An active cochlear model showing sharp tuning and high sensitivity

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Recent in vivo measurements of cochlear-partition motion indicate very high sensitivity and sharp mechanical tuning similar to the tuning of single cochlear nerve fibers. Our experience with mathematical models of the cochlea leads us to believe that this type of mechanical response requires the presence of active elements in the cochlea. We have developed an active cochlear model which incorporates negative damping components; this model produces partition displacement in good agreement with many of the mechanical and neural tuning characteristics which have been observed in vivo by other researchers. We suggest that the negative damping components of our model may represent an active mechanical behavior of the outer hair cells, functioning in the electromechanical environment of the normal cochlea.

Key words: cochlear model; active biomechanics; cochlear tuning.

Introduction

In the field of hearing research, there has been much controversy about the degree to which the sharp frequency selectivity (tuning) observed in single cochlear nerve fibers is also present mechanically in the motion of the basilar membrane. Some investigators, e.g. Evans and Wilson [3], have suggested that a 'second cochlear filter' sharpens a broad mechanical tuning to produce a sharp neural tuning. However, Kim and Molnar [5] emphasized that the apparent discrepancy between the mechanical and neural tuning should be interpreted cautiously because of physiological vulnerability and nonlinearity of cochlear-partition motion. Recent measurements of basilar-membrane motion in guinea pig [11] and cat [4] indicate that mechanical tuning in the cochlea closely resembles neural tuning when physiological disturbance to the cochlea is minimized. These new results have important implications for the theory of cochlear function.

Mathematical models of the cochlea provide a means of testing hypotheses about cochlear function. The widely accepted models of the cochlea which assume a

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passive mechanical structure are, in our experience, incapable of reproducing the recent in vivo experimental observations of sharp tuning and high sensitivity of basilar-membrane motion. We present here results from an active model for cochlear biomechanics, wherein negative damping elements in the cochlear partition provide an internal source of controlled mechanical energy. Our active model shows considerably enhanced sensitivity and sharpness of tuning of cochlear-partition motion similar to the recent experimental data. Furthermore, with changes in parameter values affecting the internal energy release, the model also simulates experimentally observed changes in sensitivity and tuning of cochlear-partition motion which typically accompany deterioration of physiological sensitivity of the cochlea [11,9].

Methods

Model results presented here are based on a finite-difference approximation of a linear, two-dimensional model of cochlear mechanics [7,8]. Although the assumption of linearity is not required by our solution methods, we have assumed linearity because it simplifies the process of selecting model parameters and allows us to focus on the active behavior of the model. The length of the cochlea in our model (x dimension) is represented by 240 discrete points and the height (y dimension) by 4 points. A FORTRAN computer program provides a time–domain solution of the model by determining the state of the cochlea and middle ear at successive instants in time in response to an impulsive pressure stimulus (click) presented at the eardrum. Of particular interest is the displacement of the basilar membrane $\xi_b(x)$ as a function of time or frequency (see Fig. 1).

The most important distinction between our cochlear model and most other models is our use of negative damping components to simulate internal sources of mechanical energy within the cochlear partition. (We presented early results from a simpler form of active cochlear model in a previous paper [6].) Each point on the cochlear partition is represented in our present model by a fourth-order mechanical
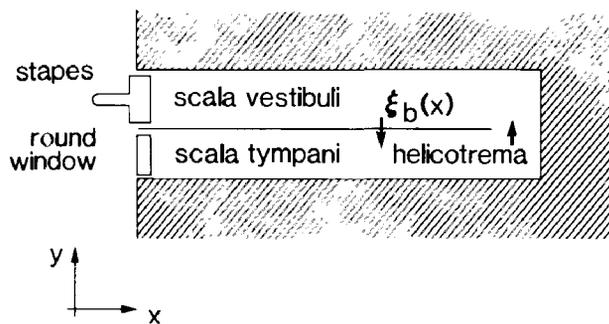

Fig. 1. Diagram of a two-dimensional cochlear model (macromechanical level) showing definition of the x and y dimensions and basilar membrane displacement $\xi_b(x)$. The positive sense of ξ_b is toward scala tympani.
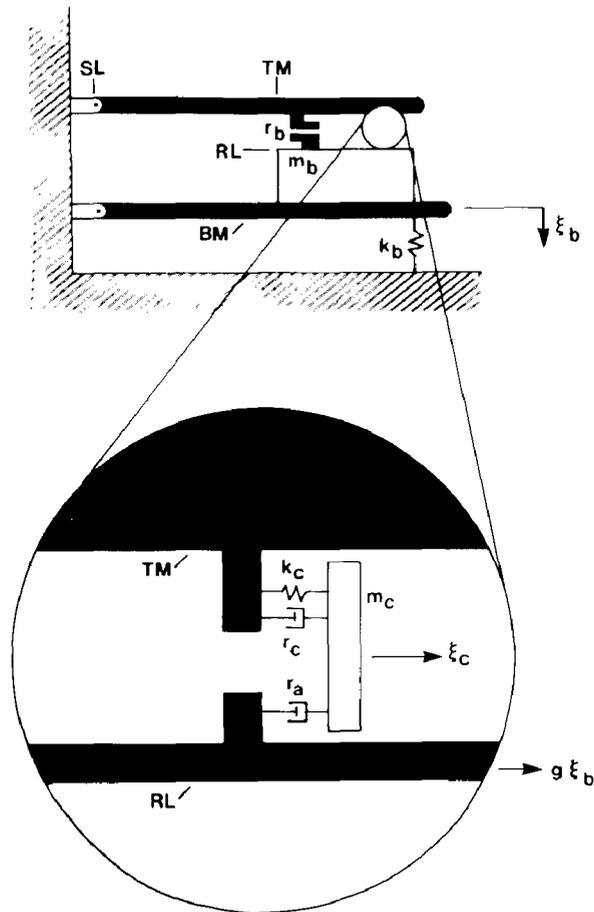
Fig. 2. Cochlear partition model with two spring-mass-damper subsystems. TM, tectorial membrane; BM, basilar membrane; SL, spiral limbus; RL, reticular lamina; k_b, m_b, r_b, stiffness, mass and damping of the basilar membrane; k_c, m_c, r_c, stiffness, mass and damping of the stereocilia of outer hair cells; r_a, active damping component; ξ_b, vertical displacement of the basilar membrane mass; ξ_c, lateral displacement of the stereocilia mass; g, ratio of the TM–RL shear displacement to ξ_b.

system consisting of two spring-mass-damper subsystems which are coupled by a negative damping component (r_a) as illustrated in Fig. 2. The first spring-mass-damper subsystem (k_b, m_b, r_b) represents the basilar membrane and is driven into oscillation by changes in fluid pressure. The second spring-mass-damper subsystem (k_c, m_c, r_c), which we associate with the stereocilia of the outer hair cells, is tuned about an octave lower than the first subsystem and serves as a control on the energy output of the negative damping element. The choice of parameters for the model was guided by structural measurements of the cat cochlea and middle-ear and by our desire to simulate the sharp tuning and high sensitivity observed experimentally. The cochlear partition parameters (k_b, m_b, r_b,

k_c, m_c, r_c, r_a) were assumed to vary exponentially with distance from the stapes in order to simplify the choice of parameters. Further details about the model and the choice of model parameters are provided in [8]. When model parameters were carefully chosen, the model solution was stable in the sense that transient responses decayed with time.

Results

Fig. 3 compares animal data based on mechanical measurements of basilar-membrane displacement with model results. In each case, the curves represent the sound pressure level (SPL) re 20 μPa at the eardrum which is required to produce a 10 Å (= 1 nm) displacement of the basilar membrane at a given place, in response to sinusoidal stimuli. A linear scaling was applied to each set of animal data to achieve a 10 Å iso-displacement criterion for all data.

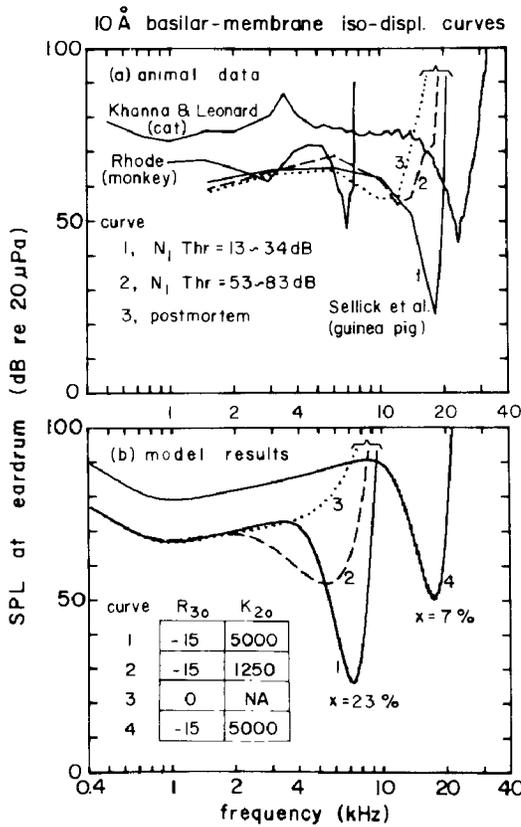The animal data in Fig. 3a represents three different animal species, two different

Fig. 3. Basilar-membrane iso-displacement tuning curves based on (a) animal data, and (b) model results. The curves indicate the sound pressure level (SPL) at the eardrum which is required to produce a 10 Å displacement of the basilar membrane.

measurement techniques, and three different groups of researchers. The data of Rhode [10] show one of his sharpest tuning curves, obtained by a Mössbauer technique in a squirrel monkey. The data of Khanna and Leonard [4] were obtained by a laser technique in a cat. The data of Sellick et al. [11] were obtained by an improved Mössbauer technique in a guinea pig. Sellick et al. noted a progressive deterioration of basilar-membrane tuning and sensitivity throughout the data collection period. As a measure of the physiological condition of the cochlea, Sellick et al. used the N_1 compound action potential of the cochlear nerve evoked by high-frequency tone bursts. The data for curve 1 in Fig. 3a were obtained when the N_1 threshold was between 13 and 34 dB SPL; curve 2 when the N_1 threshold was between 53 and 83 dB SPL; curve 3 after death of the animal. These three curves demonstrate pronounced changes in basilar-membrane tuning and sensitivity which accompany physiological deterioration of the cochlea.

The model results in Fig. 3b were obtained by taking a Fourier transform of a 40 ms response of the model to an impulse. (As stated above, the model is linear even though the cochlea is not.) Two positions on the basilar membrane are presented in Fig. 3b and are labeled by x, the percentage distance along the cochlea from base to apex. Curve 1 for $x = 23\%$ and curve 4 for $x = 7\%$ are based on a single set of the model parameter values. Curves 2 and 3 illustrate changes in the frequency response for $x = 23\%$ due to changes in cochlear model parameters which affect release of internal energy. The model parameter $R_3(x) = gr_a(x)/w_p$ is the damping component at position x which couples the two mechanical spring–mass–damper subsystems described above (g is the ratio of TM–RL shear to BM displacement ξ_h shown in Fig. 2 and w_p is the effective width of the basilar membrane). At the basal end, we have $R_3(0) = R_{30}$, and $R_3(x)$ decreases exponentially toward the apex. Curves 1, 2 and 4 in Fig. 3b were obtained with $R_{30} = -15$ (dyn · s · cm^{-3}). The fact that R_{30} is negative means it contributes energy to the system which makes the system active. The value of R_{30} was set to zero for curve 3 which makes the system passive and decouples the second spring–mass–damper subsystem. The model parameter $K_2(x)$ $= gk_c(x)/w_p$ represents the stiffness of the spring in the second spring–mass–damper subsystem; it similarly has a value K_{20} at the basal end and decreases exponentially toward the apex. Curves 1 and 4 were obtained with $K_{20} = 5000$ (dyn · cm^{-3}); the value of K_{20} was decreased to 1250 (dyn · cm^{-3}) for curve 2 in order to decrease the sensitivity of the model; the value of $K_2(x)$ is irrelevant for curve 3 because $R_3(x) = 0$.

The sensitivity and sharpness of tuning of the model results in Fig. 3b compare well with the sensitivity and sharpness of tuning of the animal data in Fig. 3a. The sensitivity at the tip of curve 1 in Fig. 3b, as indicated by the minimum SPL at the eardrum for 10 Å displacement of the basilar membrane, is within a few dB of the sensitivity at the tip of curve 1 in Fig. 3a. We have not observed this degree of sensitivity in any of our passive cochlear models. A loss of sensitivity, broadening of tuning and shift toward lower frequencies occur with physiological deterioration of the cochlea, as shown by curves 2 and 3 in Fig. 3a. These same features are simulated in the model by decreasing the stereocilia stiffness parameter K_{20} and, consequently, decreasing the energy output of the negative damping components.
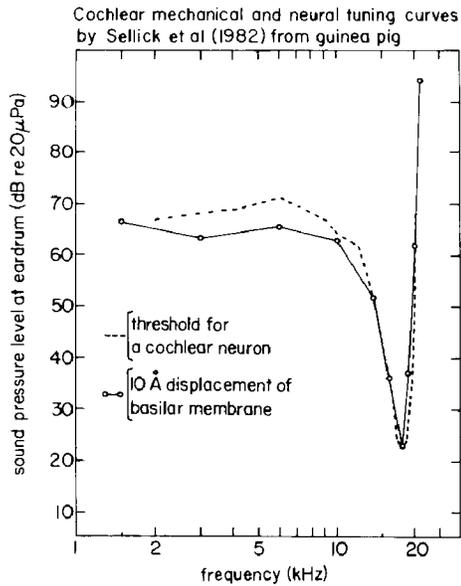
Fig. 4. Comparison between 10 Å iso-displacement tuning curve of the basilar membrane and the threshold tuning curve of single cochlear neuron on the basal region of guinea pig cochlea. These data are replotted from Fig. 10 of Sellick et al. [11] by linearly scaling their 3.5 Å curve to produce the 10 Å curve.

The internal energy output from the negative damping components was greatest for curve 1, less for curve 2, and zero for curve 3.

The tuning of the basilar-membrane data of Sellick et al., when plotted as 10 Å iso-displacement curve, is very similar to that of a single cochlear neuron. This point is illustrated in Fig. 4 where curve 1 from Fig. 3a, representing basilar membrane displacement, is replotted as a solid line, and a threshold tuning curve for a single cochlear neuron (obtained from the same animal species and in the same laboratory) is plotted as a dashed line. The similarity between basilar membrane displacement and neural response makes it reasonable for us to compare our model results directly with neural data.

The dotted lines in Fig. 5a are threshold tuning curves for two cochlear nerve fibers in one cat (No. 27) obtained by Allen [1,2]. Superimposed on Allen's data in Fig. 5a are model results (solid lines) for 10 Å basilar-membrane displacement at two positions. The agreement between curve 2 ($x = 23\%$) and the neural data is particularly close, not only at the tip of the tuning curve, but over the entire range of frequencies. The good agreement between the model results and the neural data is further emphasized by comparisons in Fig. 5b, c and d. The slope of the tuning curves in dB/octave is compared in Fig. 5b *; the model results are similar to the

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* Allen smoothed his data by a spline-fitting procedure prior to determining slope of the tuning curve and delay.
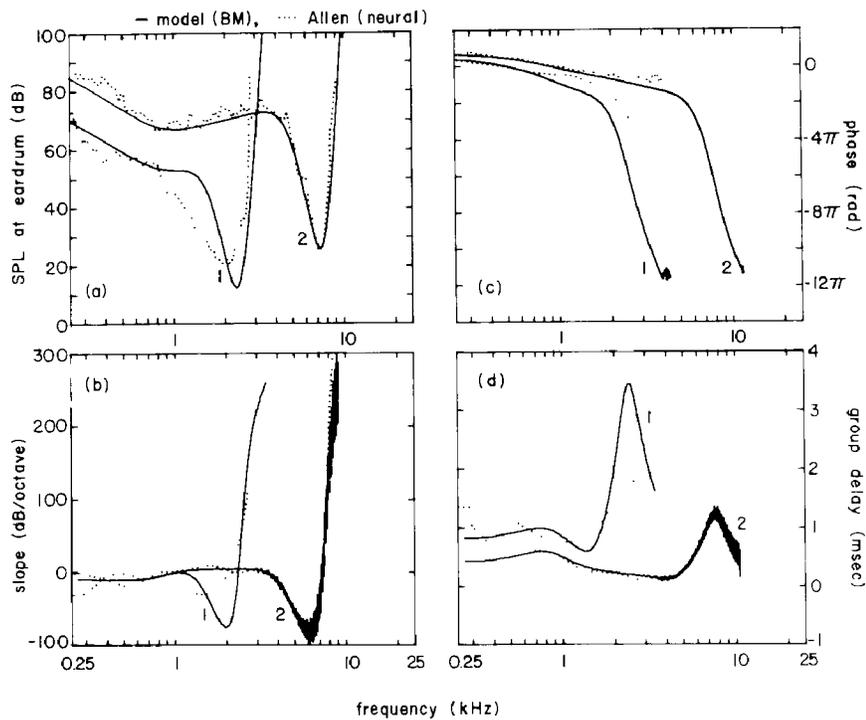
Fig. 5. Comparison between neural data (dotted lines) and model results (solid lines) for (a) threshold tuning curves, (b) slope of the tuning curves, (c) phase of the response, and (d) group delay of the response. Definitions of the positive senses used to determine the phase are as follows: (1) for the model, increase in pressure (condensation) at the eardrum and displacement of the basilar membrane toward scala tympani; (2) for the neural data, positive voltage into the earphone and decrease in neural spike discharge. Allen (pers. comm.) indicates that a positive voltage pulse into his earphone results in a condensation click. The neural phase data in (c) and (d) are plotted after removing 1.2 ms delay attributable to acoustic, synaptic and neural spike propagation delays.

neural data. The dotted line in curve 2 of Fig. 5b is not visible near the tip because it coincides with the solid line. Allen also measured phase of the neural response for the same two nerve fibers for frequencies up to about 4 kHz. The neural phase data are compared with the model phase in Fig. 5c. The group delay of the neural data and the model are compared in Fig. 5d, where the group delay of the response is defined as minus the derivative of the phase with respect to the frequency.

The agreement between curve 1 ($x = 24\%$) and the neural data in Fig. 5 is not as good as the curve 2 agreement. Further refinement of the model is needed in order to achieve better overall agreement between the model and the experimental observation.

Discussion

The model results presented here show many striking similarities to both mechanical and neural measurements of cochlear response: (1) the results from our active model are similar in sharpness of tuning and sensitivity to the most sensitive measurements of basilar-membrane motion by Sellick et al.; (2) the *same* model results are in good agreement with Allen's threshold tuning curves and group-delay phase measures in cochlear nerve fibers; and (3) the loss of sensitivity and tuning of basilar-membrane motion with physiological deterioration are simulated in the model by decreasing the internal energy output of the negative damping components. We suggest that the negative damping components in the model may represent some physical action of the outer hair cells, functioning in the electromechanical environment of the normal cochlea and serving to boost the sensitivity of the cochlea at low levels of excitation.

Acknowledgements

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