LEVEL DEPENDENCE OF THE LATENCY OF COCHLEAR TRANSIENTS

Stephen T. Neely

Boys Town National Research Hospital
555 North 30th Street, Omaha, NE 68131, USA

Introduction

An important consequence of the fact that cochlear mechanics are nonlinear is that the latency of the auditory nerve response to transient sounds is level dependent. Specifically, the latency of the neural response decreases as the sound level increases. The *cochlear component* of the latency of human auditory brainstem responses (ABR) to tone-burst stimuli has been shown to consistently decrease by about 38% for every 20 dB increase in the level of the stimulus (Neely *et al.*, 1988). Moreover, this consistent latency decrease with level holds over a wide range of tone-burst frequencies and intensities.

The level dependence of the latency of cochlear transients can be simulated in an active, nonlinear model of cochlear mechanics by applying a saturating nonlinearity to the feedback force associated with outer hair cells (Neely, 1989). The reason that this nonlinearity in the model causes the latency to vary with level in the same manner as observed in the human ABR data is not obvious. It must be that either (1) the *place* along the cochlear partition associated with the generation of the neural response changes with stimulus level or (2) the *velocity* of the transient signal along the cochlear partition varies with level.

In this paper, we examine how the cochlear place and velocity change with level with the objective of determining which has the greater influence on the latency of the neural response. The model results presented here suggest that the primary reason for the level dependence of the neural response is an increase in cochlear velocity with level.

Methods

Tone-burst stimuli were presented to an active, nonlinear, time-domain model of cochlear mechanics. The tone-bursts were Blackman-windowed tones at 4 frequencies (0.5, 1, 2, and 4 kHz) and 4 levels at each frequency (20, 40, 60, and 80 dB peSPL). The stimulus level is specified as the peak pressure at the eardrum in decibels *re* 28.28 μPa. The model response to each of the 16 stimuli was computed for 20 msec beyond onset of the stimulus.

The model equations and mathematical notation generally follow that of Neely and Kim (1986). A change was made in the representation of cochlear fluid mass in order to

simulate the decrease in scala height from base to apex. This modification improved the coupling of the cochlea to the middle ear, but did not significantly affect the latency of cochlear responses.

In order to facilitate comparison of model results with human ABR data, the model parameters were chosen so that the frequency-to-place map along the cochlear partition would be similar to a human cochlea. A time-domain formulation of the model equations was used so that the parameter controlling the force generated by the outer hair cells could vary with time to simulate a saturating nonlinearity.

Two overall measures of the model's response were recorded at each time step: (1) the locus of mechanical input to the inner hair cells (LOMI) was defined as the center of motion along the cochlear partition at each point in time; (2) the whole nerve response (WNR) was defined as the sum of the output of all inner hair cells at each point in time. These overall measures are described in more detail below.

FLUID MASS

A one-dimensional (transmission line) approximation of cochlear fluid mechanics can be written as

$$\frac{d^2}{dx^2} P_d(x) = \frac{2\rho}{H} \ddot{\xi}_p(x) \tag{1}$$

where P_d is the difference in pressure across the cochlear partition (CP), ξ_p is the average displacement across the width of the CP, H is the height of the scalae, and ρ is the density of the fluid. The dots above ξ_p indicate derivatives with respect to time. A finite-difference approximation of the spatial derivative in x results in the following equation

$$2P_d(x) - P_d(x-\Delta) - P_d(x+\Delta) = -\frac{2\rho\Delta^2}{H} \ddot{\xi}_p(x) \tag{2}$$

where $\Delta = L/(N-1)$ is a small distance along the CP over which the mechanical properties of the cochlea are lumped as a single section.

Equation (1) was derived with the assumption of constant scala height; however, the fact that the scala height decreases from base to apex has been shown to have an important influence on cochlear input impedance (Puria and Allen, 1990; Shera and Zweig, 1990). The decrease in scala height causes the effective fluid mass to increase from base to apex. In this lumped-element, transmission-line representation of the cochlea, we can identify the fluid mass as

$$m_f = \frac{2\rho\Delta^2}{H} . \tag{3}$$

The effect of decreasing scala height can be approximated by making m_f an exponentially

TABLE I. Model parameter values (cgs units).

$k_1(x) = 4 \cdot 10^8 e^{-3x}$ (dyn · cm^{-3})	$L = 3.5$ (cm)
$c_1(x) = 960 e^{-1.4x}$ (dyn · sec · cm^{-3})	$H = 0.1$ (cm)
$m_1(x) = 0.004$ (gm · cm^{-2})	$W = 0.1$ (cm)
$k_2(x) = 2 \cdot 10^8 e^{-3.2x}$ (dyn · cm^{-3})	$d_m = 10^{-7}$ (cm)
$c_2(x) = 2000 e^{-1.4x}$ (dyn · sec · cm^{-3})	$\rho = 1$ (gm · cm^{-3})
$m_2(x) = 0.037$ (gm · cm^{-2})	$b = 1$
$k_3(x) = 2.25 \cdot 10^8 e^{-3.2x}$ (dyn · cm^{-3})	$g = 1$
$c_3(x) = 0$	$N = 409$
$k_4(x) = 4.5 \cdot 10^8 e^{-3.1x}$ (dyn · cm^{-3})	
$c_4(x) = 0$	

increasing function of x

$$m_f = \frac{2\rho\Delta^2}{H} e^x . \tag{4}$$

The model results presented in this paper use Eq. (4) to represent the fluid mass. This improves the coupling of the cochlea to the middle ear in the model by decreasing the reactive (imaginary) component of the cochlear input impedance at low frequencies. This does not, however, significantly affect the latency of cochlear transients.

PARTITION IMPEDANCE

The fluid pressure difference P_d and partition displacement ξ_p are also related by the micromechanics of the cochlear partition. Two mechanical degrees-of-freedom are represented in the partition mechanics within each lumped section, so that the fluid pressure difference across the cochlear partition is related to the velocity of the cochlear partition by a partition impedance Z_p

$$P_d(x) = Z_p(x)\,\dot{\xi}_p(x) \tag{5}$$

$$Z_p = (g/b)\,[Z_1 + (Z_2(Z_3 - \gamma Z_4))/(Z_2 + Z_3)] \tag{6}$$

where $Z_1 = m_1 s + c_1 + k_1/s$, $Z_2 = m_2 s + c_2 + k_2/s$, $Z_3 = c_3 + k_3/s$, and $Z_4 = c_4 + k_4/s$ are impedance functions specified in the frequency domain, $s = i\omega$. The term Z_4 in the partition impedance represents a feedback force from the outer hair cells (OHC), implementing the hypothetical *cochlear amplifier*. The model parameter values are listed in Table I. The parameter γ controls the magnitude of the influence of the cochlear

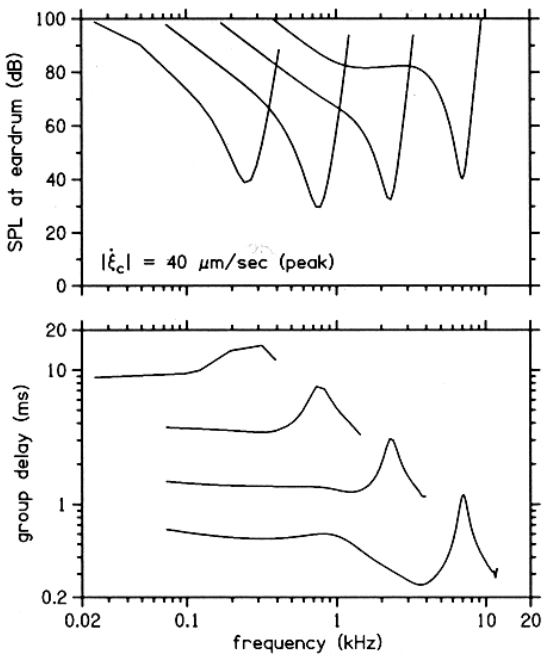

FIGURE 1 Iso-velocity tuning curves from the linear, time-domain model. The stimulus was a wide-band click presented to a simple earphone and coupler model. The linear, time-domain model response was computed for 40 msec beyond onset of the stimulus. The hair-cell velocity $\dot{\xi}_c$ at four places (corresponding to 20, 40, 60 and 80 percent distance from the base) was Fourier transformed along with the pressure at the eardrum to obtain the curves in this figure. In the upper panel the curves indicate the pressure needed at the eardrum to elicit a criterion velocity $\dot{\xi}_c$ = 40μm/sec . The lower panel shows the group delay of hair cell velocity relative to the eardrum pressure at the same four places. Group delay is defined as minus the slope of the phase with respect to frequency.

amplifier; it is constant in the frequency-domain and linear, time-domain formulations of the model and varies with time in the nonlinear, time-domain model.

For a given set of model parameters (and appropriate boundary conditions), we can use these equations to solve for P_d and ξ_p in either the frequency or time domain. For comparison with experimental data, we also identify the shearing displacement between the tectorial membrane and reticular lamina as

$$\xi_c = (g/b)\,[Z_2/(Z_2+Z_3)]\,\xi_p \tag{7}$$

The displacement ξ_c represents the mechanical input to the outer hair cells and the velocity $\dot{\xi}_c$ represents the mechanical input to the inner hair cells. Velocity was chosen as the input to inner hair cells because the iso-velocity tuning curves looked more like typical cat neural- threshold tuning curves than did the iso-displacement tuning curves.

The iso-velocity tuning curves in Fig. 1 were obtained by taking Fourier transforms of 40 msec impulse responses with $\gamma = 1$ in the time-domain model. This represents the linear version of the model. The remaining figures in this paper show "nonlinear" model results for the case in which γ was a time-varying parameter

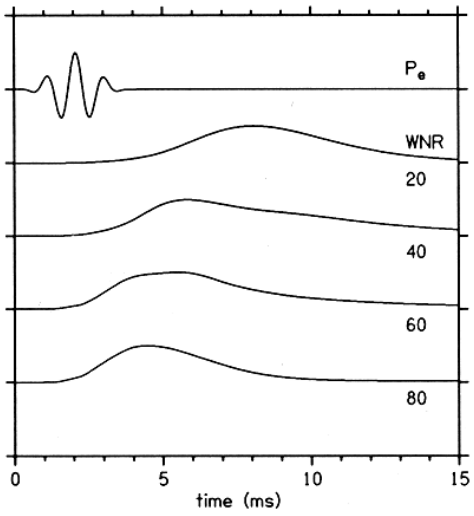

FIGURE 2 Pressure at eardrum P_e and whole-nerve response (WNR) to 1-kHz tone-bursts and four sound pressure levels. The numbers in the figure indicate the peak sound pressure at the eardrum in decibels re 28.28 μPa (peSPL). Similar results were obtained at 0.5, 2, and 4 kHz. Note that the latency of the WNR decreases as the level of the stimulus increases. The vertical scale in this figure is arbitrary. Each trace was normalized separately to the same maximum value.

$$\gamma = \begin{cases} 1, & |\xi_c| \le d_m \\ d_m/|\xi_c|, & |\xi_c| > d_m \end{cases} \tag{8}$$

making the model results dependent on the level of the stimulus. This definition of γ is equivalent to saturation of the OHC feedback force for displacements ξ_c greater than d_m (Neely, 1989).

MEASURES OF MODEL RESPONSE

The transient response within the cochlea moves as a wave packet. The locus of mechanical input to the inner hair cells (LOMI) is a measure of the location of the transient signal along the cochlear partition that was designed to track the center of the region where $\dot{\xi}_c$ was greatest. It was computed by weighting each place by the value of $\dot{\xi}_c^2$ at that place. This definition was convenient for assigning a single place to the transient signal at each time step, but is not critical to the conclusions about cochlear latency.

The whole nerve response (WNR) was computed by applying $\dot{\xi}_c$ to a simple inner hair cell model consisting of a half-wave rectifier and "leaky" integrator at each position along the cochlear partition. The time-constant of the integrator was 0.5 msec. The outputs of all integrators were summed (with equal weighting) to produce the WNR.

Results

An example of the time course of the WNR is shown in Figure 2 for the 1-kHz tone-burst at each of the 4 levels. The latency of the WNR can be measured either to (1) the peak

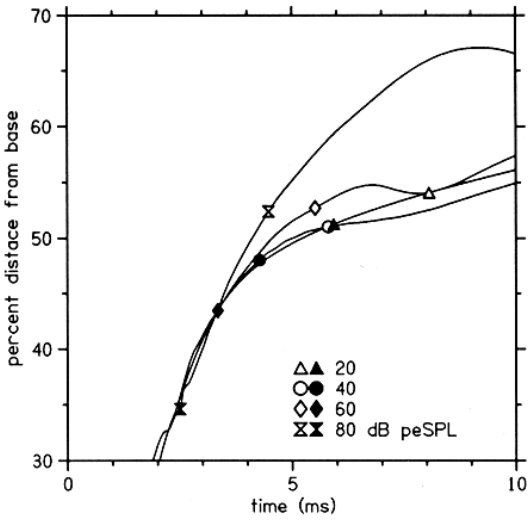

FIGURE 3 Locus of mechanical input to the inner hair cells (LOMI) and whole nerve response (WNR). The lines in this figure indicate the place at which the mechanical input to the outer hair cells is greatest based on using ξ^2_c as a weighting factor. The closed symbols indicate the time of WNR onset and the open symbols indicate the time of WNR peak. Note that the WNR peak latency at 40 dB (open circle) does not follow the trend of the other open symbols. This is due to the flattened shape of the peak of the WNR shown in Figure 2.

(maximum value) of the WNR or (2) the onset (maximum positive slope) of the WNR. Both the peak and onset latency of the WNR clearly decrease in Figure 2 as the level of the stimulus is increased. At the lowest and highest levels, the onset of the WNR precedes the peak by about 2 msec. The time difference between the onset and the peak of the WNR is largely accounted for by the difference in time between the onset and peak of the stimulus which is also 2 msec for the 1-kHz tone-burst. The onset of the WNR is probably a better measure of cochlear latency.

The latency of the WNR varies with level primarily because the time-course of the LOMI varies with level. The LOMI describes the center of activity along the cochlear partition at each point in time. In Figure 3, we see that the LOMI reaches the 1-kHz characteristic place (about 55% distance from the stapes) faster at the 80 dB level than at the 20 dB level. The velocity of the LOMI (observed as the slope of the lines in Figure 3) becomes level dependent at about 45% distance from the stapes.

We can define the place along the cochlear partition primarily responsible for the generation of the WNR as the location of the LOMI when the WNR reaches its peak value. For the 1-kHz tone-burst, this place is at 52.4% when the level is 80 dB and 54.1% when the level is 20 dB. This small change in place accounts for only a small part of the total peak latency change. Most of the change in the WNR peak latency is due to the change in velocity of the LOMI.

At each of the four levels the WNR onset latency decreases with increasing level except in one case: the 20 dB level at 4 kHz. The mechanical input to the outer hair cell may have been too small in this case to be affected by the saturating nonlinearity. The onset latency of the WNR is shown in Figure 4 for each of the 16 stimuli. The corresponding latency for the human cochlea at the same 4 levels based on analysis of human ABR data (Neely, *et al.* 1988) is represented by the dotted lines in Figure 4. In general, dependence of the WNR onset latency on level and frequency is similar to the cochlear component of the human ABR latency.

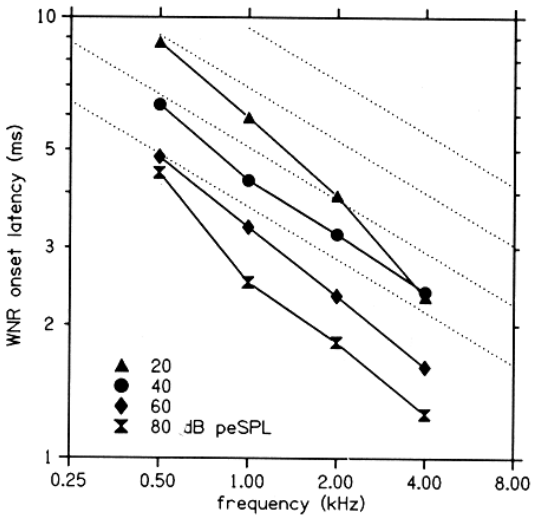

FIGURE 4. Frequency and level dependence of the WNR onset latency. The onset of the WNR was defined as the point in time corresponding to the maximum positive slope of the WNR. The dotted lines show the corresponding latency values for the human cochlea at the same four levels. These lines are based on extracting the cochlear component from human ABR latency data (Neely, *et al.*, 1988).

Discussion

COMPARISON WITH EXPERIMENT

The latency of the onset of transient responses recorded in single auditory nerve fibers also decreases as the level of the stimulus increases; however, the latency decrease may appear to be discontinuous. Post-stimulus time (PST) histograms recorded from single nerve fibers typically show several distinct peaks (Kiang, *et al.*, 1965). The latency of each individual peak does not change much with stimulus level, but earlier peaks observed at high levels are not present al low level. Thus, the onset of the transient response decreases abruptly as the stimulus level increases whenever an earlier peak becomes large enough to be observed. Similar behavior can be seen in the model results for the simulated neural response, but are not presented in this paper. The onset latency of WNR response shows more continuous variation with stimulus level because the distinct peaks seen in the response at a single place are not seen when the responses from all places are combined.

The estimates of human cochlear latency represented by the dotted lines in Figure 4 were obtained by subtracting 5 msec from measurements of the latency of ABR wave V using tone-bursts. This 5 msec is attributed to neural synaptic and propagation delay which is relatively independent of stimulus intensity and frequency (Neely, *et al.*, 1988). The model parameters could be adjusted to improve the agreement between the model results and the human latency data. In particular, the fact that the slopes of the lines in Figure 4 are greater for the model than for the human data suggests that the stiffness of the cochlear partition in the model should decrease less from base to apex.

CONCLUSIONS

The most important observation in this paper is that the latency of the WNR decreases with level mostly because the transient response moves faster along the cochlear partition near the characteristic place (for the frequency of the tone-burst) as the level increases. The

change in "the place primarily responsible for generation of the WNR" contributes much less to the change in latency than does the change in velocity of the LOMI. The fact that the frequency and level dependence of the WNR onset latency resembles that of the human ABR data suggests that this explanation may also apply to the human cochlea.

Because the cochlear velocity is determined primarily by the stiffness of the cochlear partition, these results also suggest that the stiffness of the cochlear partition is nonlinear and varies significantly with level in the vicinity of the characteristic place.

FUTURE DIRECTIONS

The method used to integrate the time-domain formulation of the equations is the same as used by Allen and Sondhi, 1980. Using a bilinear transformation of the frequency domain formulation to obtain the time-domain formulation would improve the correspondence between the frequency-domain and time-domain solutions and also improve the computational efficiency (Michel, 1989).

The nonlinear model requires that the time-varying parameter γ provide essentially a hard-limiting function for displacements greater than 1 nm. This displacement is small compared with displacements at the threshold of hearing and may need to be increased. Other more gradual limiting functions should be investigated, such as $\gamma = 1/(1 + (\dot{\xi}_c/d_m)^2)$.

Recent observations of outer-hair-cell motility suggests that these cells are intrinsically tuned to a place appropriate frequency (Brundin, *et al.*, 1989). The model equations describing the micromechanics of the cochlear partition could be reformulated to reflect this observation.

References

Allen, J.B. and Sondhi, M.M. (1979) A cochlear mechanical model of transduction. In: Psychophysical, physiological, and behavioral studies in hearing (Eds: van den Brink, G. and Bilsen, F.A.) Delft Univ. Press, Netherlands, pp 85-95.

Brundin, L., Flock, Å., Canlon, B. (1989). Sound induced motility of isolated outer hair cells is frequency-specific. Nature **342**, 814-816.

Kiang, N.Y.-S., Wanatabe, T., Thomas, E.C., and Clark, L.F. (1965). Discharge patterns of single fibers in the Cat's Auditory Nerve. M.I.T. Research Monograph No. 35., Technology Press, Cambridge, Mass., pp 32-43.

Michel, D. (1989) A model for peripheral auditory preprocessing. In: Cochlear Mechanisms (Eds: Wilson, J.P. and Kemp, D.O.) Plenum Press, London, pp 425-434.

Neely, S.T. (1989) Transient responses in an active, nonlinear model of cochlear mechanics. In: Cochlear Mechanisms (Eds: Wilson, J.P. and Kemp, D.O.) Plenum Press, London, pp 106-113.

Neely, S.T. and Kim, D.O., (1986) A model for active elements in cochlear biomechanics. J. Acoust. Soc. Am. **79**, 1472-1480.

Neely, S.T., Norton, S.J., Gorga, M.P., and Jesteadt, W. (1988) Latency of auditory brainstem responses and otoacoustic emissions using tone-burst stimuli. J. Acoust. Soc. Am. **83**, 652-656.

Puria, S. and Allen, J.B. (1990) A parametric study of cochlear input impedance. J. Acoust. Soc. Am. (submitted).

Shera, C.A. and Zweig, G. (1990) A symmetry suppresses the cochlear catastrophe. (in preparation).