THE COCHLEAR AMPLIFIER

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ABSTRACT

The recent observations of sharply-tuned basilar membrane motion and the existence of cochlear acoustic emissions provide evidence that the cochlea is an active mechanical system, capable of generating mechanical vibrations. A model of cochlear mechanics is presented in this paper to support the hypothesis that the primary function of mechanical generators in the cochlea is to amplify displacements of the basilar membrane at sound levels near the threshold of hearing. Some numerical solutions of this model show basilar membrane displacement amplitudes of about 1 angstrom for sound pressures at the eardrum of 0 dB SPL (20 μPa). The rate of energy flow out of the basilar membrane into the cochlear fluid due to the cochlear amplifier is often more than 40 dB greater than the rate of energy flow into the cochlea from the stapes. The action of the cochlear amplifier in this model may be interpreted as a piezoelectric effect which provides a delayed positive feedback to basilar membrane motion.

1. INTRODUCTION

The experimental observations in recent years of cochlear acoustic emissions (Kemp, 1978) and sharply-tuned basilar membrane (BM) displacements (Sellick et al., 1982) have forced us to modify some traditional ideas about cochlear mechanics. The existence of acoustic emissions from the cochlea indicates the presence of mechanical generators within the cochlea. If we consider the cochlea to be an active mechanical system which can utilize available biochemical energy to generate mechanical vibrations, then we can begin to explain the sharply-tuned frequency response observed in the firing rate of auditory nerve fibers directly in terms of BM displacements. A model of cochlear mechanics is presented in this paper to support the hypothesis that the primary biological function of mechanical generators in the cochlea is to amplify BM displacements at sound levels near the threshold of hearing.

2. THE COCHLEAR MODEL

We will consider a linear, two-dimensional, ideal-fluid model of cochlear mechanics (Neely, 1980). The two fluid-filled chambers are each of height H in the y dimension and length L in the x dimension; they are separated by a cochlear partition at $y=0$, which is open in the apical region $(L-L_h) < x < L$ to represent the helicotrema. Displacements of the cochlear partition in the model are the same as BM displacements. The stapes boundary at $x=0$

drives the cochlear fluid.

The cochlear amplifier will be implemented by modifying the (usually passive) representation of the mechanics of the cochlear partition. Since we are dealing with a linear model, it is convenient to characterize the partition mechanics by a complex-valued driving-point impedance Z. The driving-point impedance is defined as the ratio of pressure difference across the cochlear partition to BM velocity as a function of position x and radian frequency $\omega = 2\pi f$. The units of Z are $dyn \cdot sec \cdot cm^{-3}$.

The BM impedance Z will be defined as the sum of two parts

$$Z(x,\omega) = Z_b(x,\omega) + Z_a(x,\omega) \tag{1}$$

where Z_b represents the contribution of the mass, damping, and stiffness of the BM

$$Z_b(x,\omega) = i\omega M_1(x) + R_1(x) + K_1(x)/i\omega \tag{2}$$

and Z_a represents the effect of the cochlear amplifier

$$Z_a(x,\omega) = \frac{-(R_3)^2}{i\omega M_2(x) + R_2(x) + K_2(x)/i\omega}. \tag{3}$$

The definition of Z_a was chosen according to the restriction that the cochlear amplifier should add only one degree-of-freedom to the partition mechanics at each position. The physical interpretation for Z_a is that it represents an active biomechanical system located in the vicinity of the outer hair cells, which exerts a force on BM in parallel with the force due to fluid pressure. An alternative definition for Z_a will be presented in section 4.

The choice of numerical values for BM impedance is largely a trial-and-error process relying on physical principles and comparisons between numerical solutions of the model and experimental observations. The following mechanical parameter functions were chosen to represent a cat cochlea using as a guide the cochlear input impedance of Lynch et al. (1982) the cochlear frequency-to-place map of Liberman (1982) and the single nerve fiber response measurements of Allen (1983):

$$K_1(x) = 10^9 \exp(-2.4x) \tag{4}$$

$$R_1(x) = 400 + 10^3 \exp(-1.2x) \tag{5}$$

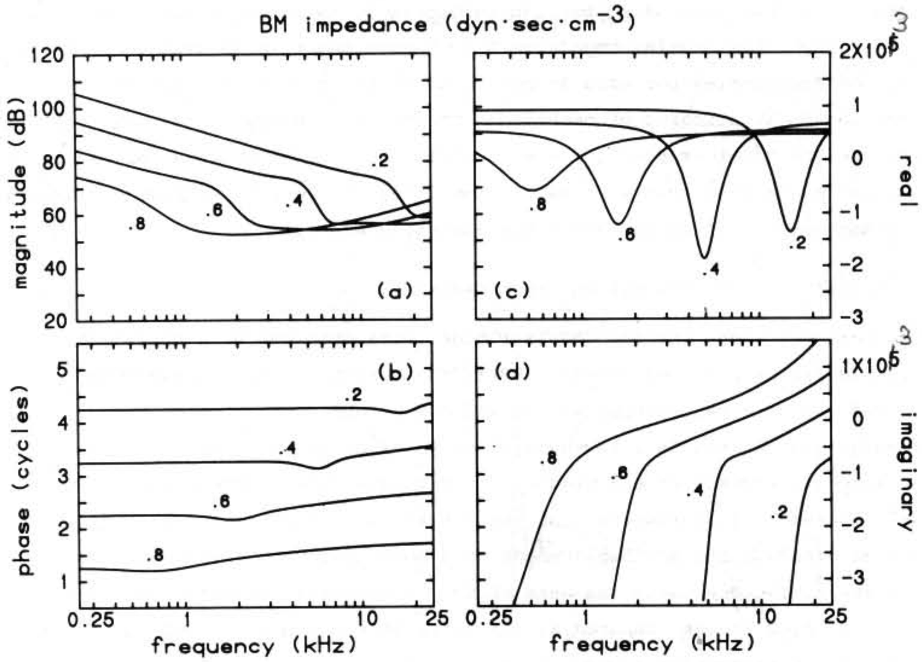

Fig. 1. The driving-point impedance Z of the basilar membrane (BM) is shown as a function of frequency at four places. The numerals next to each curve indicate the position as a fractional distance along BM. Part (a): magnitude of Z in dB re 1 dyn·sec·cm^{-3}; part (b): phase of Z with π radian (1/2 cycle) per division; part (c): real part of Z; part (d): imaginary part of Z. The impedance was computed at frequencies which are multiples of 48.8 Hz using the equations for Z given in the text.

$$M_1(x) = 10^{-3}\ \exp(1.2x) \quad (6)$$

$$K_2(x) = 250\ \exp(-2.2x) \quad (7)$$

$$R_2(x) = 10^{-4}\ \exp(1.1x) + 8\times10^{-4}\ \exp(-2.2x) \quad (8)$$

$$M_2(x) = 3\times10^{-9}\ \exp(2.2x) \quad (9)$$

$$R_3(x) = 1.0 \quad (10)$$

The BM impedance is shown in Fig. 1 at four positions: $x/(L-L_h)$ = 0.2, 0.4, 0.6, and 0.8, where $(L-L_h)$ = 2.5 cm is the length of BM. The effect of Z_a on the BM impedance is clearly seen in Fig. 1(c). At each BM position there is a resonant frequency for Z_a, at which the real part of Z_a, which is always negative, reaches its largest (most negative) value. For the parameters chosen, the real part of Z_a becomes sufficiently negative to cause the real part of the driving-point impedance Z to become negative as well for a certain range of frequencies for each BM position. Whenever Z has a negative real part, the BM is a source of mechanical energy; this energy flows out at BM and into the cochlear fluid. The energy flow out of the BM does not cause the cochlear mechanical system to become unstable, if there is sufficient damping in other regions of BM to absorb the generated energy.

3. NUMERICAL SOLUTIONS FOR BM DISPLACEMENT

Numerical solutions for the cochlear model were obtained by a time-domain, finite-difference method (Neely, 1981). The height H = 0.1 cm and length L = 2.55 cm were represented with 6 and 409 points respectively. The stimulus was defined as a low-pass click voltage, followed by simple models for earphone transducer and middle-ear (Matthews, 1980). The cochlear state was computed at 1 microsecond intervals for 20480 time-steps. The computed eardrum pressure and BM displacement at 4 positions were saved every 10 time-steps. The frequency response of BM displacement re eardrum pressure (shown in Fig. 2) was computed as the ratio of the discrete Fourier transforms of the respective 20 msec time responses. The frequency interval between data points is 48.8 Hz.

The amplitude of BM displacement in Fig. 2(a) is normalized to show the peak amplitude in dB re 1 angstrom (10^{-10}m) corresponding to 0 dB (re 20 μPa rms) sound pressure level at the eardrum. The shape and characteristic frequency of the four response curves are similar to that of typical single nerve fiber responses in cat. The amplitude of BM displacement relative to eardrum pressure in this model at 7 kHz is nearly the same as that measured by Sellick et al. (1982) in guinea pig at 18 kHz. It should be noted that the amplitude ratio shown in Fig. 2(a) would probably be larger if the model were three-dimensional and could represent BM width as being less than the entire width of the cochlea.

The slope and delay functions in Figs. 2(c) and 2(d) were computed by taking differences of adjacent points of the amplitude and phase functions, respectively. The delay function represents the slope of the phase in cycles per kHz. The "stair-step" appearance of the delay curves in Fig. 2(d) is an indication of two straight-line segments in the phase curve plotted on a linear frequency scale. This was also a characteristic feature of Rhode's (1978) observations of the phase of BM displacement in squirrel monkey.

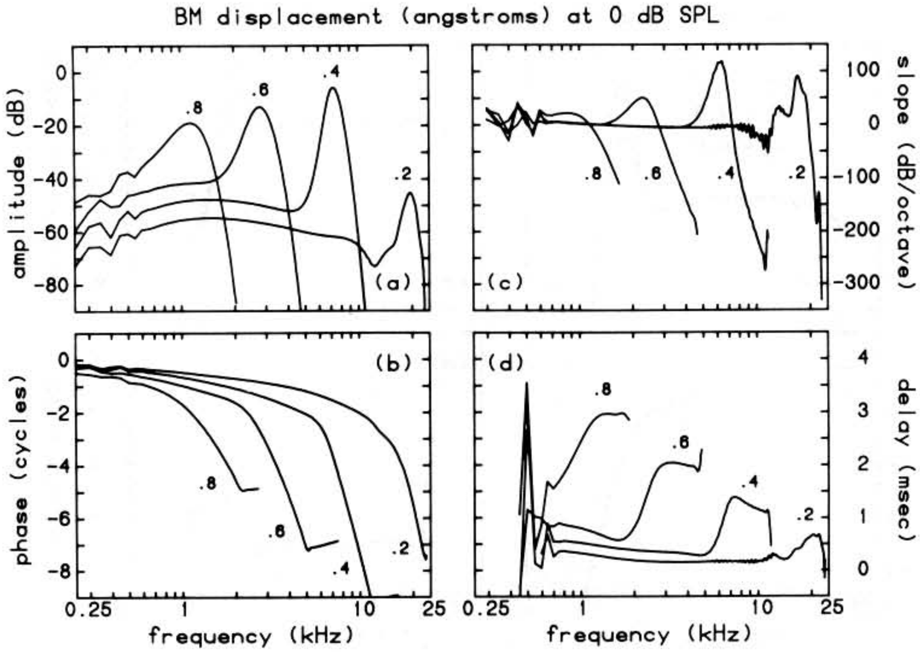

Fig. 2. Displacement of the basilar membrane (BM) re sound pressure at the eardrum. Part (a): peak amplitude of BM displacement in dB re 1 angstrom for eardrum pressure of 20 μPa rms; part (b): phase of BM displacement re eardrum pressure with 1 cycle per division; part (c): slope of the magnitude in dB/octave; part (d): delay (slope of the phase) in msec.

An attractive feature of the cochlear amplifier hypothesis is that it provides a means of explaining the deterioration of sharp tuning which is often observed experimentally in a traumatized cochlea. The loss of the tip of a tuning curve is interpreted as a loss of cochlear amplifier gain. The impedance parameter R_3 can be considered as a sort of gain control on the cochlear amplifier. Solutions of the cochlear model for $R_3 = 1.0$, 0.9, and 0.0 are shown in Fig. 3. The decreased cochlear amplifier gain clearly has a significant effect on BM displacement near the characteristic frequency. The amplitude at 7 kHz in Fig. 3(a) drops about 20 dB for $R_3 = 0.9$ and drops about 70 dB for $R_3 = 0.0$.

4. DISCUSSION

The BM impedance presented in section 2 can be "synthesized" by a mechanical system consisting of 2 masses, 2 springs, 2 positive damping elements, and 1

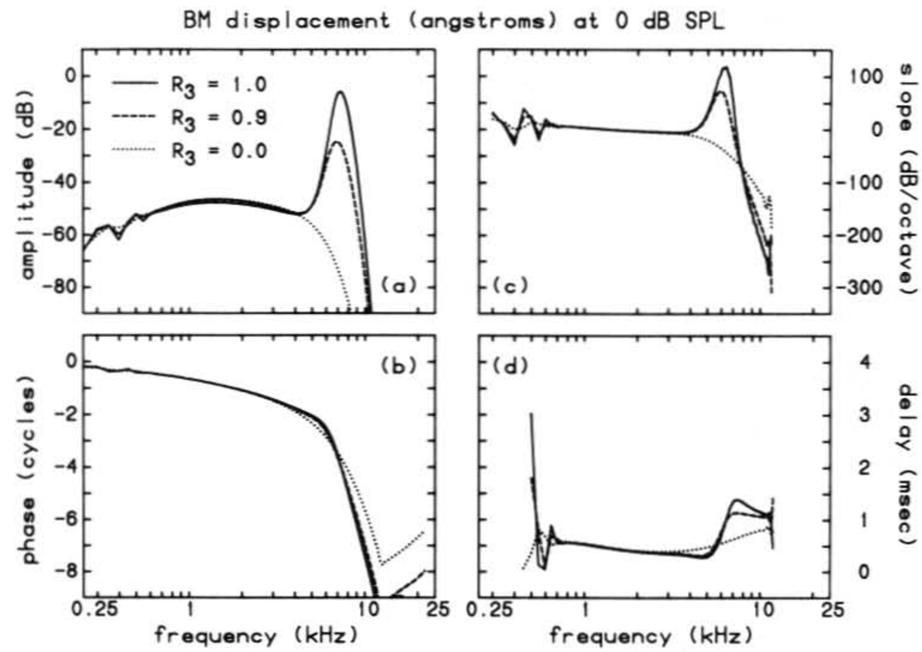

Fig. 3. Effect of changes in cochlear amplifier gain on basilar membrane (BM) displacement. Parts (a) - (d): same as in Fig. 2. The solid lines are reproduced from Fig. 2 (position 0.4, R_3 = 1.0). The dashed lines show BM displacement with R_3 = 0.9 and the dotted lines show BM displacement with R_3 = 0.0.

negative damping element. The use of negative damping in BM impedance was first presented as a means of explaining the ante- to post-mortem changes in BM displacement (Kim et al., 1980). A cochlear model with negative damping elements can produce BM displacements which closely resemble typical neural responses (Neely and Kim, 1983). Negative damping provides a convenient means of modeling active mechanical behavior in a linear cochlear model.

A more appealing physical interpretation of the cochlear amplifier is that it represents a piezoelectric action powered by the cochlear microphonic (Davis, 1981). This type of electromechanical action can be modeled as a stiffness component which has a delayed effect. The corresponding definition for Z_a would be

$$Z_a(x,\omega) = [K_3(x)/i\omega] \exp[-i\omega\, \tau(x)] \tag{11}$$

where τ is a transduction latency of several microseconds. Preliminary frequency-domain model results using Eq. (11) to implement the cochlear amplifier are very similar to those using Eq. (3). Time-domain implementation, however, is much more difficult for Eq. (11).

Non-linearities in cochlear mechanics are likely to originate in the cochlear amplifier. One plausible way of modeling a nonlinear cochlear amplifier would be to set R_3 (or K_3) to zero if BM displacement exceeds some threshold, thus simulating saturation of the cochlear amplifier.

Evidence for the existence of the cochlear amplifier is continually accumulating (Davis, 1983). Both analytical (de Boer, 1983) and numerical (Neely and Kim, 1983) model results now indicate that a cochlear amplifier is essential for producing basilar membrane displacements with the high sensitivity and sharp tuning observed experimentally.

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