Cochlear micromechanics—A physical model of transduction

J. B. Allen

Acoustics Research Department, Bell Laboratories, Murray Hill, New Jersey 07974
(Received 1 January 1980; accepted for publication 29 August 1980)

One of the basic questions which has persisted in the field of hearing theory is the still unresolved mechanical action of hair-cell transduction. The fundamental problem that has historically plagued researches is the discrepancy between mechanically measured tuning of basilar membrane motion and neurally measured tuning. In this paper we show that the difference between these two measures appears to be accounted for by a specific, physically motivated, micromechanical model. This model gives rise to a spectral zero which we identify as the "second-filter" of cochlear transduction. For high-frequency fibers this zero resides at a fixed frequency ratio below CF (characteristic frequency) while for fibers having low-frequency CF's the zero appears to go to zero frequency faster than CF. In this paper we first present and analyze the assumed mechanical model. We then briefly discuss a possible specific physical realization for the nonlinearity of cochlea mechanics. The nonlinear model is based on dynamical variations in outer hair cell stereocilia stiffness.

PACS numbers: 43.63.Bq, 43.63.Kz

INTRODUCTION

The cochlea is the organ which converts low-level acoustic signals into the auditory neural code. Its main function is to filter the stapes input signal through a continuum of very narrow bandpass filters. These narrowband signals are then half-wave rectified and modulate the firing rate of a large number of neurons, which in turn signal the central nervous system.

While this basic outline has long been documented [e.g., Kiang *et al.* (1965); Russell and Sellick (1979)], certain critical details are as yet unexplained. Recent models of basilar membrane (BM) motion have reduced the gap between the theory and the experimental BM velocity measurements [for reference see: Allen (1979); Allen and Sondhi (1979)]. These models give rise to an almost low-pass frequency response whose cutoff frequency varies with place along the BM. Although the point is controversial, from observations of the differences between mechanical and neural response, a final transformation from low-pass to bandpass appears to take place during the mechanical to neural transduction process at the hair cell level [Geisler, Rhode and Kennedy (1974); Evans and Wilson (1975); Hall (1977); Allen (1977); Zwislocki (1980)]. Since the model of Allen and Sondhi (1979) is a linear time-domain model, and since the BM response as measured by Rhode was nonlinear, a philosophical gap remains between their theory and the measurements. Allen and Sondhi were able to match Rhode's magnitude data using one value of BM damping and his phase data with a different, larger value of BM damping. Rhode's measurements were made at many different levels since it was necessary to maintain the velocity of the BM source within certain limits. Thus the model fit seems to be within the experimental variability of the cochlear nonlinearity and the measurement method. However the nature of the relationship between the input signal and the mechanical parameters (the nonlinearity) of the system has not yet been determined. Kim *et al.* (1979) and Hall (1977) have studied various nonlinear models in an attempt to understand the effects of this nonlinearity.

In this paper we develop a physical model of the transduction process which bridges the gap between BM experimental data and the neural data since it gives excellent quantitative and qualitative agreement with many experimental neural measurements. We then show that this model provides a framework which might help us understand the source of the nonlinearity properties of BM motion.

I. THE "SECOND-FILTER"

For introductory purposes, we present in this section results which argue for the validity of modeling the transfer function between BM displacement and neural response by a spectral zero. In Figs. 1(a)–(d) we show the results of model calculations which compare model tuning curves with measured neural tuning curves [Kiang and Moxon (1974)] at several different characteristic frequencies (CFs). The model tuning curves were computed in the time domain using the linear two-dimensional mechanical model of Allen and Sondhi (1979), followed by a spectral zero (an anti-resonance) systematically located below the CF (and a pole above CF). Our experience has been that any measured neural tuning curve may be closely matched by adjustment of the model spectral zero. The reader should be aware that no attempt has been made to account for the middle ear transfer function in these comparisons. The neural curves are normalized to ear canal pressure while the model tuning curves have been normalized to the model stapes displacement d_s. The measured transfer ratio between stapes displacement and ear canal pressure is approximately constant for frequencies below 1 kHz and decreases at 12 dB/oct above 1 kHz [Guinan and Peak (1966)]. Measured tuning curves normalized to stapes displacement would be useful in making more accurate comparisons.

A review of the spectral zero model of sharpening seems to be in order here. In 1974, Zwislocki and

 0001-4966/80/121660-11$00.80 © 1980 Acoustical Society of America

Redistribution subject to ASA license or copyright; see http://acousticalsociety.org/content/terms. Download to IP: 130.126.255.24 On: Fri, 15 May 2015 22:07:49

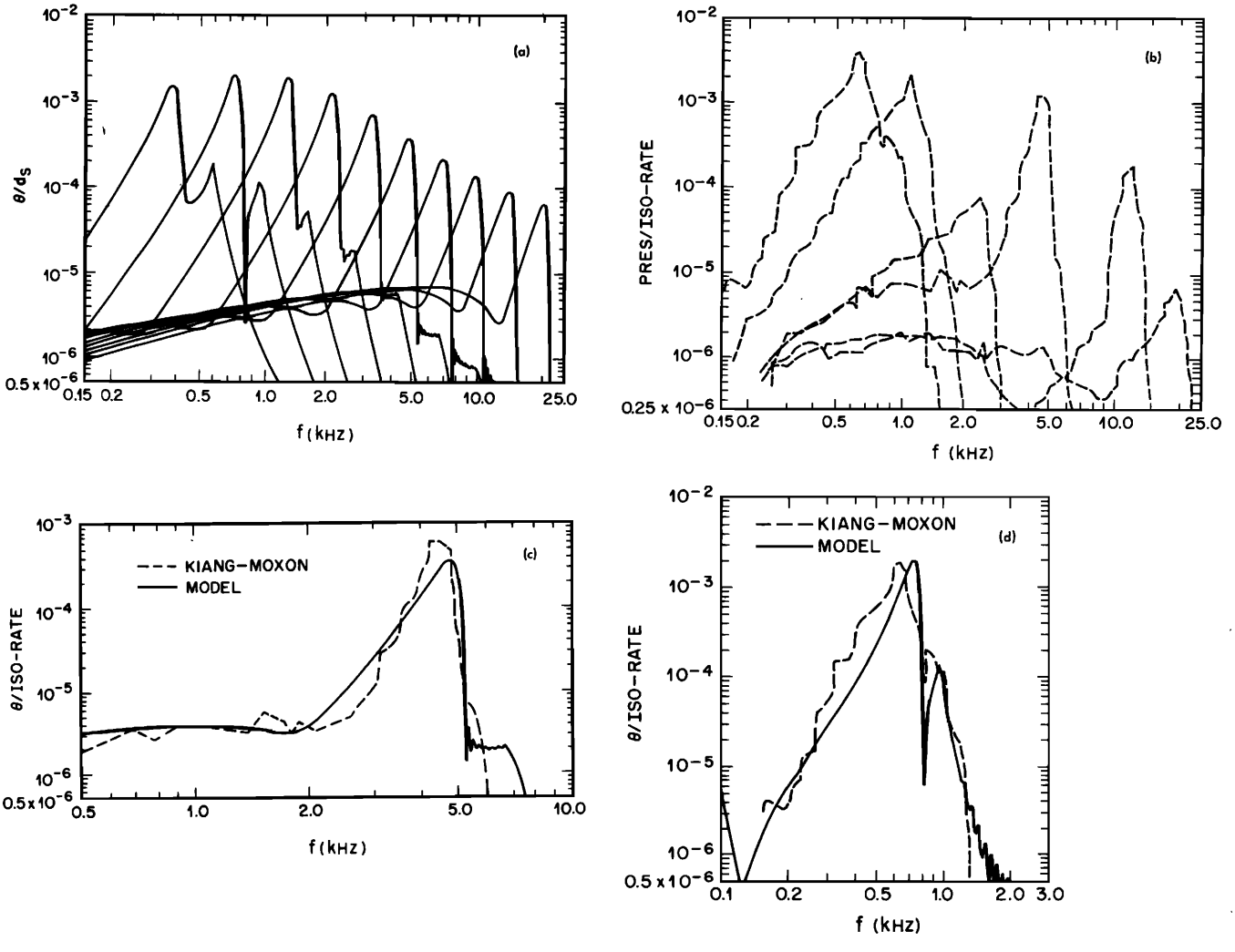


FIG. 1. In this series of figures we make comparisons between cat neural data as measured by Kiang and Moxon (1974) and the mechanical model of Allen and Sondhi (1979) modified to include the transduction filter $H_T(x, s)$, Eq. (1). (a) The model neural magnitude response at the transduction filter output normalized by stapes displacement d_s. (b) Cat neural tuning data for six different units on the same relative scale as (a). The unit having a CF of 2 kHz appears to have a raised threshold. (c) A specific comparison between the model and a neural tuning curve at a CF of 3.5 kHz. (d) A comparison between the model and a neural tuning curve for a low frequency CF.

Sokolich introduced a transduction model consisting of a difference between two components. These two components were assumed to be inner and outer hair cell signals. In this model, specific calculations were difficult because the exact nature of the two signals which were to be subtracted was not well known. Allen (1977) then introduced the idea of a spectral zero model of transduction in his Eq. (9) (see also following discussion). This model seemed to give a very good match to neural threshold data, as pointed out in that paper. The zero was physically modeled by a very special linear combination of scala pressure and BM displacement. It now seems likely that this method of physically introducing the spectral zero is not a realizable one given the microanatomy of the organ of Corti since the model required that inner hair cell stereocilia be connected to the tectorial membrane (TM).

In (1979), Kim *et al.*, published spatial phase data for single tones that showed a π phase shift below the best place (higher CF region). This led Allen (1979) to point out that the π phase shift was in agreement with the π phase shift of the spectral zero model. In 1979, Zwislocki and Kletsky introduced their spatial integral model in which they assumed that the neural signal was derivable from BM displacements by a spatial convolution with an exponential function. They also added an elastic TM and an elastic reticular lamina (RL) to the model in order to introduce sign changes in the TM–RL shear motion. While the exact details were not made completely clear, some results of a simulation were presented in their paper. Zwislocki has recently pointed out that this model does not seem to be sufficient to explain neural tuning data [Zwislocki (1980), p. 1682].

Frommer (1979) has recently introduced a second filter model based on the idea that the Spiral Sulcus (SS) changes its cross-sectional area when the BM is displaced, and that the resulting deformation causes mass flow in the TM–RL space. His analysis gives rise to an

Redistribution subject to ASA license or copyright; see http://acousticalsociety.org/content/terms. Download to IP: 130.126.255.24 On: Fri, 15 May 2015 22:07:49

exponential smoothing function which is similar in form to that of Zwislocki's (1979) smoothing function. It seems likely that all flow in Frommer's model would take place along the length of the SS since the flow resistance would be so much lower in that direction relative to the flow resistance in the TM–RL space. [Frommer describes Allen's (1977) model as a "nonlinear mathematical model involving an arbitrary parameter, the 'loss factor'." This is incorrect since the spectral zero model is by definition linear. His conclusion may have been reached as a result of some speculations which were made in Allen's paper about the nature of the BM nonlinearity being related to the cochlear damping.]

In Zwislocki's 1980 JASA paper he has introduced the idea of a resonant TM model where the mass is the mass of the TM and the compliance is the stiffness of the outer hair cell stereocilia. In the model considered here we also discuss a resonant TM. In our case however the assumed compliance is the elastic TM material rather than the stiffness of the stereocilia, as assumed by Zwislocki (1980). Thus the mode of resonance in the model presented here is quite distinct from that of Zwislocki's 1980 paper. Furthermore in the analysis given here we uncover a spectral zero in the model BM-cilia transfer response, as well as a pole, as will be shown in the following. This zero is a key issue in the present model.

In Fig. 2 we show (solid line) the cochlear map for model CF values corresponding to Fig. 1. This curve agrees quite closely with published values of cat cochlear maps. The dashed line gives the location of the assumed spectral zero frequency f_z of the transduction filter used in computing the model tuning curve. The third curve labeled f_p will be discussed. More specifically we define

x = positional coordinate along BM,

f = stimulus frequency,

$\omega = 2\pi f$, $i = \sqrt{-1}$, $s = i\omega$, $V_{BM}(x,s)$ = BM velocity,

$\Theta(x,s)$ = hair cell excitation (tuning),

$$H_T(x,s) = \frac{s^2 + 2\zeta_z(x)s + \omega_z^2(x)}{s^2 + 2\zeta_p(x)s + \omega_p^2(x)}, \quad (1)$$

where $H_T(x,s)$ is the *transduction filter* which relates Θ to V_{BM} by the relation

$$\Theta(x,s) = H_T(x,s)V_{BM}(x,s). \quad (2)$$

The roots ω_z of the numerator of $H_T(x,s)$ are the zeroes of the transduction filter of the model. The damping ratio $\zeta_z(x)$ defines the bandwidth (depth or sharpness) of the zeroes. For Fig. 2, we have assumed $\zeta(x) = 0$ in defining the root frequencies $\omega_z(x)$ and $\omega_p(x)$. Since the pole frequency ω_p is above CF and is therefore in the cutoff region, it is a less interesting feature. Thus we will concentrate on the zero for the present. For the model calculations, Eq. (1) was implemented in the time domain using second-order difference equations. V_{BM} was obtained in the time domain using the method described by Allen and Sondhi (1979).

In Fig. 3(a) we plot the phase of $\Theta(x,\omega)$ for several model tuning curves. Each curve is for a different place x on the BM. As a result of the transduction filter zero, the phase can jump by as many as π radians (depending on ζ_z) at ω_z. Since we have placed the zero in the left half s plane, the phase slope for $\omega = \omega_z$ is positive (with increasing frequency). A zero to the right of the $i\omega$ axis would have caused the phase to decrease across the zero. In Fig. 3(b) we show the phase response to a single frequency tone as a function of place x [as found by Sondhi's method, Allen (1977)].

In Fig. 4 we reproduce a figure showing neural phase as measured by Kim, Siegel, and Molnar (1979). Using their measurement technique they determined the phase resulting from a single tone stimulus over a large number of units in a single animal. They then plotted each neuron's phase response against the neuron's CF. In this way they approximately determined the

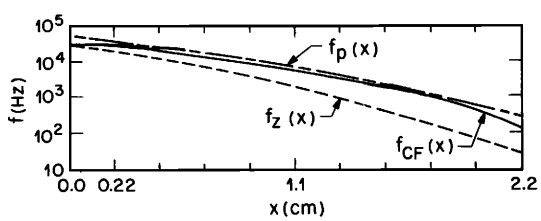


FIG. 2. We compare here the cochlear maps of the zero and pole of the model transduction filter to that of CF. The solid curve is the cochlear map of CF for the model as computed from $\omega_{CF} = [K_B/(m_B + m_T)]^{1/2}$. The model we have used for transduction is simple in that it consists only of poles and zeroes. These pole and zero frequencies vary with position along the BM.

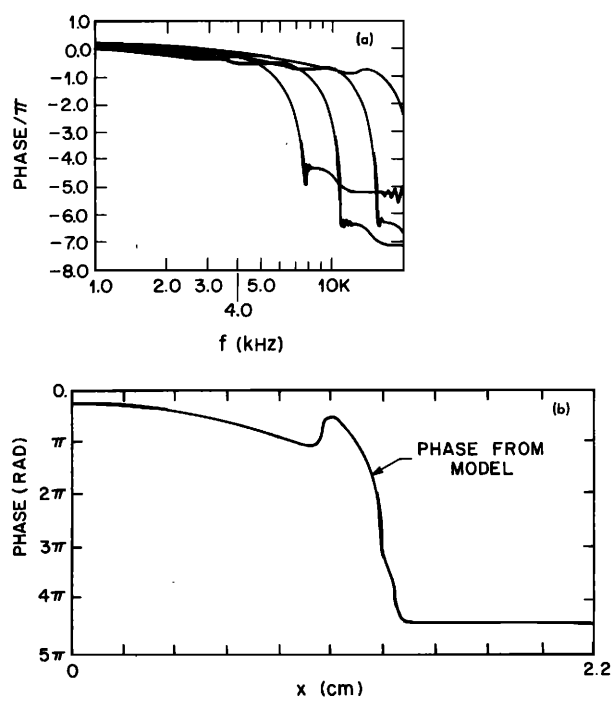


FIG. 3. As with the magnitude response, the phase, whether plotted as a function of $\log(f)$ or place x, is quite similar. (a) Phase as a function of frequency for four different measurement locations. (b) Phase as a function of location for a single frequency. In both cases the π phase reversal is a result of the spectral zero of H_T.

Redistribution subject to ASA license or copyright; see http://acousticalsociety.org/content/terms. Download to IP: 130.126.255.24 On: Fri, 15 May 2015 22:07:49

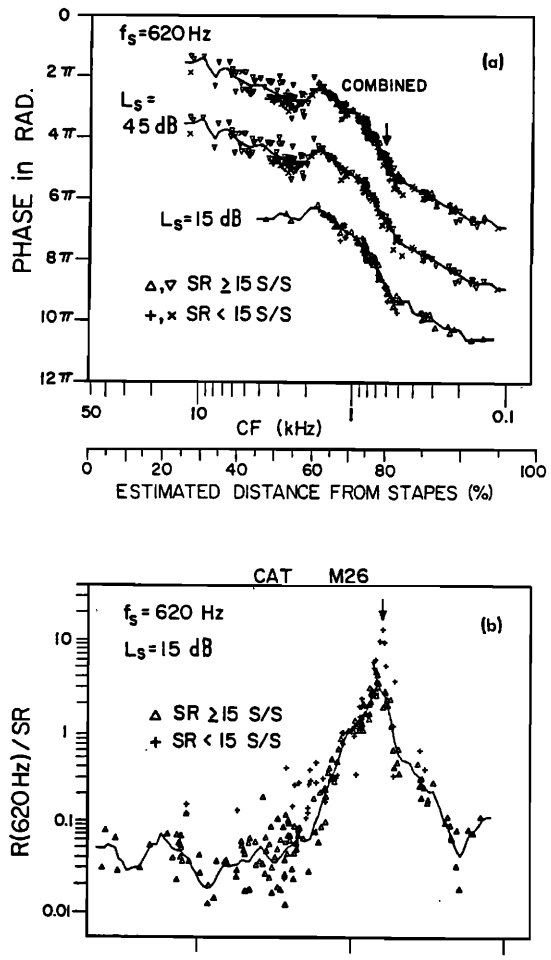


FIG. 4. This figure shows cochlear neural phase response to a single tone of frequency 620 Hz plotted as a function of place along the BM [Kim, Siegel, and Molnar (1979)]. Note the phase jump for CF's of 2 kHz. Each point corresponds to the phase (relative to the input phase) for each neuron measured in a single animal. By measuring the CF of each unit, it is then possible to obtain an estimate of the relative innervation point along the BM.

phase of the neural excitation due to the input tone as a function of position along the length of the cochlea, since CF is relatable to the innervation point on the BM by the cochlear map.[1] As may be seen in Fig. 4, Kim *et al.*, found a positive π phase shift (at 2 kHz) for units having CF's above the input stimulus frequency, in agreement with the spectral zero model π phase shift [Fig. 3(b) and Eq. (1)].

Thus the second-filter model of a left hand plane spectral zero gives excellent agreement with both the neural tuning magnitude (ear canal pressure for threshold neural isorate) and phase.

From the above evidence it appears that:

(a) the transduction filter H_T is required from a modeling point of view;

(b) the transduction filter may be modeled by a spectral zero;

(c) in some sense the cochlea transduction mechanics acts as a linear system since linear system theory concepts are applicable (e.g., zeros make up the transfer function).

As a result of the cross-correlation measurements of deBoer and Kuyper (1968), deBoer (1973), Evans (1977), and Møller (1977), it appears that the above conclusions are valid at levels well above threshold. If this interpretation of their data is correct, then the spectral zero model of the transduction filter might be useful in increasing our understanding of hair cell transduction mechanics.

II. A SIMPLE MODEL FOR RADIAL SHEAR

A concept that seems to have prevailed throughout the recent (last 20 years) history of cochlear modeling is the concept of radial (transverse) shear motion. Originally it seems to have been suggested by Kuile (1900), but first studied by G. von Békésky [1951, 1953(a),(b)], based on his vibrator measurements of the cochlear duct. von Békésy observed that the cochlear microphonic (CM) was greatest when the cochlear duct was vibrated radially. About the same time hair cell morphologists revealed the directional sensitivity of the hair cells, adding further credibility to the radial shear-motion hypothesis.

The first analytic model work seems to be that of Rhode and Geisler (1967) who attempted (unsuccessfully) to account for BM nonlinearities in their model.

In the following we present a simplified model of radial shear motion (which we will need later) in order to reveal what we feel are the basic principles (this analysis was first presented by Allen, 1978).

Consider the simplified model of the cochlear duct shown in Fig. 5(a). By comparison to Fig. 5(b) one may identify the various features of the model. The basilar membrane (BM) extents from A to E. The tectorial membrane (TM) is represented by a rigid bar (plate) DC pinned (hinged) at D. The spiral sulcus is labeled SS.

The basic question we ask is the following: Assuming that the BM is displaced by an amount ξ, what is the relative shearing displacement between TM and RL. We pick points on TM and RL that are opposite each other in the rest condition and define the distance Δ as their relative radial or transverse (z direction) separation when the BM is displaced by ξ. The displacements of the model are defined in Fig. 6.

A simple analysis of the geometry shows that triangles abc and $a'b'c'$ are similar. For small angles at vertex a we then have the proportionality

$$\xi/W_1 = \Delta/(\epsilon + h)\,, \tag{3}$$

where

ξ = BM displacement,

Δ = radial-shear-displacement,

W_1 = length $AB \approx$ length ab,

ϵ = subtectorial dimension,

h = organ of Corti height. (4)

In the following we assume that ϵ is given by the length

Redistribution subject to ASA license or copyright; see http://acousticalsociety.org/content/terms. Download to IP: 130.126.255.24 On: Fri, 15 May 2015 22:07:49

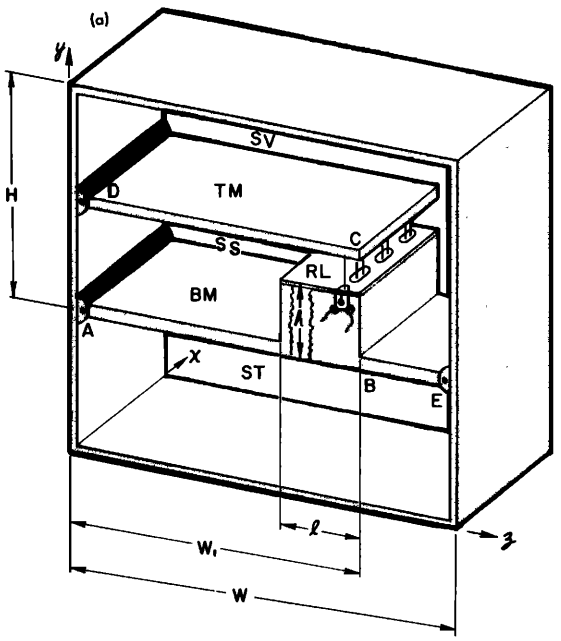
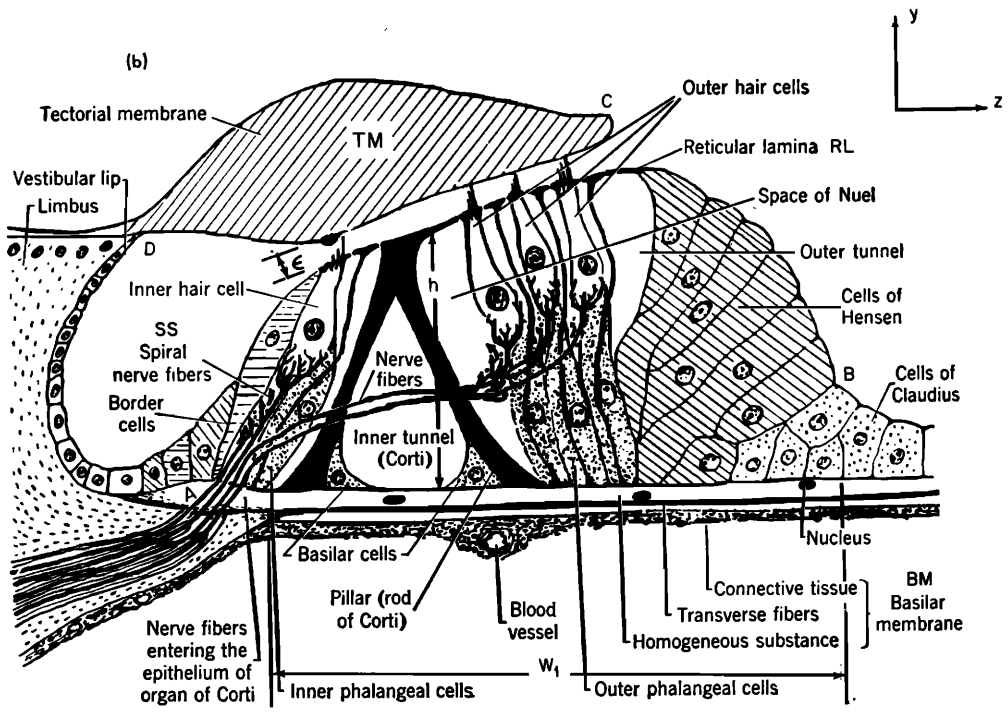


FIG. 5. We show here a labeled three dimensional representation of a cross section of the cochlea. (a) Points A, D, and E are hinge points which represent pinned boundary conditions for BM displacements. The BM extends from points A to E. (b) A two dimensional labeled cross-sectional drawing of the organ of the corti due to Rassmussen (some modifications have been made to the original drawing). Points ABCD have been indicated for reference.



of the outer hair cell stereocilia, since these stereocilia appear to be firmly fixed to both TM and RL, and that $W_1 \approx W/2$, where $W(x)$ is the BM width.

We now define a new variable $G(x)$ which we call the *shear gain*:

$$G(x) = \Delta(x)/\xi(x) . \tag{5}$$

For purposes of the present definition we assume here that the TM is rigid, a restriction which we shall later relax.

Note that the relation between Δ and ξ is linear (proportional) and instantaneous (frequency independent). It is equivalent to a lever having a displacement gain of G. The electrical equivalent is a transformer having a current gain of G.

Thus according to the above assumptions and Eqs. (3)–(5)

$$G(x) \approx 2h(x)/W(x) \tag{6}$$

since $\epsilon \ll h$. For order of magnitude calculations we will use Eq. (6). However, in the remaining sections we shall treat $G(x)$ as unknown since in the future more accurate models of $G(x)$ may be of interest.

Rhode and Geisler (1967) defined a quantity similar to $G(x)$ and determined from measurements that it went from 3 at the base ($x=0$) to 0.3 at the apex ($x=L$) (see their Fig. 4). Equation (6) is also given in Allen (1978) and in Zwislocki (1980).

Redistribution subject to ASA license or copyright; see http://acousticalsociety.org/content/terms. Download to IP: 130.126.255.24 On: Fri, 15 May 2015 22:07:49

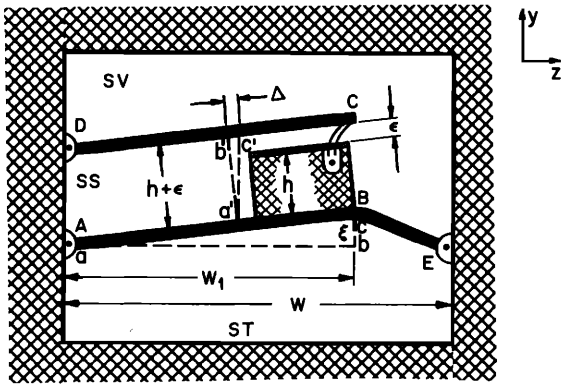


FIG. 6. A cross section showing the BM displaced. Since AB and DC are equal in length in this simplified model, BC remains parallel to AD after any BM displacement ξ. As a result, triangles abc and $a'b'c'$ are similar, and displacement Δ is proportional to the BM displacement ξ. We define this ratio as the shear gain G, namely $G(x)=\Delta(x)/\xi(x)$.

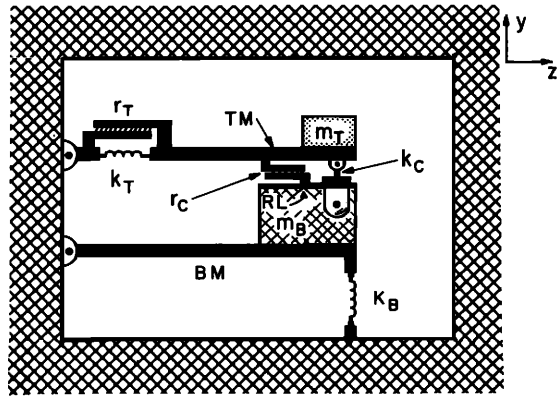


FIG. 7. In this figure we have further abstracted the physical model of Fig. 5(a) by specifically specifying the BM restoring force K_B, the BM mass m_B, the tectorial mass m_T, the cilia stiffness k_c, and the subtectorial damping r_c. Furthermore we have added the tectorial stiffness and damping k_T and r_T as discussed in the text. By allowing the TM to move independently of BM displacements, with its own resonant frequency as determined by k_T+k_c and m_T, it is possible to introduce a zero into the transfer function between TM–RL shear displacements and BM displacement.

III. THE RESONANT TECTORIAL MEMBRANE MODEL

A. The physical model

In Sec. I we presented some model results which showed the utility and parsimony of a spectral zero in modeling neural tuning data. In this section we shall develop a physical micromechanical model which physically justifies such a zero. In the following all forces, stiffnesses, masses, etc. are defined on a per unit area basis (in the plane of the BM) averaged over the BM width, and as a function of position along the length of the cochlea. This approach is common in acoustical impedance calculations.

In order to introduce a zero into the transfer function between BM displacement ξ and TM–RL shear Δ it is necessary that the tectorial membrane move independently and not be locked to BM motion through the radial shear level gain G, Eq. (5). With this end in mind we introduce an elastic connection between the body of the TM and the scala wall as shown in Fig. 7. In this figure the BM stiffness is represented by the spring K_B and the BM mass by the block labeled m_B. Since the actual BM restoring force K_B is most probably due to the bending rigidity of the BM, the representation of K_B as a spring is artificial but graphic. The cilia stiffness k_c represents stiffness with respect to radial shear; it might be thought of as a bar clamped at the RL end and pinned at the TM end. Since the space between TM and RL, the subtectorial space, is only 2–6 μm, the equation of motion between these two surfaces must include a viscous force which is shown here as the dashpot labeled r_c. A formula for r_c will be derived in Sec. V B (Allen, 1978). The tectorial membrane mass is labeled m_T, while the elastic connection to the scala wall (spiral limbus) is k_T. For reasons which will become obvious it is necessary to include a damping loss across k_T labeled r_T. This loss might represent internal friction in the TM tissue. Since the TM tissue is in a longitudinal mode of vibration its loss factor might be quite different (namely larger) than that of the bending mode of BM motion.

The basic principle of this model is that the spring-mass system of the TM, namely k_T and m_T, may resonate independently from that of the basilar membrane system of K_B and m_B. When conditions are right the TM can move with equal magnitude and in phase with the RL producing zero *relative* motion. We will show that this condition will give rise to a spectral zero in the RL–TM shear as assumed in Sec. I. We assume here that the neural excitation is simply related to the RL–TM shear.

B. The rectilinear mechanical model

In order to analyze the physical model of Fig. 7 it is helpful to redraw it in rectilinear form as shown in Fig. 8. Those not acquainted with this procedure should refer the book of H. Olson (1958), Chap. 4. The solid lines represent hinged rigid massless rods in the rectilinear

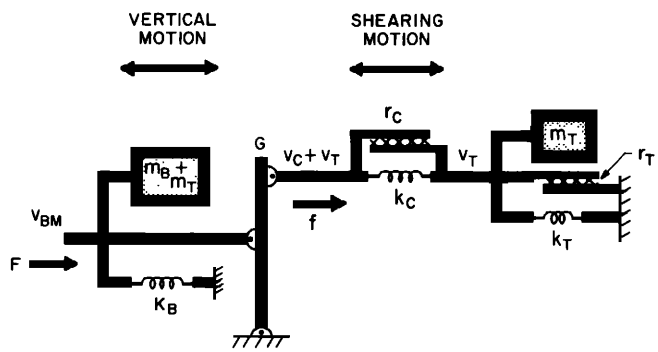


FIG. 8. In order to analyze the mechanical system described by Fig. 7 we redraw it in rectilinear form. The solid lines represent massless rigid rods or linkages. The vertical rod labeled G is a lever having a mechanical advantage of G. It represents the radial shear model which transforms vertical BM motion to radial shearing motion (Fig. 6). Springs are represented by coils, masses by boxes and the two viscous dash pots are labeled r_c and r_T. The pressure drop across the BM gives rise to force F and thus to velocity v_{BM}.

Redistribution subject to ASA license or copyright; see http://acousticalsociety.org/content/terms. Download to IP: 130.126.255.24 On: Fri, 15 May 2015 22:07:49

circuit, the coils are springs, and the boxes are masses. The radial shear model has been included as a lever having a mechanical advantage of $G(x)$ [see Eq. (5)]. The mass on the left is the sum of m_B and m_T since vertical BM motion is loaded by both masses, assuming the outer hair cell stereocilia are rigid to vertical forces.

To the left of the lever, the physical forces and displacements are vertical, while to the right they are shearing.

A number of subtle assumptions have been made in going from Fig. 7 to Fig. 8. In the physical model, Fig. 7, the lever action is nonobvious. In the rectilinear circuit Fig. 8 it is explicit. The radial stiffness of the cilia k_c is not clear in the physical model Fig. 5(a), while in the rectilinear model it is represented as the spring k_c. In a similar manner the BM bending stiffness K_B is not clear from Fig. 6 but is in Fig. 8.

The analysis of the rectilinear model is quite straightforward as discussed in Olson (Chap. 4). We first determine the "mobility" electrical equivalent and then convert it to the "classical" electrical equivalent circuit. Finally we write the system equations using the electrical equivalent circuit.

C. The electrical equivalent circuit

A straightforward and simple method for finding the electrical equivalent network is to use the mobility method (see Olson, Chap. 14). The mobility equivalent circuit may be drawn by inspection from the rectilinear model, and is given in Fig. 9. The classical electrical network is then found by forming the dual network (interchange current and voltage, L and C, R and G, and parallel with series). After performing these operations we find the classical mechanical analogue circuit shown in Fig. 10.

The BM velocity $v_{BM}(t,x)$ is $\partial\xi/\partial t$, $v_T(t,x)$ is the TM velocity, and $v_s(t,x)$ is the shear velocity between TM and RL.

IV. ANALYSIS OF THE MODEL

In the last section we went from a model of the cross-section of the cochlear duct to an electrical equivalent circuit. We are now in a position to analyze the assumed model.

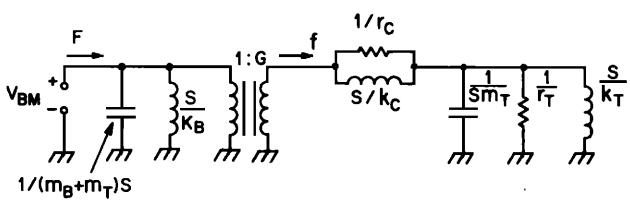


FIG. 9. By use of the mobility analogue it is possible to describe the mechanical circuit of Fig. 8 in electrical terms. The use of the mobility analogue simplifies the transformation between the mechanical and the electrical circuit.

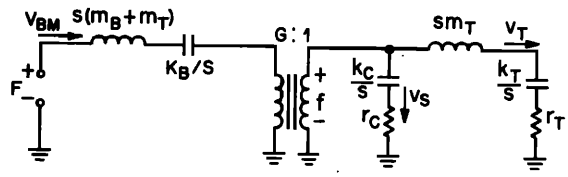


FIG. 10. The more common form of mechanical-electrical analogue is the force = voltage analogue. This analogue may be found by forming the dual of the mobility circuit. Thus the impedances of Fig. 9 are replaced by admittances and series connections are interchanged with parallel connections. The mechanical model of the cochlear duct, as shown in Fig. 5(a), has therefore been reduced to the electrical circuit of this figure.

A. The second filter

The principal question of interest is: What is the transfer function which relates $V_s(x,\omega)$ to $V_{BM}(x,\omega)$? The quantity V_s has been defined as the shear velocity between TM and RL, and it is a quantity that might well drive inner hair cell cilia. According to recent observations [Lim (1980)] these cilia do not seem to be connected directly to the TM; however, the cilia would be displaced by fluid flow across them (in a manner similar to sea grass bending in a gentle wind).

The transfer function in question may be identified as the second filter, and from the current divider law, can be shown to be

$$H_T(x,s) \triangleq \frac{V_s}{V_{BM}} = G\,\frac{sm_T + r_T + k_T/s}{sm_T + (r_c + r_T) + (k_c + k_T)/s}\,. \tag{7}$$

As in Sec. I Eq. (1) we call $H_T(x,s)$ the *transduction filter*.

The transfer function H_T consists of a zero at frequency f_z and a pole at frequency f_p where

$$f_z = (1/2\pi)(k_T/m_T)^{1/2}\,, \tag{8}$$

$$f_p = (1/2\pi)[(k_c + k_T)/m_T]^{1/2}\,. \tag{9}$$

Note that $f_p > f_z$ since $k_c + k_T > k_T$. The significance of this result is that a spectral zero, which is required to account for the difference between the mechanical and neural response, naturally follows from the model of Fig. 7. This point is one of the main results of this paper.

B. Basilar membrane impedance

A basic quantity of importance in basilar membrane macromechanics is the BM impedance, defined as the ratio of pure tone trans-BM pressure to steady state normal velocity (or force/volume velocity)

$$Z_{BM}(x,s) \triangleq -2P/V_{BM} = F/(WV_{BM}).$$

This impedance is usually assumed to be of the form

$$Z_{BM} = K_B(x)/s + R(x) + sM_0\,. \tag{10}$$

All calculated results in this paper have in fact assumed a BM impedance of this form. We hope there-

Redistribution subject to ASA license or copyright; see http://acousticalsociety.org/content/terms. Download to IP: 130.126.255.24 On: Fri, 15 May 2015 22:07:49

fore that the BM input impedance of the model proposed in Fig. 7 will be in some way consistent with Eq. (10). To a certain degree of approximation this appears to be the case, as discussed in Sec. V.C. If the input impedance to the right of the transformer were real, then Eq. (10) would hold exactly. In fact, by inspection, from Fig. 10 (or Fig. 7)

$$Z_{BM}(x,s)=s(m_T+m_B)+K_B/s+G^2(x) \times \frac{(r_c+k_c/s)(k_T/s+r_T+sm_T)}{(k_c+k_T)/s+(r_c+r_T)+sm_T} \quad . \tag{11}$$

Therefore a rigorous analysis of BM motion assuming the model of Fig. 7 is significantly more complicated than previous BM macromechanical models since the time differential equations are fourth-order rather than second-order.

V. MODEL PARAMETERS

A. The transduction filter

The model presented in the last section has some important properties: It follows from a specific physical micromechanical model, and it has a spectral zero as required in matching neural tuning data. However, before it may be seriously considered as a reasonable model we must more carefully investigate the model parameters and show that they have physically reasonable values. Since no direct measurements have been made of TM elasticity and mass, or of cilia stiffness, these values must presently be deduced from neural tuning data. Of course this makes the argument somewhat circular. However if the deduced values are reasonable (order of magnitude correct) and if the model fits the tuning-curve data accurately, as it appears to do, the model must be seriously considered and further evaluated. A critical future test of the model will be mentioned in Sec. VI of this paper where we discuss the nonlinear cochlea. In this paper only linear model calculations have been performed.

In order to recover the model parameters from tuning data it is important that we render Eq. (7) dimensionless by defining the following normalizing parameters

$$\omega_z^2(x)=k_T/m_T\,, \tag{12a}$$

$$\omega_p^2(x)=[k_c+k_T]/m_T\,, \tag{12b}$$

$$\zeta_z(x)=\tfrac{1}{2}r_T/(k_Tm_T)^{1/2}\,, \tag{12c}$$

$$\zeta_p(x)=\tfrac{1}{2}(r_c+r_T)/[(k_c+k_T)m_T]^{1/2}\,, \tag{12d}$$

$$\gamma=\omega_p/\omega_z\,. \tag{12e}$$

The radian frequencies ω_p and ω_z are the pole and zero frequencies of Eq. (7). The quantity ζ is called the damping ratio and is a measure of the damping or Q ($Q=1/2\zeta^{-1}$) of the pole or zero. Using these definitions Eq. (7) becomes

$$H_T(x,s)=\frac{G(x)}{\gamma^2}\left(\frac{(s/\omega_z)^2+2\zeta_z(s/\omega_z)+1}{(s/\omega_p)^2+2\zeta_p(s/\omega_p)+1}\right)\,. \tag{13}$$

The normalizing variables $\omega_z,\omega_p,\zeta_z,\zeta_p$ are physically meaningful since they may, in principle, be identified easily from the transfer function spectrum. The frequencies ω_z and ω_p may be identified from the null and peak frequencies in the spectrum, and ζ_z and ζ_p from the zero and pole bandwidths. The pole frequency ω_p appears to be sufficiently above CF that it cannot be observed in normal tuning data. For the same reason ζ_p is not observable. However we do have the bound on ω_p

$$\omega_p>\omega_{CF}\,. \tag{14}$$

By simple calculations for different ζ_z values in the model we have found that ζ_z must be greater than $\frac{1}{10}$ to give a reasonable match to tuning curves for frequencies near ω_z. Thus we have

$$\zeta_z(x)>\tfrac{1}{10}\,. \tag{15}$$

From the defining Eq. (12a,b)

$$\omega_p^2-\omega_z^2=k_c/m_T>0\,. \tag{16}$$

giving the obvious result [Eq. (12e)]

$$\gamma=\omega_p/\omega_z>1\,. \tag{17}$$

In order to relate k_T and k_c we use Eqs. (12a,b,e)

$$k_c=(\gamma^2-1)k_T. \tag{18}$$

Assuming $\gamma>2$ then

$$k_c>3k_T\,.$$

For large $\gamma=\omega_p/\omega_z$ we may therefore replace k_c+k_T by k_c [for example in Eqs. (12b,d)]. Also from Eqs. (12) it follows that

$$\zeta_p/\zeta_z=(1+r_c/r_T)/\gamma\,. \tag{19}$$

The parameter r_c may be directly modeled from the geometry of the subtectorial space as follows [Allen (1978)].

B. Model for subtectorial damping r_c

Assume, as shown in Fig. 11, that TM and RL are two plates separated by a viscous fluid of viscosity η. If the width of the upper plate is l, the distance between them, ϵ, and their relative shearing velocity is v_s, which results from a shearing force f. We may then calculate the resistance r defined by

$$r\triangleq f/v_s\,.$$

The solution to this problem is well known and is given in any basic textbook on fluid mechanics as

$$r=l\eta/\epsilon\,. \tag{20}$$

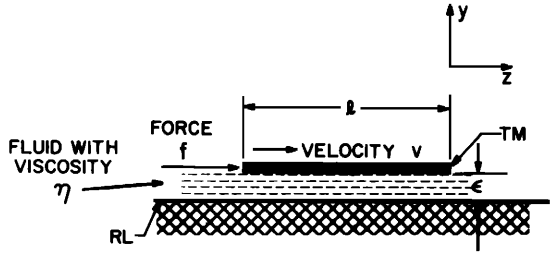


FIG. 11. The circuit element r_c may be associated with the viscous drag between TM and RL (see Fig. 5). The TM is modeled as the upper plate having a shear force f driving it. The terminal velocity of the TM is given by $v=f/r$ with r given by Eq. (20).

Redistribution subject to ASA license or copyright; see http://acousticalsociety.org/content/terms. Download to IP: 130.126.255.24 On: Fri, 15 May 2015 22:07:49

We then define

$$r_c = r/W \tag{21}$$

since the acoustic resistance r_c is found by dividing r by the BM width W. We assume that for endolymph $\eta = 0.015$ (g/cm-s). The parameters l and ϵ are either known or are easily measured [$\epsilon \approx 4 \times 10^{-4}$ (cm), $l \approx 0.015$ (cm)] for any given animal. This source of damping seems to be in excellent agreement with damping estimates derived from model calculations using Eq. (10) [Allen (1978)] where

$$R(x) = r_c G^2(x) . \tag{22}$$

C. Analysis of BM impedance

We now look at a simplifying approximation of Z_{BM}, Eq. (11). Using the definition of the transduction filter $H_T(x,s)$, Eq. (7), we may rewrite Z_{BM} as

$$Z_{BM} = s(m_T + m_B) + \frac{K_B}{s} + \frac{k_c}{s}\left(1 + \frac{s r_c}{k_c}\right) G H_T(x,s) . \tag{23}$$

The most important frequency region is $\omega < \omega_{CF}$, namely below cutoff. Again we assume that $\omega_{CF} < \omega_p$.

As may be deduced from Eq. (13), for $\omega < \omega_{CF} < \omega_p$ the denominator (pole) of H_T may be approximately replaced by the low-frequency dominant stiffness term $(k_c + k_T)/s$. Next we define the cilia damping frequency ω_c

$$\omega_c = k_c / r_c . \tag{24}$$

We shall show that $\omega_c \gg \omega_p$, giving for $\omega < \omega_p \ll \omega_c$ the constraint $\omega/\omega_c \ll 1$. Thus $|s r_c/k_c| = \omega/\omega_c$ may be ignored compared with 1 in Eq. (23). From these two approximations we find the following approximate expression for Z_{BM}

$$Z_{BM} = s(m_T + m_B) + \frac{K_B}{s} + \frac{k_c G^2(x)}{(k_c + k_T)}\left(s m_T + r_T + \frac{k_T}{s}\right) . \tag{25}$$

According to the above approximations the BM impedance remains second order as assumed in Eq. (10); however the resulting impedance values have been modified by the micromechanical superstructure.

It remains to be shown, as assumed, that $\omega_c/\omega_p \gg 1$. From Eqs. (12a,b,e) and (18)

$$k_c = m_T \omega_p^2 (1 - 1/\gamma^2) , \tag{26}$$

$$\omega_c/\omega_p = \epsilon m_T \omega_p (1 - 1/\gamma^2)/\eta l . \tag{27}$$

From the following approximate values for the parameters

$$l \approx 0.015 \text{ (cm)}, \quad \eta \approx 0.015 \text{ (g/cm-s)},$$

$$\epsilon \approx 4.0 \times 10^{-4} \text{ (cm)}, \quad \gamma \approx 3.0 ,$$

$$m_T > 0.2 m_B \approx 0.008 \text{ g/cm}^2 ,$$

we find from Eq. (27)

$$\omega_c/\omega_p > 0.013 \omega_p .$$

Thus for frequencies greater than 12 Hz, $\omega_c > \omega_p$, or for $\omega < \omega_p$, $\omega \ll \omega_c$ and the approximation in the numerator of Eq. (23) is justified.

The above calculations demonstrate that commonly assumed model parameters for Z_{BM} [Eq. (10)] are consistent with the model suggested here. They also specify the properties of the spectral zero and the pole in the TM–RL shear signal.

VI. A NONLINEAR MICROMECHANICAL MODEL

The nonlinear properties of the cochlea have been well documented in the recent literature. Clearly, for any micromechanical model to be useful it must account for these nonlinearities, such as combination tone generation, two-tone suppression, known threshold, and Q_{10} variations with input level. Toward this end we propose that the stereocilia stiffness k_c be a decreasing function of signal level (i.e., the cilia become limp with increased SPL). We feel that there are many qualitative justifications for such a proposal. First, Flock (1977) has pointed out that the outer hair cell cilia are composed of the protein actin. Based on the structural composition of the actin filaments Flock has proposed that the cilia bending moment (k_c) could possibly be variable. Second, the cilia appear to grow limp after strong sound stimulation [Hunter–Duvar (1977)]. Third, stimulation of the COCB efferent neural system, which terminates at the outer hair cells and thus might effect k_c directly, seems to modify neural tuning in a way which is consistent with decreased k_c in the model. Fourth, the rapid loss of the tip of the tuning curve of the receptor potential [Russell and Sellick (1978)] near CF seems consistent with this hypothesis since as k_c goes to zero the CF decreases toward the zero of H_T [see Eq. (25)]. Fifth, the apparent increase in BM damping might be accounted for by decreased k_c since as k_c decreases r_c is "turned on" in the sense that a greater velocity is allowed across the TM–RL interface (increasing the effective mechanical damping).

The ultimate test of these ideas must await a more complete nonlinear simulation of this model and better experimental data. Many experiments, which might strengthen or weaken the proposed model, suggest themselves.

VII. PHYSICAL MEASUREMENTS

The basic premise of this paper is that the transfer function which relates neural to mechanical response consists of a spectral zero below CF. Based on some preliminary calculations we have estimated the zero frequency ω_z from existing neural data and have found that ω_{CF}/ω_z is about one octave. The calculated tuning curves give excellent quantitative agreement with neural measurements. Since a zero has a π phase shift, a more accurate way of measuring ω_z or ζ_z may be by measuring this phase jump. This could be done for many different CFs and as a function of level.

There presently seems to be very little information on the TM mass m_T; by measuring the cross-sectional area of TM it should be possible to obtain an approximate estimate of $m_T(x)$. Values for $\epsilon(x)$ are available; however apparently $l(x)$ has not been measured.

Redistribution subject to ASA license or copyright; see http://acousticalsociety.org/content/terms. Download to IP: 130.126.255.24 On: Fri, 15 May 2015 22:07:49

The neural response pole ω_p and zero ω_z might be independently observed if the BM could be driven directly while observing neural rate, thereby removing the BM macromechanics (the low-pass filter) from the response.

A possible explanation of the alligator–lizard neural data of Weiss *et al.*, (1978) might be the pole and zero of $H_T(x,s)$. If $K_B(x)$ were set to a large constant in the model we could remove BM resonance as we presently model it in the mammalian cochlea. This might account for the lack of observed tonotopic mechanical BM organization.

Finally, we feel that there appears to be one important flaw with this model that we would like to point out.

This model seems to predict a cochlea microphonic (CM) having a sharpened frequency response, assuming that CM (recorded differentially) is proportional to TM–RL shearing displacements. Schmiedt and Zwislocki (1977), on the other hand have shown that in the middle turn of the gerbil the CM frequency response is quite similar to the mechanical response as measured by Rhode in squirrel monkey.

VIII. CONCLUSIONS

In this paper a physical micromechanical model of cochlea transduction has been introduced and developed. Although a full analysis of a nonlinear version of the model is not yet practical, the linear results presented here are strongly encouraging in that they qualitatively agree with many diverse pieces of data. Of particular interest is the close agreement between the model and neural tuning data, both in magnitude and phase. The novel feature of the present model is the radial resonant tectorial membrane which affects the transduction mechanism by introducing a spectral zero into the transfer function between basilar membrane motion and inner hair cell excitation.

ACKNOWLEDGMENTS

This work was not done in isolation. I would like to thank the following people for valuable contributions and encouragement: M. M. Sondhi, C. Thompson, D. A. Berkley, and J. L. Flanagan.

[1]From cochlear theory we know that the BM response as a function of place x to a pure tone is similar to that of the variable $x_p = -1/a \log(\omega/\omega_{max})$ at a single place x, where the parameter a is given by the slope of the cochlear map, and ω_{max} is the intercept. We define the variable x_p as "pseudo-place" due to its similarity to the true place variable x. According to the above assumptions one may show that the tuning phase as a function of $x_p(\omega)$ at a single place, or of position $x(\omega_{CF})$ as a function of frequency are similar.

Allen, J. B. (1977). "Cochlear Micromechanics—A Mechanism for Transforming Mechanical to Neural Tuning within the Cochlea," J. Acoust. Soc. Am. **62**, 930–939.

Allen, J. B. (1978). "A Physical Model of Basilar Membrane Dissipation," J. Acoust. Soc. Am. **63**, 543(A).

Allen, J. B. (1979). "Cochlea Models 1978," Symp. on Models of the Auditory System and Related Signal Processing Techniques, Münster, Ger., in Scandanavian Audiology, Suppl. 9.

Allen, J. B. , and Sondhi, M. M. (1979). "Cochlear Macromechanics—Time Domain Solutions," J. Acoust. Soc. Am. **66**, 123–132.

de Boer, E., and Kuyper, P. (1968). "Triggered Correlation," IEEE Trans. Biomed. Eng. **15**, 169–179.

de Boer, E. (1973). "On the Principle of Specific Coding," Dyn. Syst., Measurement & Control (Trans. ASME), 265–273.

Evans, E. F. (1977). "Frequency Selectivity at High Signal Levels of Single Units in Cochlear Nerve and Nucleus," in *Phychophysics and Physiology of Hearing*, edited by E. F. Evans and J. P. Wilson (Academic, London).

Evans, E. F. and Wilson, P. J. (1975). "Cochlear Tuning Properties: Concurrent Basilar Membrane and Single Nerve Fiber Measurement," Science **190**, 1218–12|21.

Flock, A. (1977). "Physiological Properties of Sensory Hairs," in *Psychophysics and Physiology of Hearing*, edited by E. F. Evans and J. P. Wilson (Academic, London).

Frommer, G. H. (1979). "Fluid Motion in the Mammalian Organ of Corti," Acta Oto-Laryngol., Suppl. 363.

Geisler, C. D., Rhode, W. S., and Kennedy, D. T. (1974). J. Neurophysiol. **37**, 1156–1172.

Guinan, J. J., and Peak, W. T. (1966). "Middle Ear Characteristics of Anesthetized Cats," J. Acoust. Soc. Am. **41**, 1237–1261.

Hall, J. L. (1977). "Spatial Differentiation as an Auditory 'Second filter': Assessment on a Nonlinear Model of the Basilar Membrane," J. Acoust. Soc. Am. **61**, 520–524.

Hunter–Duvar, I. M. (1977). "A Scanning Study of Acoustic Lesions of the Cochlea," in *Inner Ear Biology*, edited by M. Portman and J. M. Aran, INSERM **68**, pp. 385–396.

Kiang, N. Y. S., Watanabe, T., Thomas, E. C., and Clark, L. F. (1965). *Discharge Patterns of Single Fibers in the Cat's Auditory Nerve*, MIT Research Mono. No. 35 (MIT Press, Cambridge, MA).

Kiang, N. Y. S., and Moxon, E. C. (1974). "Tails of Tuning Curves of Auditory-Nerve Fibers," J. Acoust Soc. Am. **55**, 620–630.

Kim, D. O., Siegel, J. H., and Molnar, C. E. (1979). "Cochlear Nonlinear Phenomena in Two-Tone Responses, Symp. on Models of the Auditory System and Related Signal Processing Techniques, Münster, Ger.," Scand. Audiol., Suppl. 9.

Kuile, E. ter. (1900). "Die Uebertragung der Energie von der Grundmanbran auf die Haarzellen," Pflueg. Arch. ges Physiol. **79**, 146–157.

Lim, D. J. (1980). "Cochlear Anatomy Related to Cochlear Micromechanics. A Review," J. Acoust. Soc. Am. **67**, 1686–1695.

Møller, A. R. (1977). "Frequency Selectivity of Single Auditory-Nerve Fibers in Response to Broadband Noise Stimuli," J. Acoust. Soc. Am. **62**, 135–142.

Olson, H. F. (1958). *Dynamical Analogies* (Van Nostrand, New York).

Rhode, W. S., and Geisler, C. D. (1967). "Model of the Displacement between Opposing Points on the Tectorial Membrane and Reticular Lamina," J. Acoust. Soc. Am. **42**, 185–190.

Russell, I. J. and Sellick, P. M. (1978). "Intracellular Studies of Hair Cells in the Mammalian Cochlea," J. Physiol. **284**, 261–290.

Schmiedt, R. A., and Zwislocki, J. J. (1977). "Comparison of Sound-Transmission and Cochlear-Microphonic Characteristics in Mongolian Gerbil and Guinea Pig," J. Acoust. Soc. Am. **61**, 133–149.

von Békésy, G. (1951). "Microphonics Produced by Touching the Cochlear Partition with a Vibrating Electrode," J. Acoust.

Redistribution subject to ASA license or copyright; see http://acousticalsociety.org/content/terms. Download to IP: 130.126.255.24 On: Fri, 15 May 2015 22:07:49

Soc. Am. **23**, 29–35.
von Békésy, G. (1953a). "Description of Some Properties of the Organ of Corti," J. Acoust. Soc. Am. **25**, 770–785.
von Békésy, G. (1953b). "Shearing Microphonics Produced by Vibrations Near the Inner and Outer Hair Cells," J. Acoust. Soc. Am. **25**, 786–790.
Weiss, T. F., Peak, W. T., Ling, A., and Holton, T. (1978). "Which Structures Determine Frequency Selectivity and Tonotopic Organization of Vertebrate Cochlear Nerve Fibers; Evidence from Alligator Lizard," in *Evoked Electrical Activity in the Auditory Nervous System*, edited by Naunton and Fernandez (Academic, New York).
Zwislocki, J. J., and Kletsky, E. J. (1979). "Tectorial Membrane: A Possible Effect on Frequency Analysis in the Cochlea," Science **204**, 639–641.
Zwislocki, J. J. (1980). "Five Decades of Research on Cochlear Mechanics," J. Acoust. Soc. Am. **67**, 1679–1685.

Redistribution subject to ASA license or copyright; see http://acousticalsociety.org/content/terms. Download to IP: 130.126.255.24 On: Fri, 15 May 2015 22:07:49