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AN ACTIVE COCHLEAR MODEL WITH NEGATIVE DAMPING IN THE PARTITION: COMPARISON WITH RHODE'S ANTE- AND POST-MORTEM OBSERVATIONS

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ABSTRACT

Results are presented from a two-dimensional model for cochlear mechanics with active properties represented by the inclusion of negative damping in the impedance of the cochlear partition over a limited region, or with passive properties without negative damping. Model solutions were obtained using both a finite-difference method in the frequency domain and a Green's-function method in the time domain. Results from our active model are similar to Rhode's ante-mortem observations of basilar-membrane motion in the squirrel monkey, and results from our passive model are similar to Rhode's post-mortem observations. We suggest from these results: 1) that an active source of mechanical energy in the cochlear partition may underlie normal cochlear mechanical response; 2) that the loss of this energy source upon death may be responsible for the early post-mortem broadening of tuning and peak shift; and 3) that a later reduction in the stiffness of the cochlear partition may be responsible for further shifts of the amplitude peak and of the phase pattern occurring hours after death.

INTRODUCTION

We present in this paper our recent results from a model for cochlear mechanics where active mechanical behavior is incorporated. A novel feature of our model is the presence of a controlled energy source in the cochlear partition represented by negative values of the damping of the partition impedance over a certain localized region of the partition. Our results demonstrate, in a plausible cochlear mechanical model, a marked influence exerted by the presence of a source of mechanical energy in the cochlear partition upon the sensitivity and sharpness of tuning observed near the peak of the response to a single-tone stimulation. Cochlear-partition motion in our active model shows higher sensitivity and sharper tuning than in a conventional passive model where damping values are assumed to be positive everywhere along the partition. In the following sections of this paper, we describe the assumptions of our model and compare the model cochlear-partition displacement with Rhode's (1973) experimental data from the squirrel monkey. We note close similarity between our active model results and Rhode's ante-mortem observations, and between our passive model results and Rhode's post-mortem observations. In addition, we show profiles of power flux density over the basal and partition boundaries of the model for the active and passive conditions of the model.

MODEL

Two implementations of a cochlear model (Neely, 1978; Matthews, 1979) have been adapted for the present study. Both versions make the same set of assumptions about the cochlea:

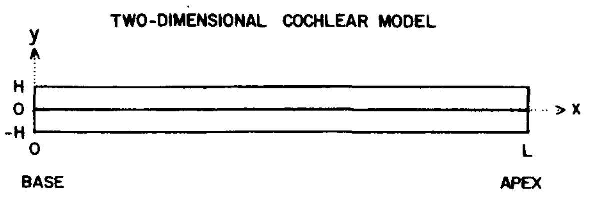

Fig. 1. Diagram of a two-dimensional cochlear model.

1) All quantities of the model are constant with respect to the z axis, and the cochlea is represented as a two-dimensional, rectangular chamber filled with fluid and divided into two symmetric halves (scalae) by a partition (Figure 1);
2) The fluid is incompressible, inviscid and satisfies Laplace's equation, $\nabla^2 P(x,y)=0$, where $P(x,y)$ is the pressure at (x,y);
3) The upper and lower walls are rigid;
4) At $x=L$, corresponding to the apical end, we have $P(L,y) - P(L,-y)=0$, for $0<y<H$, where H is the height of each scala;
5) At $x=0$, corresponding to the basal end, we have

$$\frac{\partial P(0,y)}{\partial x} = - \frac{\partial P(0,-y)}{\partial x} = \rho A_s \cos(\omega t), \text{ for } 0<y\leq H,$$

where ρ is the fluid density, A_s is the amplitude of the stapes acceleration, and ω is the angular frequency of excitation;
6) The partition displacement is very small compared with the scala height;
7) There is no longitudinal coupling within the partition;
8) The partition dynamic characteristics are linear, and described in the frequency domain by impedance parameters, $Z(x) = R(x) + j[\omega M(x) - K(x)/\omega]$ where $R(x)$, $M(x)$, and $K(x)$ are the damping, mass and stiffness parameters of the partition.

We have used the following parameter values:
1) cochlear length, $L = 2.2$ cm;
2) scala height, $H = 0.1$ cm;
3) fluid density, $\rho = 1.0$ gm.cm^{-3};
4) partition mass, $M(x) = 0.01$ gm.cm^{-2} for all x;
5) partition stiffness, $K(x) = K_o \exp(-4.5x)$ dyne·cm^{-3} where x is distance from the base in cm, and $K_o = 10^9$, or 0.4×10^9;
6) partition damping, $R(x) = 200$ dyne·sec·cm^{-3} for all x, or $R(x) = f_R(x)$.

The two cochlear model implementations of this study use different solution methods: a finite-difference method in the frequency domain (Neely, 1978); and a Green's function method in the time domain (Matthews, 1979). For the conventional case of passive partition characteristics without negative damping, the solutions obtained from the two methods are in excellent agreement. Comparison of the solutions for the active cases will be made in the Discussion section.

RESULTS

In Figure 2-A and -B, model results of amplitude and phase of the ratio of the cochlear-partition displacement to the stapes displacement are shown for one stimulus frequency of 1550Hz versus distance along the cochlea for three conditions: 1. The partition damping R(x) has negative values over a certain region as shown in Figure 3 and the stiffness parameter K_o is equal to 10^9; 2. $R(x)=200$ for all x and $K_o=10^9$; 3. $R(x)=200$ for all x and $K_o=0.4 \times 10^9$. From Figure 2-A, it can be noted that the model response amplitudes for conditions 1 and 2 are similar in the basal region but quite different in the

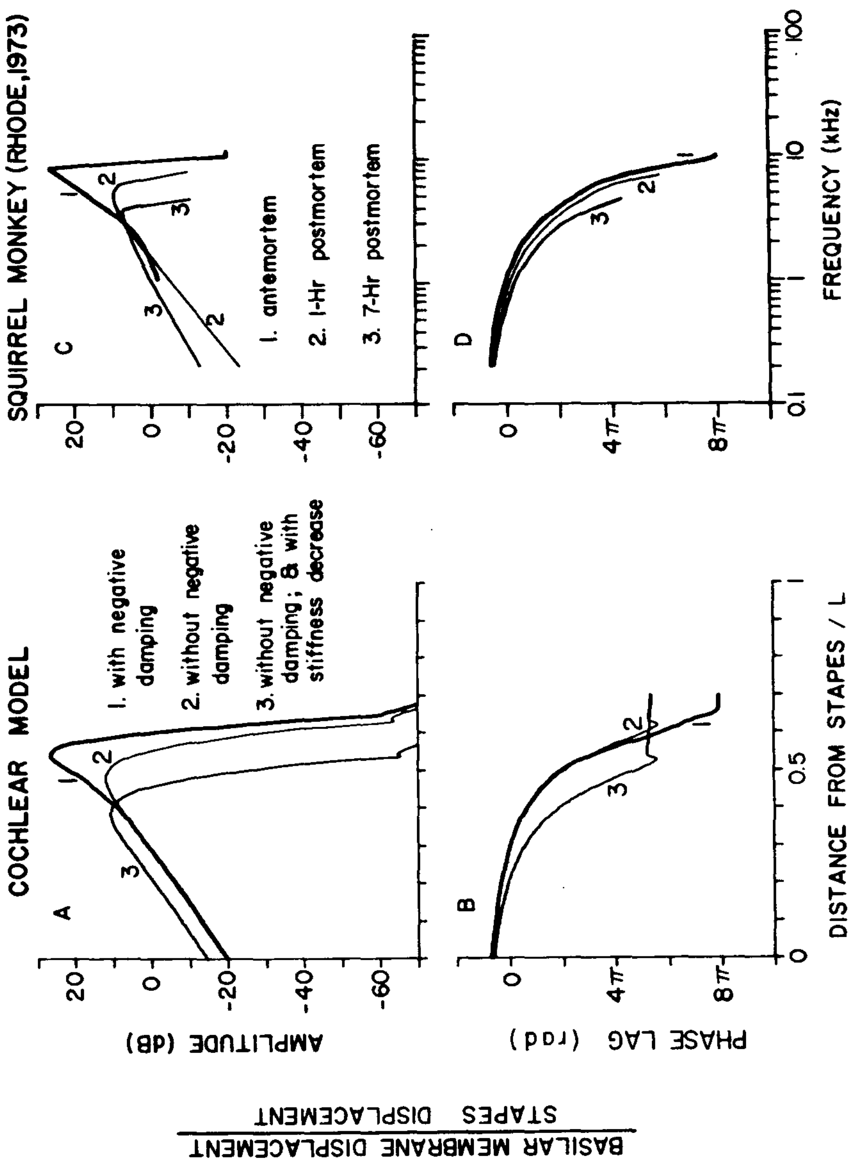

Fig. 2. A and B: Amplitude and phase of cochlear-partition displacement relative to the stapes displacement of the model (frequency-domain solution) for a stimulus frequency of 1550 Hz versus distance from the stapes. The three conditions correspond to different parameter values of the partition. For all three conditions, the x position was represented by 400 points and the y position was represented by 16 points. For the phase, positive senses are the inward displacement of the stapes, and the displacement of the partition to the scala tympani. C and D: Amplitude and phase of basilar-membrane displacement relative to the stapes displacement for one position along the basilar membrane of the squirrel monkey versus a logarithmic scale of stimulus frequency. C and D are redrawn from Fig. 3 of Rhode (1973).

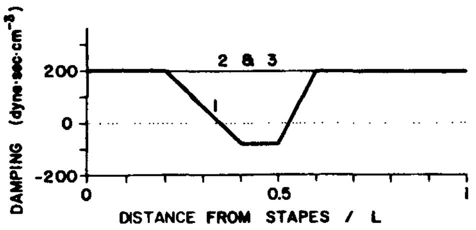

Fig. 3. Damping profiles for the three conditions used for the model results shown in Figure 2-A and -B. The profile of condition 1 is referred to as $f_R(x)$ *in the text.*

region around the peaks. The response for condition 1 shows a sharper peak which is shifted slightly toward the apex and larger in amplitude than the response for condition 2 where there was no negative damping in the partition. In spite of the marked difference in response amplitudes near the peaks, the response phases for conditions 1 and 2 (Figure 2-B) are quite similar in most of the regions except in the phase plateau region apical to the peaks. In this region, condition 1 shows a larger amount of total phase shift than condition 2. Model responses for conditions 2 and 3 in Figure 2-A and -B show that a decrease in the stiffness coefficient K_0 leads to a basal shift of both the amplitude and phase, with little change in the shapes of the response curves.

In Figure 2-C and -D, Rhode's (1973) experimental results of amplitude and phase of the ratio of the basilar-membrane displacement to the stapes displacement are shown for one position along the basilar membrane versus a logarithmic scale of stimulus frequency for three conditions. The antemortem response shows a sharper peak which is shifted slightly to the high-frequency side and larger in amplitude than the postmortem responses. Differences in the response amplitudes for the antemortem and the 1-Hr postmortem conditions are quite prominent in the frequency region near the peaks but are inconspicuous in the frequency region below the peaks. The 7-Hr postmortem response appears to be of similar shape to the 1-Hr postmortem response but shifted to the low-frequency side.

A complication in comparing the model and experimental results shown in Figure 2 is that the horizontal axes of the two cases are different: A linear scale of distance from the stapes for the model results, and a logarithmic scale of stimulus frequency for the experimental results. We do not yet have model results for different stimulus frequencies. However, plots of basilar-membrane displacement on a linear scale of distance along the cochlea for one stimulus frequency are expected to be fairly similar to plots of basilar-membrane displacement on a logarithmic scale of the stimulus frequency for one position of the basilar membrane. This general similarity is expected from the "shift invariance" property observed in experimental results (Bekesy, 1960, p. 461-462; Rhode, 1971, Fig. 8), as well as in cochlear models (e.g., Sondhi, 1978). To the extent that the shift invariance is a reasonable approximation for our comparison of results in Figure 2, we note that the salient features of postmortem changes observed in the animal are fairly well reproduced by the model results in Figure 2-A and -B. Results of this model suggest that the rapid changes in basilar-membrane motion after death may be due to the loss of an internal energy source in the cochlear partition and that the slower changes occurring over several hours from death may be due to a decrease in the stiffness of the partition.

In Figure 4, we show profiles of power flux density, i.e., the time-averaged power per unit area, over the basal and partition boundaries. Here, positive flux densities correspond to flow of energy into the fluid; negative densities to flow of energy from the fluid (into the cochlear partition). For steady state conditions with sinusoidal excitation as we consider here, the x-component of the power flux density, $E_x(0,y)$, over the basal boundary is (de Boer, 1979)

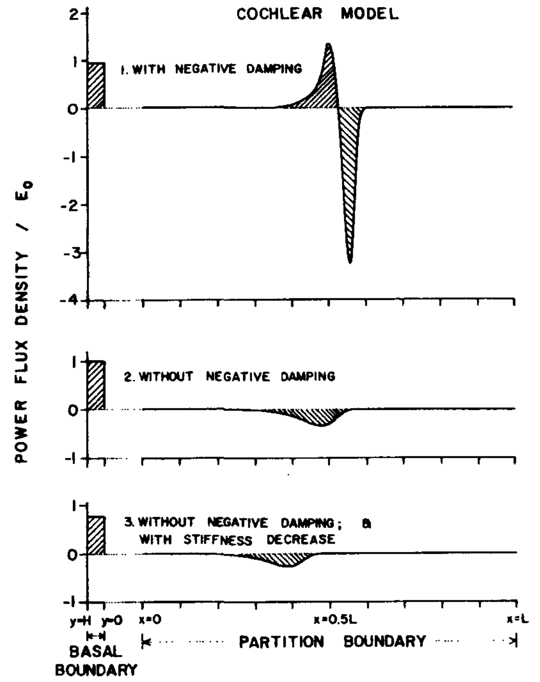

Fig. 4. Profiles of power flux density normalized with E_o *for the three conditions used for the model results shown in Figure 2-A and -B.* E_o *is equal to 0.43 erg* $\cdot$ *sec*$^{-1}$ $\cdot$ *cm*$^{-2}$ *which corresponds to the power flux density at* $x=0$*, and* $y=H$ *for condition 2. For all three conditions, a constant stapes displacement (*10^{-6} *cm) is applied. Positive values correspond to energy flow into the fluid and the negative values correspond to energy flow from the fluid into the partition.*

$$E_x(0,y) = 0.5\ P(0,y) \cdot V_x(0,y) \cdot \cos[\theta_1(y)],$$

where $P(0,y)$ and $V_x(0,y)$ are the peak amplitudes of sinusoidal time variation of pressure and x-component of velocity at position $(0,y)$, and $\theta_1(y)$ is the phase difference between $P(0,y)$ and $V_x(0,y)$. Plots in Figure 4 for the basal boundary show $[E_x(0,y) + E_x(0,-y)]$ versus y for $H>y>0$. The left-most cross hatched areas in Figure 4 thus represent total power into the fluid through the basal boundary, i.e., the power into the fluid through the oval window minus the power out of the fluid through the round window.

Similarly, the y-component of the power flux density over the upper surface of the partition is

$$E_y(x,0^+) = 0.5\ P(x,0^+) \cdot V_y(x,0^+) \cdot \cos[\theta_2(x)],$$

and over the lower surface of the partition

$$E_y(x,0^-) = 0.5\ P(x,0^-) \cdot V_y(x,0^-) \cdot \cos[\theta_3(x)].$$

Plots in Figure 4 for the partition boundary show $[E_y(x,0^+) - E_y(x,0^-)]$ versus x for $0>x>L$. This represents the total power into the fluid from both sides of the partition at position x. The $E_y(x,0^-)$ part is subtracted from $E_y(x,0^+)$ because the y-component of the power flux at the lower surface is pointing into the partition from the fluid.

The middle cross-hatched area above zero in Figure 4-1 represents the power delivered from the negative-damping region of the partition into the fluid, and the right-most cross-hatched area below zero in Figure 4-1 represents the power dissipated in the positive-damping region of the partition. The lower two panels of Figure 4 show profiles of power flux density for conditions 2 and 3 where the damping is positive everywhere along the partition (Figure 3). The major difference between these conditions and condition 1 is that, for conditions 2 and 3 over the partition boundary, there is only a region of power dissipation and no region of power source. We have verified that, for each condition shown in Figure 4, the total power into the fluid is equal to the total power taken from the fluid, as expected from conservation of energy. It is interesting to note that, for condition 1, the total power delivered from the negative-damping region of the partition (i.e., the middle cross-hatched area of Figure 4-1) is 1.5 times the total power delivered through the basal boundary (i.e., the left-most cross-hatched area of Figure 4-1). This gain in power through the internal energy source of the model underlies the substantial increase in the response near the peak for condition 1 of the model.

DISCUSSION

The hypothesis of active mechanical behavior of the cochlea was suggested by Gold (1948) and Kemp (1979). Strong support for this hypothesis is provided by a form of tinnitus where spontaneously emitted tones can be detected in the ear canals of some human subjects whose thresholds of hearing are in the normal range (Kemp, 1979). Our model results presented in this paper demonstrate specific effects of incorporating a source of mechanical energy into the partition of the model. To the extent that our active and passive model results shown in Figure 2 simulate Rhode's ante- and post-mortem observations, our model results support the hypothesis of active mechanics in a normal cochlea. It is unknown what kind of mechanisms may underlie the hypothesized internal energy source in the cochlear partition. Our conjecture is that energy available through cellular metabolism in the cochlear partition may be somehow transduced into mechanical energy. [Note: The appearance of negative damping in the cochlear-partition point impedance could also conceivably be produced by some form of longitudinal coupling within the cochlear partition. Longitudinal coupling could not, of course, produce spontaneous oscillations in the absence of external energy input through the stapes.]

The hypothesis of active cochlear mechanics is compatible with the hypothesis of bidirectional coupling of electrophysiological and mechanical processes in the cochlea. Bidirectional coupling has been suggested from various observations of physiologically vulnerable behavior: 1) in the ear-canal sound pressure, regarding "echoes" in response to brief transient stimuli (Kemp, 1978; Anderson and Kemp, 1979) and regarding distortion products in response to continuous two-tone stimuli (Kim, 1980); 2) in basilar-membrane motion (Rhode, 1973; Robles, Rhode and Geisler, 1976; Lepage and Johnstone, 1980); and 3) in psychoacoustic (Smoorenburg, 1972) and neural (Siegel, Kim and Molnar, 1977; Kim, Siegel and Molnar, 1979; Kim, Molnar and Matthews, 1980) responses regarding distortion products which are interpreted to be associated with basilar-membrane motion. [For further discussions of bidirectional coupling, see Kim, Molnar and Matthews (1980), and Kim (1980).] The hypotheses of active mechanics and bidirectional coupling in the transduction in the cochlea are consistent with various observations that noxious disturbances reduce sensitivity and frequency selectivity of individual inner hair cells (Sellick and Russell, 1978) and of single cochlear neurons (e.g., Kiang, Moxon and Levine, 1970; Robertson and Manley, 1974; Evans, 1974; Dallos and Harris, 1978; Robertson and Johnstone, 1979).

As stated earlier in this paper, the solutions obtained from the two implementations of the model are in excellent agreement for conditions 2 and 3 which have no negative damping in the partition. For condition 1, which has negative damping in the partition, the time-domain solution was not stable. The time-domain solution of the model to a smoothly-gated sinusoidal stimulus initially approached the pattern obtained with the frequency-domain method, but the model response subsequently entered into irregular, unstable oscillations rather than remaining in a steady-state condition. We have not yet determined whether this instability of the model response is due to an instability of the physical condition modeled, or due to inaccuracies in the model implementation. However, we did observe that, for damping profiles with less pronounced negative values, the time-domain solution was stable and in good agreement with the frequency-domain solution.

In addition to further study of the stability properties of active models and their computational implementations, other extensions of this work are needed. We feel that the most important extension is the incorporation of both active and nonlinear behavior into the same model for cochlear mechanics. This may be helpful in understanding how a damping profile such as that shown in Figure 3 might arise under a particular condition of stimulation. Such an understanding would allow us to examine model response for various stimulus frequencies for a fixed position along the cochlear partition which can be compared with Rhode's observations more directly. In view of the success of nonlinear cochlear models having increases in damping with increasing response for reproducing a wide range of nonlinear phenomena observed (Kim, Molnar and Pfeiffer, 1973; Hubbard and Geisler, 1972; Hall, 1974; Matthews, Cox, Kim and Molnar, 1979), it should be interesting to investigate cochlear models where similar nonlinear behavior is combined with active behavior, for example, with respect to the questions of cochlear mechanical stability and the tendency to spontaneous oscillation.

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