma that damages the outer hair cells. After recording tuning curves from the noise damaged cells, they found a systematic loss of outer and/or inner hair cells associated with the noise trauma neurons. They then correlated the hair cell loss to the frequency response of the associated tuning curves. In this paper we model the Liberman and Dodds noise damaged tuning curves by associating the loss of normal outer hair cells with a decrease in the basilar membrane stiffness (increased compliance).

We believe that the compressive and frequency dependent cochlear nonlinearities that have been observed in the basilar membrane response and in inner and outer hair cell receptor potentials (for a review see Allen, 1988) are a related phenomenon, and we propose a model for the nonlinear cochlea based on this approach. In this model, the outer hair cell length changes, which occur during cell depolarization (Brownell *et al.* 1985), dynamically increase the basilar membrane compliance. The effect of this dynamically modified compliance would be a compression of the dynamic range of the basilar membrane motion, and therefore of the excitation to the inner hair cells. This nonlinearity is important to compress the dynamic range of the acoustic signal to match that of the inner hair cells.

This model is being offered as a physically realizable alternative to the active (negative-resistance) cochlear amplifier model of Neely and Kim (1983).

Neural Excitation Patterns

One of the basic problems in cochlear modeling is the determination of the model parameters from physical data in a systematic way. Frequency domain models give a response along the basilar membrane for a given input-signal frequency, whereas the experimental data (neural tuning curves) to be matched are functions of frequency for a given position along the basilar membrane. To side step this computational problem, it is possible to transform the neural tuning curve data to place. These place tuning curves are called *excitation patterns* in the literature. This transformation represents a major simplification of the data-fitting process. If the neural excitation patterns are accurately fitted by the model in the place domain for several well separated frequencies, then the frequency tuning data should fit as well.

The transformation to excitation patterns is best understood by example. Fig. 1 shows a family of normal cat tuning curves collected by Liberman. Liberman has also measured the

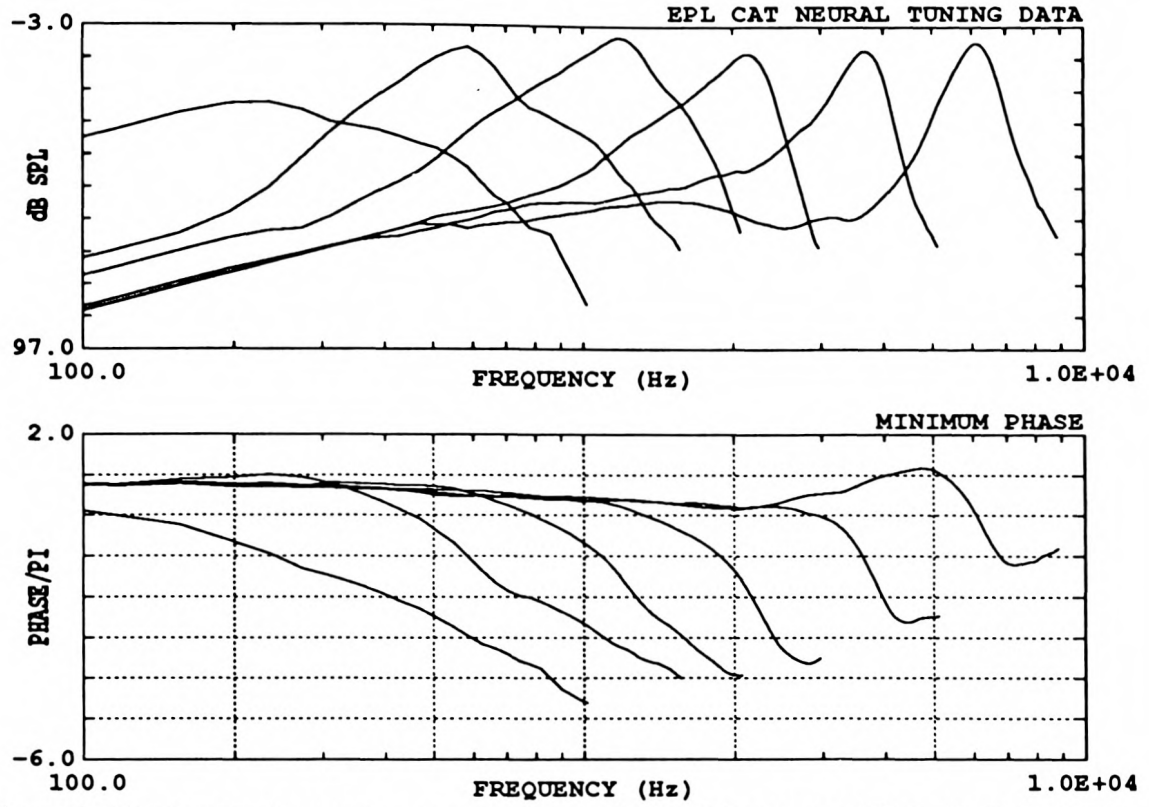

Figure 1: This family of cat tuning curves was provided by Liberman and Delgutte. The phase was generated by the Fourier Transform minimum phase method.

relation between the characteristic frequency (CF) and position on the basilar membrane $f_{CF}(x)$. Our procedure then is the following. First compute the phase for each tuning curve using the minimum phase method. The complex frequency responses are then loaded into the response matrix $\Theta(x_i, f_j)$, where x_i is the index that labels each tuning curve, and f_j is frequency. To find x_i, look across frequency to find $f_{CF}(x_i)$, the frequency of the maximum of $|\Theta(x_i, f_j)|$. Then use $f_{CF}(x)$ to determine x_i, the row index for each tuning curve, from the f_{CF} of the row. The excitation pattern is then $\Theta(x_i, f_j)$ vs. x_i for any given f_j, as shown in Fig. 2. These threshold response are for single tones as a function of position along the basilar membrane. The lower panel of Fig. 2 shows the derived phase along the basilar membrane for a given frequency. Since this phase was generated from the tuning curves using the minimum phase method, it is not necessarily the phase that one would measure neurally. The models, however, approximately match this phase. The close match demonstrates that the models approximately have a minimum phase response.

Modeling the Tuning Curve Data

In this section we show model fits to the neural excitation patterns of Fig. 2. The macromechanical model is the two-dimensional model of Sondhi (1979). The micromechanical model being used is the resonant tectorial-membrane model described in [Allen, 1980; Allen, 1988]. The basilar membrane to cilia transfer function $H_T(x, \omega)$ is used to modify the basilar membrane displacement response to give the cilia displacement. The difference between the 1980 model and the one here is in our choice of model parameters and the addition of a resistive element to the basilar membrane impedance. The comparison of the model to the neural data was made using a simple middle ear model.

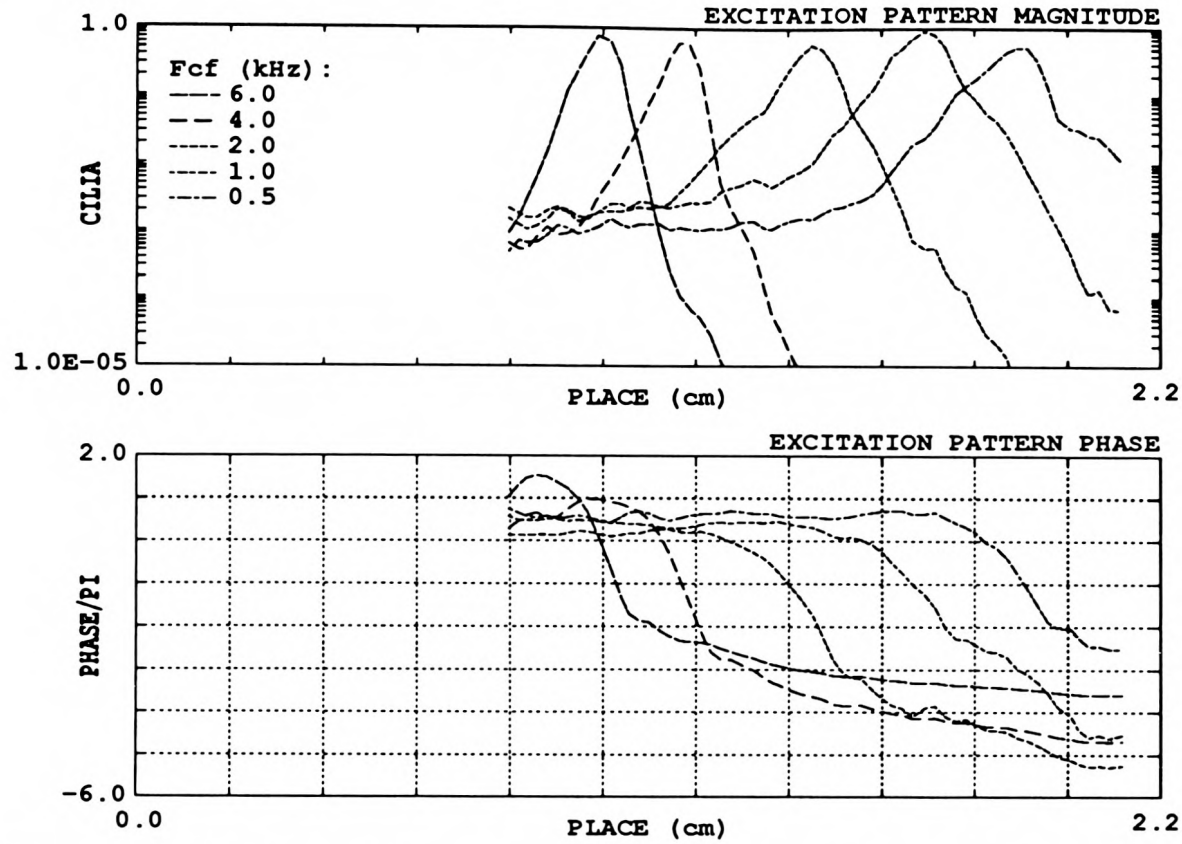

Figure 2: Transforming neural data tuning curves to place gives excitation patterns. These are more readily compared to model responses, since the model also gives excitation patterns for each input frequency.

THE TRANSDUCTION FILTER

The transduction filter $H_T(x,\omega)$ is defined as the transfer function, assumed here to be linear, between the basilar membrane displacement and the inner hair cell stereocilia displacement. In this paper $H_T(x,\omega)$ consists of three parts, which we call $G(x)$, $H_{TM}(x,\omega)$, and $H_{TR}(\omega)$. *First* is the lever action of the transduction gain $G(x)$, which is defined as the ratio of the cilia displacement to the BM displacement, under the condition that $k_c << k_T$. In Allen (1980) a formula was given for this gain (Eq's. 5 and 6) in terms of the physical variables. The estimate of G used here was heuristically determined in the process of fitting the neural data. It is desirable to have a large value of the transduction gain to increase the hair cell excitation. However, a large value of G seemed inconsistent with fitting the data. *Second*, is the effect of the elastic coupling between the limbus and the tectorial membrane $k_T(x)$. This elastic element introduces a pole and a zero into the transfer function, as described in Allen (1980, Eq. 13), and shown in Fig. 3, upper right hand panel. *Third* $H_{TR}(\omega)$ is defined as a first order high pass filter which represents the viscous fluid layer driving the stiffness-dominated inner hair cell stereocilia. H_{TR} is the transfer function developed between the tectorial membrane to reticular lamina (TM-RL) shear displacement and the cilia displacement, coupled via fluid viscosity. This component of the transduction filter is given by

$$H_{TR}(\omega) = \frac{j\omega}{j\omega + 2\pi f_c}. \quad (1)$$

If the inner hair cell cilia were attached to the underside of the tectorial membrane, then this highpass filtering action would not be present since there would be no slip condition. From the above equation, at low frequencies the cilia respond with the velocity of the shear, whereas at high frequencies, the cilia follow the TM-RL shear displacement. In the model,

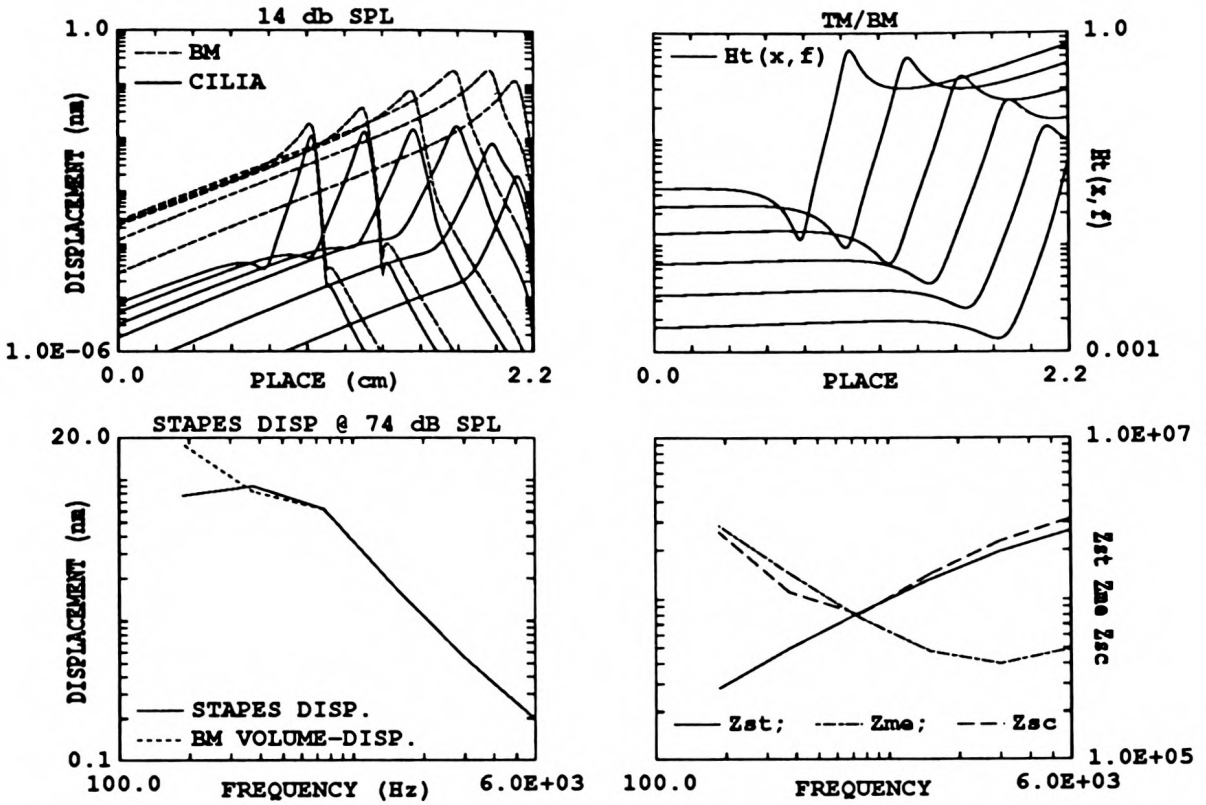

Figure 3: Model responses for octave frequencies between 6 kHz and 182.5 Hz, assuming an eardrum pressure of 14 dB SPL.

$f_c = 5.0$ kHz. As may be seen from the model response in the upper right panel of Fig. 3, the cilia move with the TM-RL shear-displacement for frequencies above f_c, and with the shear-velocity below f_c (Dallos, 1984).

Putting the three factors together gives the transduction filter

$$H_T(x,s) \quad = \quad G(x)\, H_{TR}(s)\, H_{TM}(x,s) \tag{2}$$

shown in Fig. 3 upper right panel.

SUMMARY OF MODEL EXCITATION RESPONSES

A summary of the model responses is given in Fig. 3. The upper left panel shows the model basilar membrane center-line and cilia rms displacements at octave frequencies between 6.0 kHz and 187.5 Hz at 14 dB SPL. The basilar membrane displacement is derived from the per unit length volume-displacement by dividing by the basilar membrane width. The lower left panel shows the stapes rms displacement at 74 dB SPL. Also shown in this panel is the volume integral of the basilar membrane displacement. The stapes volume-displacement and the basilar membrane volume-displacement should be equal at all frequencies. Because of the boundary conditions that have been assumed at the helicotrema, these two integrals are not exactly the same (Puria and Allen, 1990). The difference between them is due to fluid flow through the model helicotrema. The lower right panel shows the stapes input impedance Z_{sc}, the ossicle impedance Z_{me}, and their sum Z_{st}, which is proportional to the eardrum impedance.

In Fig. 4 the dashed lines give the model cilia excitation patterns, magnitude and phase, at the frequencies 0.5, 1.0, 2.0 4.0 and 6.0 kHz. The units in the upper panel are in nanometers (nm), and correspond to 74 dB-SPL constant pressure in the model ear canal. The solid lines are the neural data from Liberman. The amplitude scaling for the neural curves is arbitrary, but all curves are scaled by the same factor. The lower panel shows the

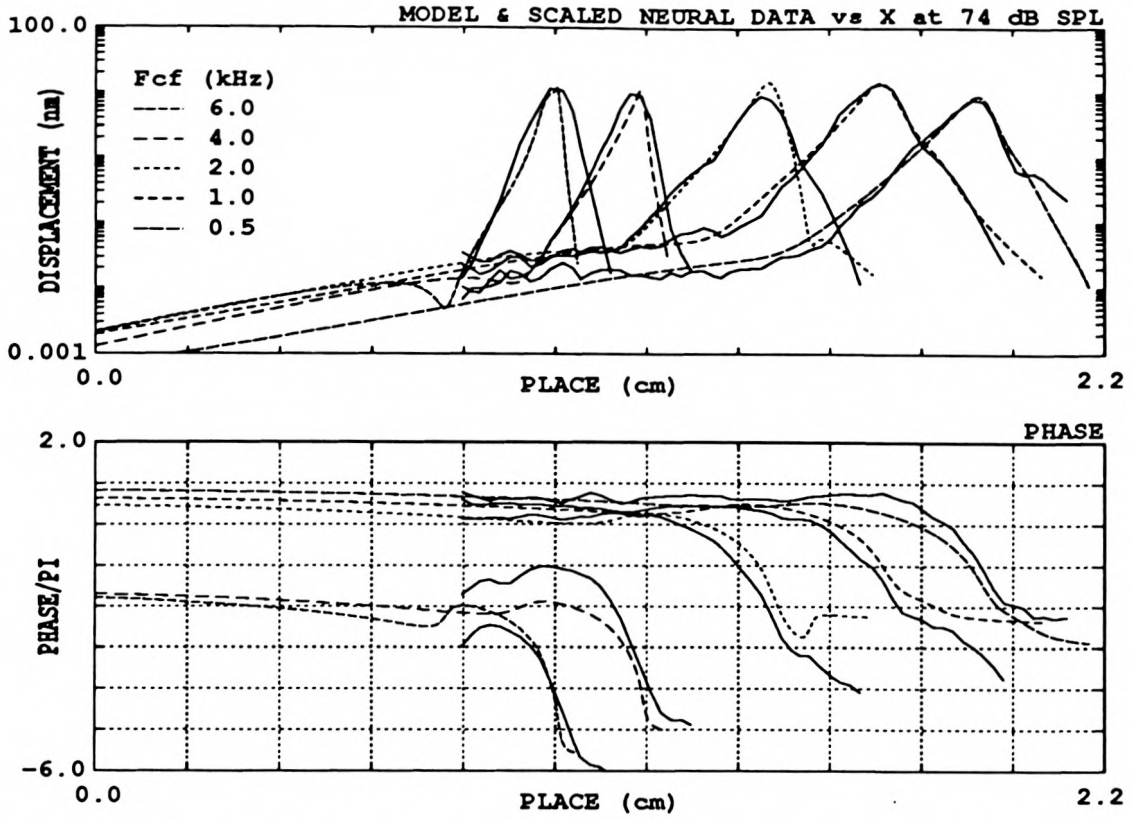

Figure 4: The solid curves are the neural data of Liberman and the dashed lines are the model responses in nanometers for a 74 dB SPL stimulus.

excitation pattern phase for the model (dashed lines) and of the neural data (solid lines) for the octave frequencies. The 4.0 and 6.0 kHz phase curves have been displaced down by $2\pi n$, where n is an integer, to separate them for clarity of plotting. The neural data is the same as shown in Fig. 2. The most significant deviation between the model and the neural data is in the phase curves for the 4 kHz tuning curves where the curves are π radians apart below CF (at 0.5 cm). There is also a trend for the model data to show a slightly greater phase lag than the neural minimum-phase result. This effect may also be seen by comparing Fig. 1 to Fig. 5.

Model Tuning Curves

After computing the model response at 7 locations along the basilar membrane for a large number of frequencies we find the results shown in Fig. 5. This figure should be compared to Fig. 1. An important degree of freedom that remains in comparing these curves is the threshold sensitivity of the model hair cell. For both Fig. 4 and 5 we would like to know if the sensitivity of the BM at the characteristic frequency (f_{CF}) is realistic. A discussion of the sensitivity question may be found in Hudspeth (1983). Denk and Webb (1989) have shown that hair cells transduce their cilia Brownian motion. The magnitude of this motion depends on the real part of the mechanical impedance of the stereocilia *in situ*. Hair cell sensitivity is an important and open question that has caused many to speculate on the need for a cochlear amplifier in the basilar membrane (Neely and Kim, 1983; Mountain and Hubbard, 1989; Patuzzi *et al.* 1989). Estimates of cilia displacements are complicated by the uncertainty introduced by the unknown transduction filter. It is not known if inner hair cells are velocity or displacement sensitive in vivo. Dallos (1984) has estimated that there is a velocity to displacement transition with a transition frequency of about 1 kHz. In the present model we assume a similar velocity to displacement as described in Eq. 1, but with $f_c = 5.0$ kHz.

It is assumed here that the rate threshold for the cat corresponds to an eardrum pressure

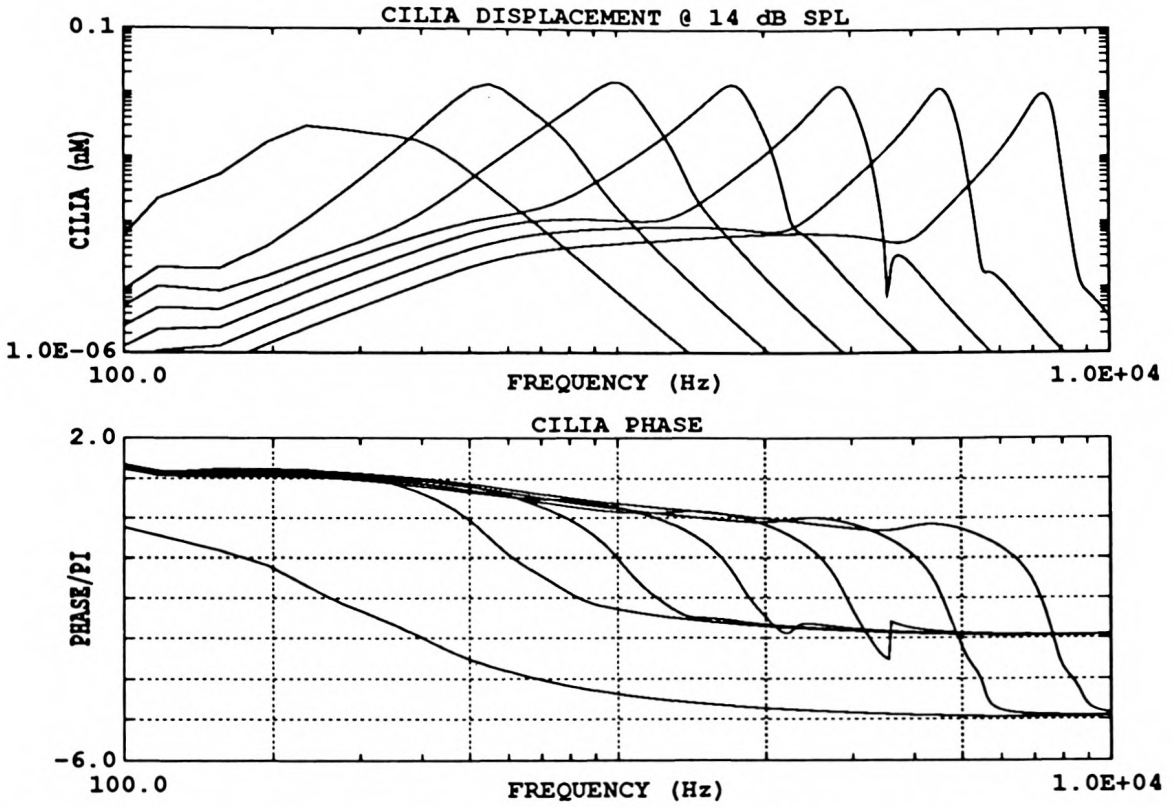

Figure 5: Once the model parameters have been determined, it is practical to compute the frequency tuning curves at points along the basilar membrane. These tuning curves are shown here, and should be compared to Fig. 1. As before, the upper panel is the cilia displacement in nanometers for a stimulus level of 14 dB SPL. The lower panel is the corresponding phase.

of 14 dB SPL. From Fig. 3, the model BM motion is 120 pm at the CF of 1 kHz and 14 dB SPL. The stapes displacement at 1 kHz for the model is 3.5 picometers at 14 dB-SPL. This means that the model basilar membrane has a gain of 31 dB at 1 kHz. Threshold displacements as low as 0.1 nm (100 pm) for cilia displacements have previously been estimated by Hudspeth, A.J. (1983). Nuttal *et al.* (1990) found basilar membrane displacements of 0.5 nm at 35 dB for his most sensitive animals. They also showed BM displacement data for several animals that showed a nonlinear input-output response growth at 80 pm for 50 dB SPL. Sellick *et al.* (1983) estimated the BM threshold at 350 pm, while Robles *et al.* (1986) have estimated the BM threshold at 1.9 nm.

THE BASILAR MEMBRANE STIFFNESS

During the parameter fitting process it was found that the basilar membrane stiffness was much more sensitive than other parameters in its effect on the basilar membrane tuning curve. Fig. 6 shows this effect. In this figure the basilar membrane stiffness was modified by a relative factor of 0.3 to 1.0 times the normal value (the value that gave a match to the tuning curve data). From this figure one may see that the tip of the model tuning curve becomes less sensitive by 40 dB and the tail of the model tuning curve is more sensitive by about 10 dB. There are several reasons for these changes in the model. First, as the stiffness decreases, the CF shifts toward the base. This means that the CF is shifting into the 'zero' (f_z) of the resonant tectorial membrane transfer function. Because of the presence of the zero, the CF threshold rises dramatically. A second important effect is the hyper-sensitive tails of the tuning curve. As the volume of fluid motion at the CF is reduced, the volume-motion in the tail increases because the net fluid motion must remain constant, as required by conservation of fluid mass. These model results should be compared to those of Liberman for noise damaged cochlea.

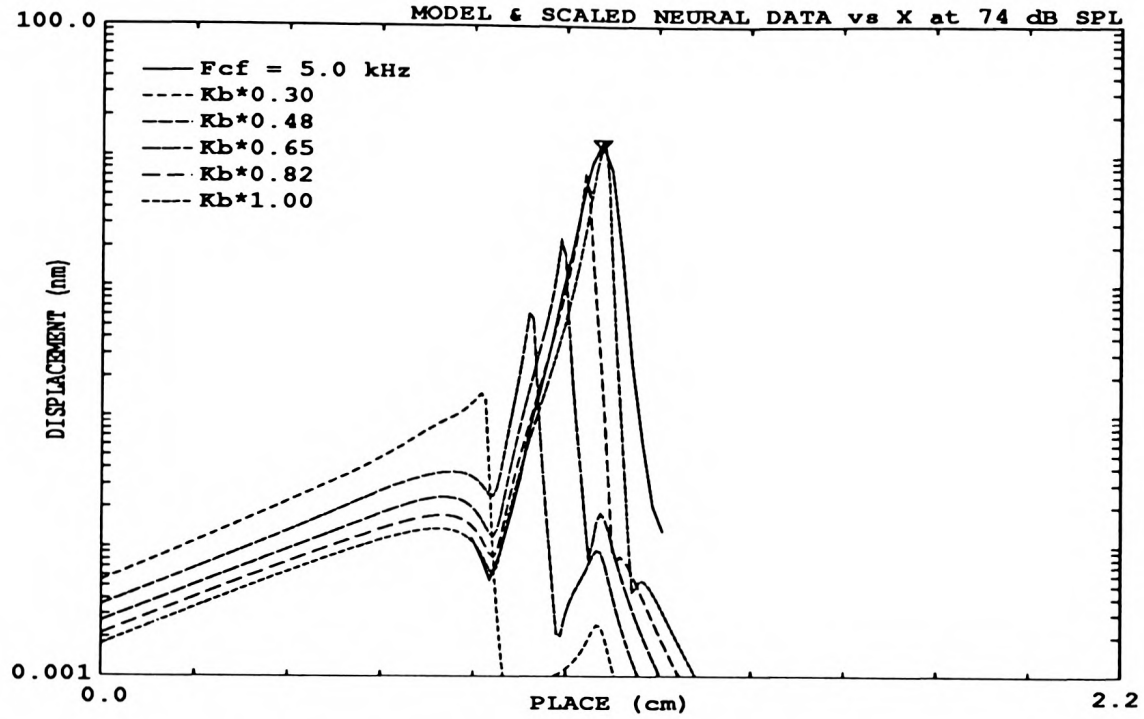

Figure 6: For an input frequency of 5.0 kHz, $K_{BM}(x)$ was varied from 30% to 100% of its normal value. This response should be compared to the tuning curves for damaged outer hair cell as found by Liberman.

Discussion: A Nonlinear Cochlear Model

A nonlinear version of this model remains to be explored, and an approach toward this end is described next. As the basilar membrane displacement increases with level, the depolarization of the outer hair cell increases due to the increased shearing of the sterocilia of the outer hair cell at the higher input levels. We propose that as the cell depolarizes, the induced hair cell shortening *reduces* the basilar membrane stiffness in the way assumed in Fig. 6. The published sensitivity of the hair cell length changes is 20 nm/mv (Santos-Sacchi and Dilger 1987). In Fig. 6 the stiffness changes are uniform along the basilar membrane, whereas in the nonlinear model they would be signal dependent and thus nonuniform. Since the stiffness variations would be low-pass filtered by the membrane capacitance of the outer hair cells, the stiffness variations would not follow the signal on a cycle-by-cycle basis. In this sense, the model could be characterized as a nonlinear parametric model. If the stiffness variations at high frequencies (e.g. 10-20 kHz) do not follow the signal waveform, then the term 'cochlear amplifier' does not apply to this class of model. It is an 'active' model in the usual electrical engineering sense, just as the Davis model of the hair cell is 'active.' However, this use of the term 'active' is not what is usually meant in cochlear modeling, where the term is frequently used interchangeably with the term 'cochlear amplifier', implying gain on a cycle by cycle basis. The details following the cell depolarization which lead to the basilar membrane stiffness change are presently unknown and we have assumed here that such a dependence is plausible. To study the site of the nonlinearity in a more systematic way, it may be helpful to model the frequency response of the $2f_1 - f_2$ distortion product for constant f_2. These distortion products may be modeled using quasi-linear techniques by introducing voltage sources in series with K_{BM} to represent the generation of the nonlinear components. From the equivalent model of the micromechanical circuit (Allen, 1980, Fig. 10), a source in series with K_{BM} would see the series impedance of the tectorial membrane, which has a minimum at f_z. This suggests that the nonlinearity might have maximum coupling to the fluid at this frequency.

A little analysis shows that this would give a maximum of the distortion product amplitude when $2f_1 - f_2 = f_z$. First we argue that the distortion product is generated at, or near, x_2, which is defined as the f_2 place. Next we define $\beta(x) = f_z(x_2)/f_2(x_2)$ as the ratio of f_z to f_2 at x_2. It follows that the distortion product amplitude will have its maximum at $f_2/f_1 \simeq 2.0/(1+\beta)$. For β in the range of 0.7 to 0.5, as it is in this model, this would give a best frequency ratio of 1.18 to 1.33, which is close to the range of observed maximum values (Wilson, 1980).

References

Allen, Jont B. (1980). "Cochlear micromechanics - A physical model of transduction," J. Acoust. Soc. Am. **68**(6) 1660-1670.

Allen, Jont B. (1988). "Cochlear signal processing," *Physiology of the Ear*, edited by A. F. Jahn and J. Santos-Sacchi, Raven Press, New York, 243-270.

Brownell, W.E., Bader, C.R., Bertran,D., and de Rabaupierre, Y. (1985). "Evoked mechanical responses of isolated cochlear outer hair cells," *Science*, **227** 194-196.

Dallos, Peter (1984). "Some electrical circuit properties of the organ of Corti. II. Analysis including reactive elements," Hearing Research **14** 281-291.

Denk, W. and Watt, W.W. (1989). "Thermal-noise-limited transduction observed in mechanosensory receptors of the inner ear," Physical Review Letters **63** 207-210.

Hudspeth, A. J. (1983). "Mechanoelectrical Transduction by Hair Cells in the acousticolateralis Sensory System," *Annu. Rev. Neurosci.*, **6** 187-215.

Liberman, M. C. and Dodds, L. (1984). "Single Neuron Labeling and Chronic Cochlear Pathology III: Stereocilia Damage and Alterations of Threshold Tuning Curves," Hearing Research **16** 55-74.

Mountain, D.C., and Hubbard, A.E. (1989). "Rapid force production in the cochlea," Hearing Research 42 195-202.

Neely, S.T. and Kim, D. O. (1983). "An active cochlear model showing sharp tuning and high sensitivity," Hearing Research. **9** 123-130.

Nuttal, F., Dolan, D. F., and Avinash, G. (1990). "Doppler Vibrometer Measurements of Basilar Membrane Motion in the Guinea Pig," abstract 293, poster 23, 13th ARO Midwinter Meeting.; See paper in this proceedings.

Patuzzi, R. B., Yates, G. K., and Johnstone, B. M. (1989). "Outer hair cell receptor current and sensorineural hearing loss," Hearing Research 42 47-72.

Puria S., and Allen, Jont B. (1990). "A Parametric Study of the Cochlear Input Impedance," J. Acoust. Soc. Am., In Press

Robles, L., Ruggero, M.A., Rich, N.C. (1986). "Basilar membrane mechanics at the base of the chinchilla cochlea. I. Input-output functions, tuning curves, and response phases," J. Acoust. Soc. Am. **80** 1364-1374.

Santos-Sacchi, J. and Dilger J. P. (1987). "Whole cell currents and mechanical responses of isolated outer hair cells," Hearing Research **35**, 143-150.

Sellick, P.M., Patuzzi, R., and Johnstone, B.M. (1983). "Comparison between the tuning properties of inner haircells and basilar membrane motion," Hearing Research **10** 93-100.

Sondhi, M. M. (1979). "Method for computing motion in a two-dimensional cochlear model," J. Acoust. Soc. Am.**63** 1468-1477

Wilson, J.P. (1980). "The combination tone, $2f_1 - f_2$, in psychophysics and ear-canal recording," in *Psychophysical and Physiological and Behavioral studies in Hearing*, edited by G. van den Brink and F. A. Bilsen, Delft Univ. Press.

Comments and discussion

LYON

In your first step, you convert iso-response tuning curves to "excitation patterns" that appear to be in terms of an iso-intensity situation. This would be a sensible transformation for a linear system, such as your model, but how can it be interpreted for a system with a strong input-output compression nonlinearity, such as the cochlea from which the data were taken ?

ALLEN

I agree with your observation which you make in your paper that the frequency dependent compression of the type that has been observed in the basilar membrane response will have an impact on the response characteristics as the input level is varied. These nonlinear properties make the job of modeling BM responses much more difficult. The question then is one of the philosophy of how to go about this difficult task. Two points need to be made about this.

The first point goes back to my paper in Keele (Allen, 1988) where I discussed the three regions of the amplitude and frequency space where we see different nonlinear behavior. Observations of basilar membrane nonlinearities are considerably reduced in the apical region of the cochlea (for example, for frequencies below 4 or 5 kHz and for levels below about 60 to 65 dB-SPL.) Evidence for this statement is documented in my Keele paper. It follows that the effects you describe are most important in the base of the cochlea, which I have not attempted to modeled for this conference. As I said in Keele, we must be very careful about not generalize the effects we see in the base of the cochlea to the apex region.

Second, in a nonlinear system it is helpful if one can hold the signal to the nonlinear element constant when specifying the systems response. In the case of the basilar membrane, there is not one nonlinear element but a nearly continuous distribution of nonlinear elements. In the case of neural tuning curves, such as I have been trying to match, we have not only the basilar membrane nonlinearity, but also the hair cell rate level nonlinearity. In making a tuning curve one attempts to minimize the nonlinear effect of the inner hair cell transduction nonlinearity by measuring the locus of pressures as a function of frequency that produce a constant output firing rate. The analogous measurement in the case of basilar membrane measurements would be to hold the excitation to the nonlinear elements constant. To the best of our present knowledge, this nonlinear element is the outer hair cell, which is controlled by the receptor voltage. Since the experimenter does not have direct control of this voltage, the basilar membrane velocity or displacement is typically help constant. This implies that the nonlinearity is varying over the course of the measurement, which greatly complicates both the interpretation and modeling of the measurement.