

SCANDINAVIAN AUDIOLOGY

SUPPLEMENTUM 9.

**MODELS OF THE AUDITORY SYSTEM  
AND RELATED SIGNAL  
PROCESSING TECHNIQUES**

Organized and edited by  
M. HOKE and E. DE BOER

PROCEEDINGS FROM THE WORKSHOP HELD AT  
MÜNSTER, FEDERAL REPUBLIC OF GERMANY  
SEPTEMBER 1978

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COCHLEAR MODELS - 1978

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0. ABSTRACT

Two important concepts at the forefront of most cochlear modeling work today are the need for nonlinear basilar membrane mechanics and the need for a "second-filtering" mechanism at the transduction site of the hearing system. Other less controversial topics are one vs. two-dimensional models and the use of the WKB method for obtaining analytical results for frequencies below the cut-off frequency.

DEFINITION OF TERMS

CF	Characteristic frequency	m	BM Mass
V <sub>BM</sub>	BM velocity	H	Scala height
BM	Basilar membrane	x	Positional coordinate along BM
ρ	Density	p	Pressure at BM surface
V <sub>ST</sub>	Stapes velocity	Z	BM Impedance
m <sub>eff</sub>	Effective BM mass	K	BM stiffness
ST	Stapes	ω	Radian frequency 2πf
1	1/√-1	ω <sub>max</sub>	CF at stapes

1. INTRODUCTION

In this paper we review the present state of cochlear modeling with an emphasis on the most recent developments in two-dimensional cochlear mechanics, second-filter sharpening mechanisms and cochlear nonlinearities. Two important concepts are at a forefront of most cochlear modeling work today. The first of these is the need for a "second-filter" mechanism at the transduction site of the hearing system and the second is the need for nonlinear basilar membrane mechanics.

Recently detailed arguments on each of these points of view have independently been put forth. Kim and Molnar (H2,1975) have reviewed the need for signal dependent (nonlinear) mechanical damping. They argue that based on present evidence there is no need for a second-filter and tentatively conclude that the mechanical and neural systems are directly coupled. According to their working hypothesis the nonlinear mechanics at threshold levels becomes very sharply tuned as a result of the small mechanical damping. Thus they argue that the observed differences between neural and mechanical tuning are a direct result of the stimulus level.

Evans on the other hand (E4,1974) has presented compelling arguments on the need for a "private, physiologically vulnerable second-filter." As a result of studies where simultaneous neural and mechanical measurements were made on cats, Evans and Wilson (E6,1974) came to the conclusion that the mechanics must be linear and that a second-filter is required between the mechanical and neural systems.



Hall, who represents a third point of view, has made numerous numerical model studies using a nonlinear transmission line model followed by a second-filter model based on spatial differentiation (G3, 1977a; B1, 1974). He found that both nonlinear mechanics and the second-filter are necessary in order to successfully model combination tone effects and two-tone suppression in order to frequencies below the characteristic frequency (CF). His model has also been successful in modeling Zwicker's psychophysical masking period pattern data (G2, G3, 1977) (as a time domain version of two-tone suppression) which uses a very low frequency (20 Hz) suppressor (B3, 1978).

In this paper I shall present a point on view of these issues which argues for both nonlinear basilar membrane mechanics and a linear transduction-stage sharpening mechanism (second-filter). My approach differs from that of Hall in that I have studied two-dimensional mechanical models and have used a different approach to the second-filter problem.

2. One vs. Two Dimensions

The cochlea is a three-dimensional, coiled, fluid-filled mechanical chamber divided into two sub-chambers (actually three if Reissner's membrane is considered) by the basilar membrane (BM). Because of this one might ask why we are interested in one and two-dimensional models. The answer is of course that a good model, by definition, should be the simplest possible model of the cochlea that accurately captures the principles of its operation. At one level, it is possible to do this with the one-dimensional, transmission line model. However, when one is interested in making detailed comparisons between physical measurements and a particular model, the one-dimensional models are not quantitatively adequate. We illustrate this in Fig. 1 where we compare the results of: (a) the one-dimensional model without effective BM mass correction [as discussed by Sondhi (A5, 1978), Eq. (39a)], (b) the one-dimensional model with effective mass correction  $m_{eff} = m + \frac{1}{3}\rho H$ , (c) the two-dimensional model response of Allen and Sondhi (A3, 1979), and (d) Rhode's measurements.

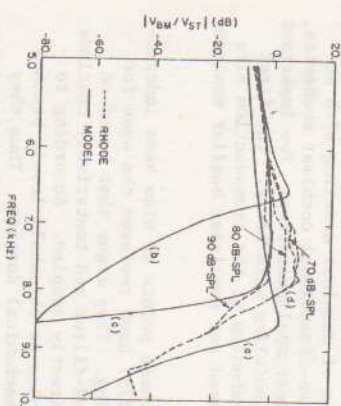


Fig. 1. Comparison of (a) one-dimensional model with no effective mass, (b) one-dimensional model with effective mass, (c) two-dimensional model of Allen and Sondhi (A3, 1979). All model parameters are identical in this figure. The dashed lines (d) are data of the Rhode (animal 69-473) made at several different sound pressure levels, showing the frequency dependent nonlinear response.

The three sets of calculations are based on identical model parameters. The point we wish to make here is the following. The assumptions made in deriving the one-dimensional model are more restrictive than those which are required for the more general two-dimensional model. Thus when two model responses differ for the same set of parameters, the two-dimensional model must be used if

quantitative comparisons are to be made. As the scala height H becomes small the various model responses become equal. However, for any realistic choice of scala height H and BM mass m, the one-dimensional model is inadequate for frequencies in the neighborhood of the characteristic frequency (CF). As may be seen Fig. 1, the one-dimensional model (Fig. 1b) is in good agreement with the two-dimensional model (Fig. 1c) for frequencies below CF as long as the effective mass of the scala fluid is included. When the scala fluid mass is ignored (Fig. 1a), the CF for the one-dimensional model may be closer in frequency to the 2-D result, but the low frequency response (below CF) does not have the proper gain  $|G(x, \omega)|$  where  $G(x, \omega) = \frac{V_{BM}}{V_{ST}} \frac{V_{BM}}{V_{ST}}$  and  $V_{ST}$  are the velocities of the basilar membrane and the stapes. It was shown by Allen and Sondhi (A3, 1979) that the high frequency slope can be made to agree with that of Rhode by the inclusion of a small amount of longitudinal BM stiffness.

3. WKB Approximation

As first pointed out by Zwetg et al. (A6, 1976) the one-dimensional model may be accurately integrated by an approximation technique called the WKB method. The 1-D model is most accurate in the frequency region below  $\omega_{CF}$ . We may therefore limit the model equation to the valid frequency region and then use the WKB method to find the solution. For frequencies below resonance the basilar membrane impedance  $Z(x, \omega)$  may be approximated by the stiffness term alone

$$Z(x, \omega) = \frac{-2P}{V_{BM}} \approx \frac{K(x)}{I_{\omega}} \quad \omega < \omega_{CF} \quad (1)$$

This still yields an interesting model since the resulting impedance is a function of both the position x and the radian frequency  $\omega = 2\pi f$ .

The 1-D model equation describing the pressure  $P(x, \omega)$  is [assuming an input of the form  $\exp(i\omega t)$  with  $\omega < \sqrt{K(x)/m}$ ]

$$\frac{\partial^2 P(x, \omega)}{\partial x^2} + \frac{\omega^2}{c(x)^2} P(x, \omega) = 0 \quad (2)$$

where

$$c(x) = \left[ \frac{HK(x)}{2\rho} \right]^{1/2}$$

$K(x) = K_0 e^{-2\alpha x}$  = BM stiffness  
 $H$  = Scala height  
 $P$  = Scala pressure  
 $\rho$  = Scala fluid density  
 $m$  = BM mass.

Equation (2) accurately models the BM response for frequencies below CF but not near CF and therefore it cannot be integrated across CF. As a result, only one boundary condition is applicable, namely the one at the stapes [Sondhi, (A5, 1978), Eq. 43b]

*Handwritten note:*  $H(x) = \frac{A R(x)}{B m \omega \sqrt{K(x)}}$



$$\frac{\partial p}{\partial x} \Big|_{x=0} = -i\omega p_{ST}^V(\omega), \quad (3)$$

where  $V_{ST}$  is the stapes velocity. By application of the WKB approximation, we may find the forward traveling wave component under the WKB assumption that reflections along the length of the cochlea may be ignored. Using this approximation, only one boundary condition is required. The WKB solution to Eq. 2 is

$$P(x, \omega) = A \sqrt{\frac{c(x)}{\omega}} \exp \left[ -i\omega \int_0^x \frac{dt}{c(t)} + i\omega t \right] \quad (4)$$

The integral is easily evaluated and the boundary condition Eq. (3) may be used to find the unknown constant A. As a result of this calculation

$$\begin{aligned} \frac{P(x, \omega)}{P(0, \omega)} &= \sqrt{\frac{c(x)}{c_0}} \exp[i\omega(t-\tau(x))] \\ &= \exp \left[ -\frac{1}{2} \alpha x + i\omega(t-\tau(x)) \right] \end{aligned} \quad (5)$$

and

$$\begin{aligned} G(x, \omega) &= \frac{V_{BM}(x, \omega)}{V_{ST}} = \frac{-2Z(\omega)}{Z(x, \omega)} \frac{P(x, \omega)}{P(0, \omega)} \\ &= \frac{-2Z(\omega)}{Z(x, \omega)} \exp \left[ -\frac{1}{2} \alpha x + i\omega(t-\tau) \right] \end{aligned} \quad (6)$$

where

$$\tau(x) = \int_0^x \frac{dx}{c(x)} = \frac{e^{\alpha x} - 1}{\alpha c_0} \quad (7)$$

$$\begin{aligned} Z(\omega) &= P(0, \omega) / V_{ST} \leftarrow \text{one chamber} \quad (8) \\ c_0 &= c(0) \leftarrow \text{2 chambers} \quad (9) \end{aligned}$$

One immediately useful result is an expression for the cochlear input impedance

$$Z(\omega) = \frac{i\omega p c_0}{\alpha c_0} \frac{1}{1 + \frac{\alpha^2}{2}} \quad (10)$$

The equivalent electrical circuit for this input impedance is a parallel inductor and resistor as shown in Figure 2. From Eq's. (1,6,10) we find

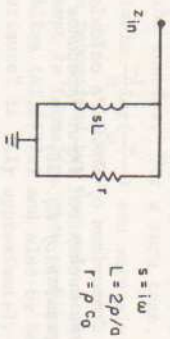


Fig. 2. Equivalent electrical circuit for the mechanical cochlear input impedance as found by the WKB method.

$$|G(x, \omega)| = \frac{2\omega^2 p c_0}{1 + \alpha^2 c_0^2 / 2 |K_0|} e^{-3\alpha x / 2} \quad (11)$$

The results predicted by these equations are consistent with both 1-D and 2-D models at a given point x on the BM for frequencies sufficiently below CF.

The important results here are the 6-12 dB/oct magnitude slope of the velocity transfer function  $|G|$  Eq. (11), the frequency-independent group delay (phase slope)  $\tau(x) = -\partial\phi/\partial\omega$  for frequencies below CF Eq. (7), and the expression for the cochlear input impedance Eq. (10). Note further that Eq. (5) shows that under the conditions assumed, namely for frequencies less than CF, the pressure is slightly attenuated and delayed by an amount  $\tau(x)$  independent of frequency. Thus for frequencies less than CF the mechanical response of the cochlea acts like a delay line having delay  $\tau(x)$ .

Variants of Eq's. (6,7) were used recently by Allen and Sondhi (A3,1979 Eq's. 33,34) to match Rhode's mechanical data which has a 6 dB/oct slope for frequencies well below CF. According to Eq. (11), a 6 dB/octave slope of  $|G|$  implies that  $\omega > \alpha c_0 / 2$ . Assuming exponential stiffness variation, this

condition may be written as  $\omega > \frac{\alpha \omega_{max}}{2} \sqrt{\frac{mL}{2p}}$ , where  $\omega_{max}$  is the largest CF  $\left[ \omega_{max} = \sqrt{K_0/m} \right]$ .

To the extent that the nonlinear effects are isolated to the CF region, and assuming [as discussed by Sondhi, (A5,1978)] that the major source of the input impedance results from the frequency region below CF, all of the above results approximately hold for nonlinear models. Sondhi found that the input impedance is not greatly affected by the choice of models or the response near CF. Sondhi's model results shown in his Fig. 11 are consistent with Eq. (10). [Sondhi (A5, 1978) used the parameters of his Fig. 5 rather than those of Fig. 6, as indicated in the figure caption]. In Fig. 3 we compare Sondhi's input impedance calculation to that of Eq. (10) with  $c_0 = 9.35 \times 10^3$  (cm/sec). The low level (but conceptually important) nonlinear cochlear reflections observed recently by Kemp (D2,1979) in the ear canal are clearly not accounted for by this simple linear theory. Any nonlinear mechanical CF related effects in live animals would, in principle, be present in cochlear input impedance measurements. Nonlinear CF effects would probably affect the input impedance impulse response (pressure response at the stapes to a stapes velocity pulse) at large delays  $[t > 2\tau(x_0)]$  and at small relative levels. However, at this point comprehensive model simulations have not yet been published on nonlinear model input impedance.



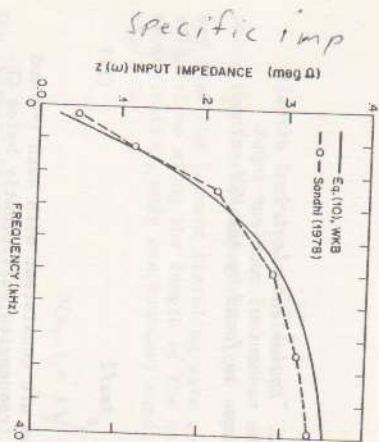


Fig. 3. Comparison of Sonzhi's calculation of the mechanical input impedance and the results of Eq. 10.

3. Need for a Second-Filter

The results of Eq. (11) highlight one of the key issues in cochlear models today. Eq. (11) indicates that the velocity transfer gain below CF (in the linear response region) must vary by less than 12 dB/oct, and when  $\omega > \frac{2}{3} \omega_0$ ,  $|G|$  must vary by 6 dB/oct (Rhode's measurements show 6 dB/oct). Neural and receptor potential measurements on the other hand indicate a totally different result with slopes for frequencies below CF as large 300 dB/oct. Under some conditions the slope even changes sign. Every modeling attempt directed at a resolution of this contradiction has supported, in my opinion, the need for a second-filter at the transduction stage (the hair cell).

The use of the terminology "second-filter" is perhaps unwise since the term has been proposed by so many in such a variety of forms. By second-filter as used here we mean that the hair cell excitation function  $\theta(x,t)$  is given by a linear transformation of BM pressure  $P(x,t)$  and displacement  $\xi(x,t)$ . Since BM velocity  $v(x,t) = d\xi/dt$  is a linear transformation of the displacement, velocity derivatives  $\theta = 3v^2/3x^2$  [Hall (C3,1977a)], the recent spatial integral model of Zwislocki (C6,1979), and the linear two component (LTC) transformation of Allen (C1,1977b)  $\theta = ap + bf$ . They do not include nonlinear transduction operations such as neural interactions. Nonlinear transduction models have the unfortunate property that the resulting neural excitation depends upon the nature of the time waveform and therefore cannot be treated as a filter which modifies the frequency content of the exciting waveform. Strictly speaking only a linear transformation may act as a filter.

Besides the large disparity between the mechanical gain and neural slopes below CF the neural phase response data measured by Kim and Molnar (H2,1975) also show important differences between neural and mechanical response. They have measured the neural phase response to a single tone for a large number of fibers in individual animals, and have plotted the data as a function of each fiber's CF. Note that this method neatly avoids the middle ear transfer

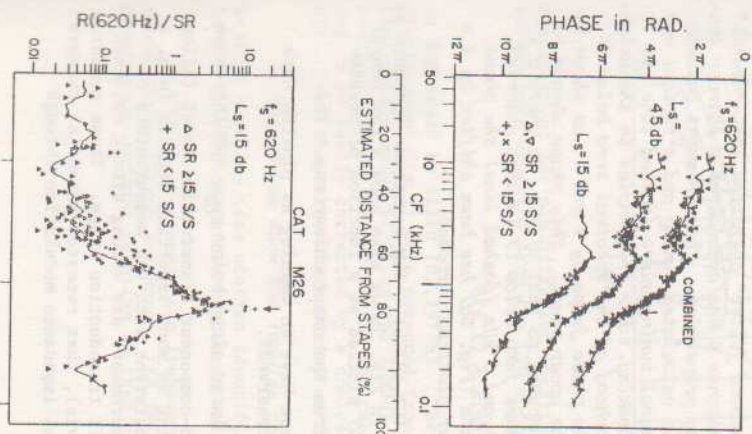


Fig. 4a,b. Kim et al. (H6, 1979) measured the neural phase and spike rate to a single frequency tone over a large number of fibers, for a single animal. They then plotted the phase and normalized rate as a function of  $\log(\omega_{CF})$ , where  $\omega_{CF}$  is the best frequency of each fiber measured. This phase may approximately be viewed as the neural phase to a pure tone as a function of position along the basilar membrane. The rate function is strongly distorted by the saturation of the neural system and therefore is difficult to interpret directly.

function since only one input frequency is used. Their method is approximately equivalent to measuring the phase as a function of position along the length of the cochlea. For a pure tone, response as a function of place  $x$  and the variable  $\frac{-1}{a} \log\left(\frac{\omega}{\omega_{max}}\right)$  are very similar. This property of the cochlea has long been recognized but has only been approximately formulated analytically. One attempt to formalize this property is the so called "shift-invariance" discussed by Allen (A1,1977a) and also by Sonzhi (A5,1978, Appendix B). While "shift-invariance" is only approximately valid in the real cochlea, it is a useful concept that has long been recognized (e.g. constant Q, or 1/3 octave filters).

The results of Kim and Molnar (H2) reproduced in Fig. 4(a,b) show neural phase and normalized rate as a function of  $\frac{-1}{a} \log\left(\frac{\omega}{\omega_{max}}\right)$  might be called "pseudo-place"]. The startling result is that a  $\pi$  phase shift occurs at



a place having a CF 1.5 octaves below the input frequency. Since this phase jump appears to be correlated with the input excitation frequency. It is not believed to be a result of a local mechanical distortion on the BM but is characteristic of a minimum-phase zero (zero in the left half s-lu plane). The rate function Fig. 4b does not look like a neural tuning curve because of the effect of neural rate saturation. In Fig. (5a,b) we show the results of the

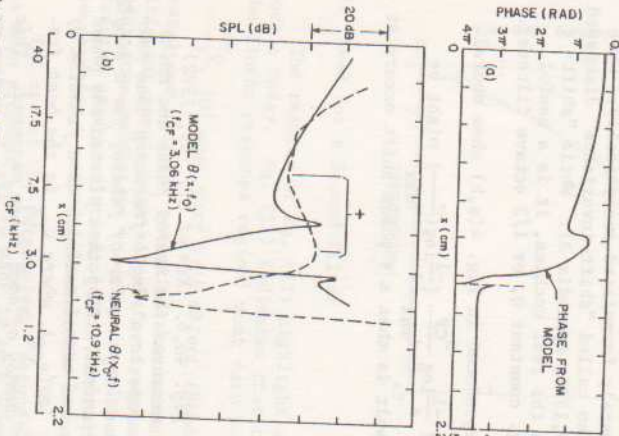


Fig. 5a,b. "Neural" magnitude and phase from the two-dimensional mechanical model as computed by the linear two-component transduction model of Allen (CI, 1977). In that model in order to derive neural tuning we subtract the 5<sup>th</sup> pressure from the BM displacement. For low frequencies the pressure and displacement are the same function of frequency and thus cancel. Near CF they go out of phase by π and therefore add at CF and above. As a result of this "second filter" operation, the "neural" response θ has considerably sharper tuning properties. The agreement between our calculated tuning and a typical cat neural tuning curve (dashed line) is striking. For frequencies in the neighborhood of the spectral zero below CF the phase jumps by π rad as shown by the upper panel. This phase should be compared to that of Fig. 4a where a π phase jump below CF is also observed. Beyond 3 kHz (dashed line) the phase data (Fig. 5a) has been shifted by 2 π for plotting purposes.

the second-filter model proposed by Allen (CI,1977b). The magnitude response as a function of place is given in Fig. 5b. In Fig. 5b we also show a cat neural place  $\frac{-1}{g} \log(u)$ , where a has been derived from the cat cochlear map. The absolute coordinates for the neural response have no meaning as plotted here (however relative differences have been preserved).

Both the magnitude response with its large slope below  $\omega_{CP}$  and the phase jump of π radians are explained by the two-component transduction model (Allen, CI,1977). While this model is still lacking in many important details (e.g. a physical realization) it appears to be consistent with the measurements of Russell and Sellick (R2,1979). Their measurements are strong direct evidence that sharpening must occur at the hair-cell transduction stage. These measurements also support the old idea (of H. Davis), that receptor potential changes are a direct result of hair-cell electrical impedance modulation through motion of the cilia.

According to the Allen LTC (linear two component) transduction model, the second-filter is equivalent to a minimum phase spectral zero just below CF as discussed by Allen (CI,1977, Eq. (9)).

Since spatial differentiation models do not appear to exhibit the π phase shift or equivalently the positive slopes in the magnitude of the tuning curve (region labeled "+" in Fig. 5b) it seems unlikely according to the measured phase jump of Fig. 4a that these models can be correct.

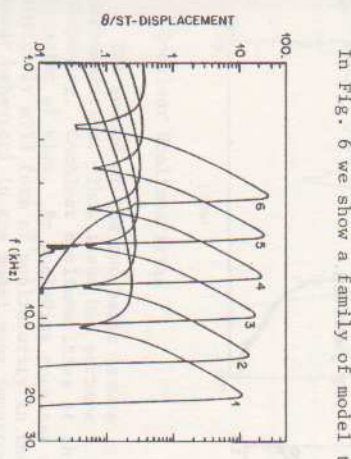


Fig. 6. Family of model neural tuning curves for six stations along the basilar membrane. These results were obtained using the linear two-dimensional time domain mechanical model of Allen and Sondhi (A3,1979). For this figure  $K_0 = .55 \cdot 10^{10}$ ,  $R_0 = 400$ ,  $m = .05$ ,  $H = .1$ ,  $L = 2.2$ ,  $\alpha = 2.2$  (CGS).

In Fig. 6 we show a family of model tuning curves normalized to stapes displacement for six different locations along the basilar membrane. These curves were computed from the LTC model

$$\theta(x,t) = a(x)p(x,t) + b(x)\xi(x,t) \quad (12)$$

as discussed by Allen (CI,1977b). The pressure  $p(x,t)$  and basilar membrane displacement  $\xi(x,t)$  were computed from the linear two-dimensional mechanical time domain model of Allen and Sondhi (A3,1979). Figure 7 compares the model cochlear map to that estimated for cat. The lack of fit in the 1.2 < x < 2.0 region is easily corrected by a choice of a slightly different function for  $K(x)$ . For the sake of simplicity we did not make this modification here.

In Fig. 8a we show the impulse response of  $\theta(x_0,t)$  for station 4 on the basilar membrane (see station identification numbers in Fig.'s 6,7). Fig. 8b is the Fourier transform magnitude and phase corresponding to Fig. 8a.

In Fig. 9 we compare the frequency response of station 5 to a neural tuning curve [Kiang and Moxon, (E8,1974), unit M92-23]. The mechanical damping was reduced relative to that of Fig. 6.



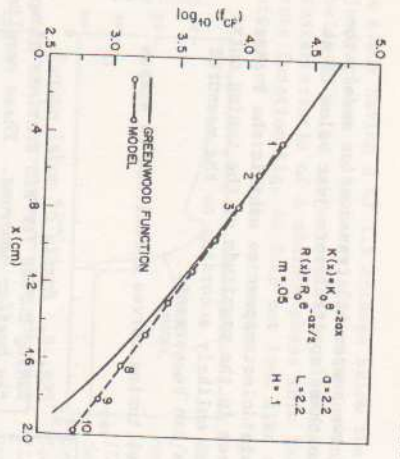


Fig. 7. Cochlear map for model parameters used in Fig. 6 as determined from the model tuning curves. The solid line is the Greenwood cochlear map function.

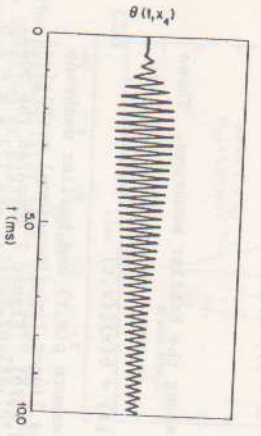


Fig. 8. a) Model neural impulse response for station 4. b) Magnitude and phase as found by Fourier transforming impulse response.

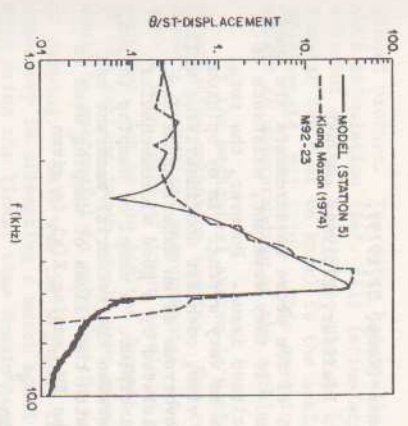
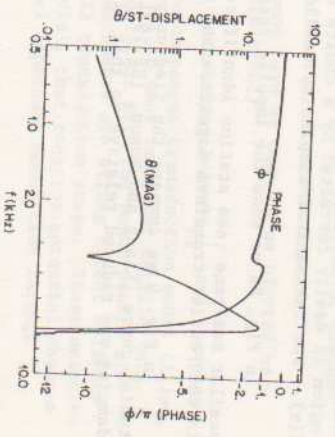


Fig. 9. Model neural response magnitude compared to a neural tuning curve of Kiang and Moxon (88, 1974) M92-23. The neural data has been inverted and scaled in amplitude to best fit the model data. The frequency scale is absolute for both plots.

4. Cochlear Nonlinearities

The second of the two basic issues in cochlear modeling today is cochlear nonlinearities. This issue has perhaps a longer history than that of cochlear sharpening. Cochlear nonlinearities at this point seem inevitable from a modeling point of view. By including cochlear nonlinear mechanical damping (a relatively mild form of nonlinearity in the sense that the system retains its linear behavior) in the model many important phenomena may be modeled. The nonlinear damping model is presently the only one known which explains all of these phenomena. Experimental results that are explained (or are at least consistent with the nonlinear damping model hypothesis) are:

- a) CF related BM velocity growth with SPL (Rhode D3, 1971; D6, 1978),
- b) Decreasing mechanical CF with increasing SPL (Rhode D3, 1971; D6, 1978),
- c) Distortion component generation and subsequent propagation (Kim, Molnar, H2, 1975; Hall B1, 1974),
- d) Decreased tuning sharpness (increased bandwidth) of: the mechanical system, the receptor potential, the cochlear microphonic and neural tuning, with increasing SPL (Rhode, D4, 5, 6, 1974, 1971, 1978; Russell and Sellick, F2, 1978; Dallos F1, 1973; Evans, E4, 5, 6, 1974, 1977, 1975),
- e) Observed differences between critical BM as measured by classical (simultaneous) masking vs. pulsation threshold (nonsimultaneous) techniques (Houtgast, G1, 1973),
- f) Two-tone suppression observations (Sachs and Kiang, E9, 1968; Houtgast, G1, 1973; Kiang and Moxon, E8, 1974; B2, Hall, 1977),
- g) Zwicker's "Masking Period Pattern" (Zwicker, G2, G3, 1977a, b; Hall, B3, 1978), (this appears to be a form of two-tone suppression),
- h) Receptor potential frequency response data and amplitude growth (single frequency) data vs. SPL (Russell and Sellick, F2, 1978),



- 1) Nonlinear input impedance measurements (Kemp, D2, 1979).
- 1) Time domain nonlinearities (Goblick, Pfeiffer, E7, 1969, see B5)

To varying degrees, many, or even all, of the above measurements are open to some question, as are their explanations. If they were not, existence of evidence supporting cochlear nonlinearities would likely be a closed issue. However, the total without some future revolutionary point of view, cochlear nonlinearities will eventually probably be accepted by almost everyone as an experimental fact. This process could perhaps be greatly accelerated by a good micro-mechanical physical model which embodies the above principles. A model of damping (Allen, A2, 1978) based on viscous fluid shearing between the tectorial membrane and the reticular lamina gives good agreement with the values of damping used in model studies. According to that model, the BM damping  $R(x)$  is given approximately by:

$$R(x) = \frac{\eta}{\epsilon} \left[ \frac{2h}{W(x)} \right]^2 \quad (13)$$

where  $\eta$  = fluid viscosity,  $h$  = organ of corti height,  $\epsilon$  = subreticular-space height, and  $W(x)$  = BM width. In CGS units:  $\eta = .01$ ,  $h = .03$ ,  $\epsilon = 2.5 \times 10^{-4}$ ,  $W(0) = .02$ ,  $R(0) = 360$ .

#### 5. Discussion

Given the opinions which we have so strongly expressed up to this point, the reader might reasonably ask what overall purpose cochlear nonlinearities serve. For those familiar with the data, one answer seems almost obvious: The nonlinear damping (as proposed in nonlinear cochlear models) acts to compress (attenuate) the frequency components of  $\theta(t, x)$ , the neural excitation, near  $\omega_{CF}(x)$  (in a logarithmic or exponential manner) in order to increase the dynamic range of the filters. Thus the nonlinear damping acts as a mechanical automatic gain control. The price paid for this increased dynamic range is: 1) a gradual decrease in frequency selectivity with increased SPL, and 2) harmonic frequency distortion.

The neural narrow-band filters which result from the second-filter action on the mechanical response serve three functions: 1) to reduce the bandwidth of the signal driving the neuron to an information rate that the neuron can handle, 2) to improve the signal to noise ratio (the perceptual ability to separate tones in noise), and 3) to remove distortion products created by the nonlinear mechanics. From this functional point of view the nonlinear damping and the second-filter seem somewhat reasonable. If the above point of view is correct it is not yet presently clear how the damping is made nonlinear, or how the second filter might physically operate.

#### 6. Summary

While probably running the risk of being prematurely philosophical we have attempted to present a unified point of view which attempts to broadly draw on (much of) the experimental cochlear data presently available. Many other important and relevant factors have not been mentioned in this discussion such as how the nonlinear damping might arise, how pressure and displacement might jointly interact on the cilia, or how the outer hair cells enter into the

global picture. The outer hair cells are coupled to the efferent system and OOSH stimulation (Ref. E11) (stimulation of the outer hair cells through the efferent system) also gives rise to broadened tuning about CF in a manner very similar (as best we know) to the nonlinear level dependent mechanical damping (Weiderhold, E11, 1970). This experimental fact seems to be an important clue toward an understanding of the cochlear nonlinearity.

If the mechanical system is nonlinear, as we presently believe, a further interesting question remains. How could nonlinear damping have affected Rhode's mechanical measurements? It was necessary for Rhode to drive the cochlea with a wide range of input levels in order to measure its output frequency response, due to the limited dynamic range of the measurement system. If each of the various input levels gave rise to a different BM damping, no linear model would be successful in matching the measurements with one value (the linear case) of damping. This was the argument that Allen and Sondhi (A3, 1979) found necessary in attempting a match model responses to Rhodes magnitude and phase data using the linear time domain two-dimensional model. Wide band noise cross correlation measurement methods [such as "rev-cor," de Boer, (E2, 3, 1968, 1973; Evans E5, 1975)] seem to be a convenient means by which one might skirt this signal dependent damping problem since they use a stationary noise signal to measure the signal dependent system "frequency response" of the cochlear filters, unlike the "nonstationary" pure tone stimuli used by Rhode.

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#### TRAVELLING WAVES AND COCHLEAR RESONANCE

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#### 1. INTRODUCTION

The principal elements that determine the mechanics of the cochlea are: the mass of the fluids filling the canals and the stiffness of the cochlear partition (i.e. the basilar membrane and its associated structures). See figure 1-a for the simplified geometry of the cochlea. The first theories that sought to explain Beke's observations on the movement pattern of the basilar membrane, were based on just these two elements: fluid mass and membrane stiffness (Zwislocki 1948, Dallos 1973). It proved simple to explain the formation of travelling waves in the basal part of the cochlea. Because the stiffness diminishes with increasing distance from the windows, the wave amplitude must increase to keep the energy constant. From a certain point on, the effect of ever-present a vibration maximum, at a location that depends on frequency, is explained. In later theories (e.g. Fletcher 1951) the effect of the mass of the cochlear partition was taken into account. In those theories the partition shows true resonance, at each location there is one frequency for which the mechanical impedance is minimal and near that frequency the wave amplitude may be expected to be maximal. The resonance frequencies are evenly distributed over the audible frequency range. (For a review of these theories see Zwislocki 1953 or Geisler 1976.)

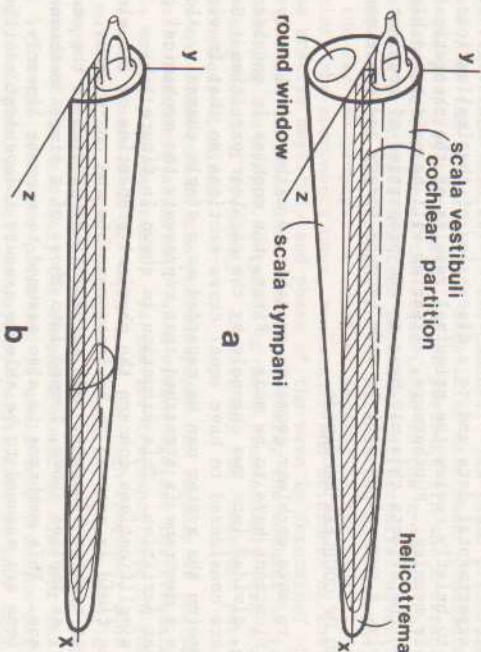


Fig. 1-a,b. Simplified geometry of the cochlea, see text.