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A new nonlinear model of the cochlea

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A NEW NONLINEAR MODEL OF THE COCHLEA

Iowa State University   PH.D.   1980

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A new nonlinear model of the cochlea

by

Steven Frederick Oakland

A Dissertation Submitted to the

Graduate Faculty in Partial Fulfillment of

The Requirements for the Degree of

DOCTOR OF PHILOSOPHY

Co-majors: Biomedical Engineering
             Electrical Engineering

Approved:

 In Charge of Major Work

 For the Major Departments

 For the Graduate College

Iowa State University
Ames, Iowa

1980

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LIST OF SYMBOLS

Symbol	Description	Dimensions
b	width of cochlear partition	L
c	compliance (or capacitance) per unit length	L^3T^2/M
∂, d, D	differentials	—
D	flexural rigidity	ML^2/T^2
e	ratio of tension to strain	M/T^2
E	Young's modulus of elasticity	M/T^2L
f	frequency, or tensile force per unit length, or force per unit volume, depending upon context	T^{-1} M/T^2 M/L^2T^2
F	force	ML/T^2
G	acoustic conductance per unit length	L^3T/M
j	square root of -1	—
L	length dimension	L
m	mass per unit area	M/L^2
M	mass dimension	M
p	pressure, or as subscript, refers to cochlear partition	M/T^2L —
P	complex pressure	M/T^2L
q	volume velocity	L^3/T
Q	complex volume velocity	L^3/T
r	damping per unit area	M/L^2T
R	acoustical resistance per unit length	M/L^5T
s	complex frequency, or width of stretched partition or plate, depending upon context	T^{-1} L
S	cross sectional area	L^2

t	time, or	T
	as subscript, refers to scala tympani	—
T	time dimension	T
u	average velocity	L/T
v	velocity, or	L/T
	as subscript, refers to scala vestibuli	—
x, y, z	displacement, or	L
	as subscripts, refer to direction	—
Y	volume displacement of cochlear partition, or acoustic admittance per unit length, depending upon context	L^3 L^3T/M
Z	acoustic impedance per unit length	M/L^5T
Γ	dimensionless compliance per unit length	—
κ	stiffness per unit area	M/L^2T^2
λ^2	dimensionless tensile force per unit length	—
μ	coefficient of viscosity	M/LT
ν	Poisson's ratio	—
Π	dimensionless pressure	—
ρ	mass density	M/L^3
τ	thickness of the cochlear partition	L
ψ	dimensionless volume displacement per unit length	—
ω	radian frequency	T^{-1}

I. INTRODUCTION

Of all the senses, hearing probably ranks second only to sight in
importance. Our ears enable us to talk with each other, to enjoy beautiful
music, or to be warned of danger by a siren or horn. People who lose their
hearing lose their ability to effectively communicate.

Deafness may be caused by a number of factors. Some people are born
deaf. Others may lose their hearing by disease or by accident. If the
auditory nerve is damaged or destroyed by accident or by diseases such as
meningitis, deafness may result. Diseases such as epilepsy can affect the
parts of the brain which perceive sound. Sudden or prolonged loud noises
may cause separation of the basilar membrane from the auditory nerve
fibers, resulting in total or partial hearing loss. Infection in the nose
or throat may find its way up the Eustachian tube to the ear. If not
treated promptly, serious damage may occur in the middle ear, the eardrum,
or even the cochlea.

Many pathological conditions in the external and middle ear can be
corrected with today's surgical techniques. Problems within the cochlea,
however, are not easily corrected. It is possible to open a portion of the
bony cochlea by manipulating surgical instruments inserted through the ear
canal. In fact, special devices have been placed within cochleae to
directly stimulate auditory nerve fibers. Such stimulation has had only
limited success and is reserved for people whose auditory neurons are not
stimulated effectively by any other means.

It is hoped that a better understanding of the normal excitation of
auditory nerve fibers will encourage the development of more effective

prostheses. Therefore, it is the purpose of this dissertation to provide a better understanding of the auditory perception process at the level of the auditory nerve stimulus.

The literature is rich with data from studies of the auditory system. Unfortunately, contradictions exist, making it difficult if not impossible to obtain a universally acceptable "theory of hearing."

One reason the ear is difficult to analyze is the fact that the hearing process is not linear. The frequency spectrum of the response of a linear system contains only those components which are present in the excitation. (These components may change in amplitude and phase, but not frequency.) It is noted that the auditory system is nonlinear because tones are heard which correspond to frequencies not present in acoustical stimuli.

It is not surprising that the auditory nonlinearity was discovered by a musician. In the year 1714, the Italian composer and violinist, Giuseppi Tartini (1692-1770), observed that if he sounded two violin strings simultaneously, a third musical tone could be heard (Jones 1935). Tartini taught his pupils to make use of the _terzi_ _suoni_ (third sounds) to tune their violin strings.[1]

Tartini probably heard tones corresponding to the difference frequency f_1-f_2, where f_1 and f_2 are the frequencies of vibration of the two strings (Vieth 1805). More recent studies have shown that combination tones corresponding to $f_1-n(f_2-f_1)$ are more audible than the difference tone (Weber 1829; Goldstein 1967).

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[1] Independent discoveries of combination tones were evidently made in 1745 by the German organist Georg Andreas Sorge (see Tyndall 1873, p. 276) and in 1751 by the French musician Jean-Baptiste Romieu (see Young 1800; Jones 1935).

Understanding of the operation of a complex system such as the auditory system is achieved by breaking the system into simpler parts. The operation of the complete system cannot be fathomed until each part is understood. To analyze a physical system, a model is helpful. If the characteristics of the model are similar to those of the physical system, one can gain understanding about the system by studying the model.

The human ear can detect sounds over a frequency range of nearly 10 octaves. Yet the human can discriminate between sounds which differ in frequency by only 0.3%. This frequency selectivity has been characterized by linear models, which are reviewed in Chapter II. To date, however, no model has adequately explained the existence of combination tones.

The hypothesis of this dissertation is that the compliance of the cochlear partition, the frequency-selective part of the cochlea, is a function of the displacement of the partition. This variation of compliance with displacement is responsible for the generation of combination tones. The hypothesis will be proved by applying Hooke's law for elastic solids to the cochlear partition.

Further, it will be shown that under normal operation the characteristics of the fluids in the scalae vestibuli and tympani are linear. The fluids provide inertial and damping forces, but are not responsible for the generation of combination tones.

II. REVIEW OF MATHEMATICAL MODELS OF COCHLEAR MECHANICS

A. Introduction

Based on Helmholtz's (1895) theory of hearing, the vibration of the basilar membrane was assumed for many years to consist of standing waves. However, direct observations of the basilar membrane showed that waves traveled in one direction, from the stapes to the helicotrema (von Bekesy 1960). The traveling wave phenomenon has been explained in terms of models mathematically similar to electric transmission lines. The development of these models is summarized in this chapter.

All physical models are based on the fact that the cochlea (see Figures 1 and 2) consists of two fluid-filled compartments, the scalae vestibuli and tympani, separated by the scala media. Bekesy observed that the entire scala media vibrates as a unit, i.e. Reissner's membrane vibrates in phase with the basilar membrane (von Bekesy 1960). In many models, therefore, the scala media is represented by a vibrating membrane called the cochlear partition.

The cochlear partition separates the scala tympani from the scala vestibuli throughout the length of the cochlea, from the stapes (basal) end almost to the apex. At the apex, however, the two scalae are not separated. This junction is called the helicotrema.

The cochlea is coiled around the auditory nerve, as shown in Figure 2. Nerve cells extend along the basilar membrane to the Organ of Corti, where they innervate the receptor cells. The receptor cells are responsible for transducing mechanical energy of the cochlear partition to
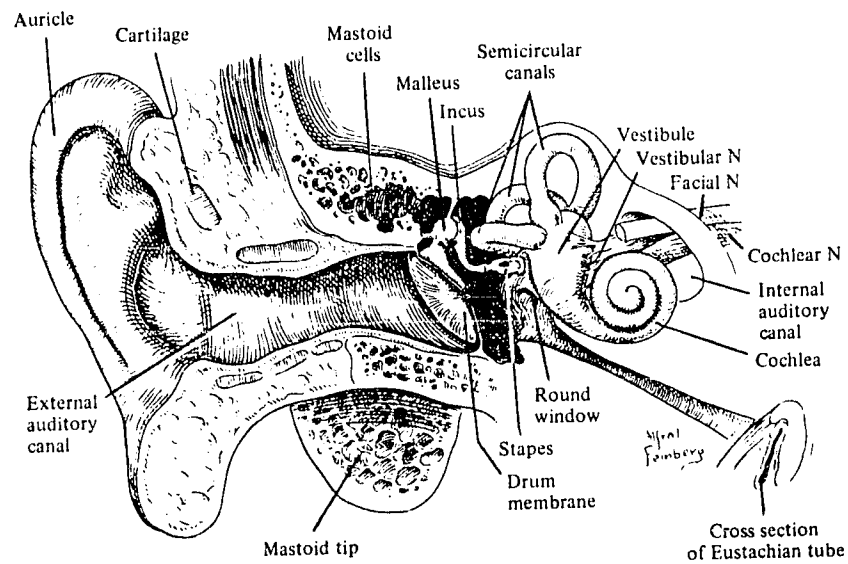
Figure 1. Cross section of the human ear (Davis and Silverman 1970, p. 48).
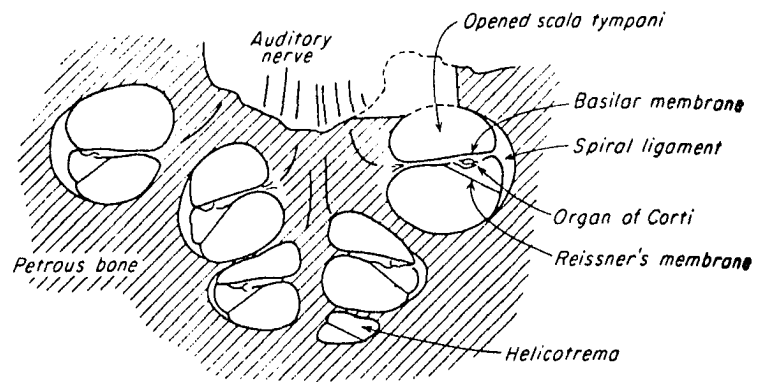
Figure 2. Cross section of the human cochlea (von Bekesy 1960, p. 470).

electrochemical energy. The latter is transmitted by nerve cells to the brain as action potentials.

In this chapter studies of cochlear models are reviewed. These models are the results of previous attempts to characterize the motion of the basilar membrane. Most of the models are analogous to electrical transmission lines. The electrical parameters of the transmission line vary along the length of the line in the same manner that physical parameters of the cochlea change throughout its length.

A sketchy development of the transmission line model is given by Zwislocki (1965). However, he fails to provide much documentation for his equations. A reader unfamiliar with the principles of fluid mechanics has trouble understanding the theory relating the transmission line model to the cochlea. Without this understanding, however, a reader of the literature cannot determine what assumptions have been made in the development of a particular model.

Unfortunately, the author knows of no source of background information, other than texts of fluid mechanics. Therefore, the next section is included to provide a review of the mechanics of motion as applied to cochlear models. The theory is based entirely on Newton's second law of motion and the principle of conservation of mass.

B. Theory

To simplify the equations of the physical models, the cochlea is assumed uncoiled, as shown in Figure 3. Viergever (1978) has shown that this simplification gives negligible errors in the calculation of the vibration of the cochlear partition.
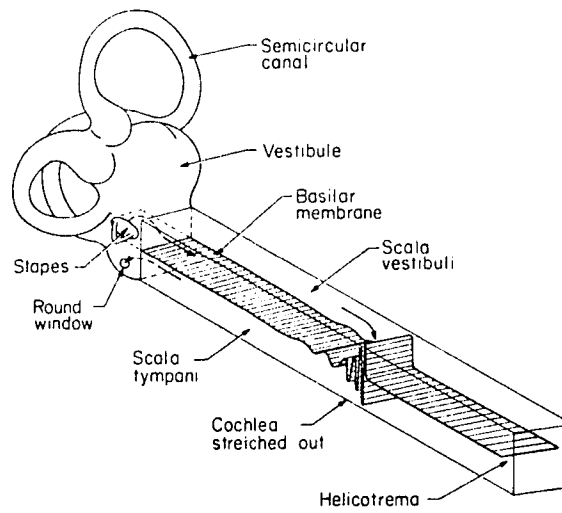
Figure 3. Simplified model of the cochlea (Zweig et al. 1976). Displacement of the basilar membrane is exaggerated.

The shape of a cross section of the cochlea does not significantly influence the behavior of the model. The cross section shown in Figure 3 is square, but it could just as well be circular (as in Figure 4) or any other shape. The size of the cross section, however, is important. The cross sectional area of the scala vestibuli is S_v; that of the scala tympani is S_t (see Figure 4). As shown in Figures 1-4, the area is largest near the stapes and gradually decreases with increasing distance from the stapes.

The coordinate system shown in Figure 4 will be assumed throughout the remainder of this dissertation. Distance x is positive if directed away from the stapes. A positive displacement of the cochlear partition is directed downwards, the positive y direction.

The equations of motion of cochlear fluids are given first. The relationship between the motion of fluids and the motion of the cochlear partition is given next. Then the equation of motion of the cochlear partition is given. The analogy between these equations and a segment of an electrical transmission line is also shown.

1. Equation of motion of cochlear fluids

The fluid in the volume element $S_v \Delta x$, shown in Figure 4, must obey Newton's second law of motion. The sum of forces per unit volume in the x direction may be written as (Bird et al. 1960, pp. 76-78)

$$\rho \frac{\partial v_x}{\partial t} = f_x - \frac{\partial p}{\partial x} \qquad (2.1)$$

where v_x is the x component of velocity, ρ is the mass density of the
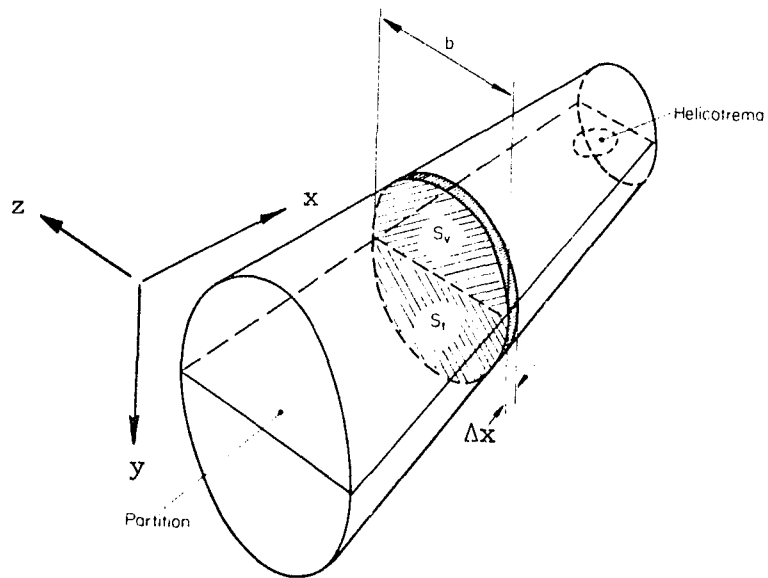
Figure 4. Simplified model of the cochlea showing the volume elements
in the scalae vestibuli ($S_v \Delta x$) and tympani ($S_t \Delta x$) (Dallos
1973, p. 138).

fluid, p is the pressure, and f_x is the sum of convective, viscous, and gravitational forces per unit volume.

If equation 2.1 is integrated over the cross sectional area S_v, the motion in the scala vestibuli is described in terms of the volume rate of flow, q_v, where

$$q_v = \int_{S_v} v_x \, dS \tag{2.2}$$

If convective, viscous, and gravitational forces are ignored, and if ρ is constant throughout the cross section, equation 2.1 becomes (Zwislocki 1965; Dallos 1973, p. 142)

$$\rho \frac{\partial q_v}{\partial t} = -\frac{\partial}{\partial x}(p_v S_v) \tag{2.3}$$

where p_v is the pressure averaged over the area S_v.

For the scala tympani, equation 2.1 becomes

$$\rho \frac{\partial q_t}{\partial t} = -\frac{\partial}{\partial x}(p_t S_t) \tag{2.4}$$

where q_t and p_t are the tympanic counterparts of q_v and p_v, respectively.

If the cross sectional area S_v of the scala vestibuli changes with distance x more slowly than does the average pressure p_v (i.e. if $(\partial S_v/\partial x)/S_v \ll (\partial p_v/\partial x)/p_v$), the right side of equation 2.3 is approximated by $-S_v(\partial p_v/\partial x)$. This approximation is made if equations 2.3 and 2.4 are written in terms of acoustic impedance.

Making the analogies of pressure to voltage and volume velocity to current, the acoustic impedance is defined as the ratio of complex pressure P to complex volume flow rate Q (Seto 1971, p. 115). In terms of acoustic impedance, equation 2.3 becomes

$$\frac{dP_v}{dx} = - Z_v Q_v \tag{2.5}$$

where Z_v, the acoustic impedance per unit length of the scala vestibuli, includes only the inertial component $s\rho/S_v$.

Some authors approximate viscous effects by including a damping term R_v (Zwislocki 1965; Dallos 1973, p. 142). In this case,

$$Z_v = R_v + s\rho/S_v \tag{2.6}$$

Similarly, the acoustic impedance per unit length of the scala tympani is written as

$$Z_t = R_t + s\rho/S_t \tag{2.7}$$

where

$$\frac{dP_t}{dx} = - Z_t Q_t \tag{2.8}$$

2. Equation of continuity

From the principle of conservation of mass, rate of accumulation within a volume element $S_v \Delta x$ equals the sum of the rates of flow into the element through each face. The resulting equation, called the equation of continuity, is given by (Dallos 1973, p. 140)

$$\frac{\partial \rho}{\partial t} S_v \Delta x = \rho q_v \Big|_x - \rho q_v \Big|_{x+\Delta x} - \rho u_p b \Big|_x \Delta x \tag{2.9}$$

where

$$u_p(x) = b^{-1} \int_b v_p(x,z) \, dz \tag{2.10}$$

is the y-directed velocity of the cochlear partition at a position x, averaged over the width b.

The first two terms on the right side of equation 2.9 represent the flow across the area S_v at x and x+Δx, respectively. The third term represents the rate of displacement of fluid due to movement of the cochlear partition in the y direction. Dividing by Δx and taking the limit as Δx goes to zero gives

$$S_v \frac{\partial p}{\partial t} + \frac{\partial}{\partial x}(\rho q_v) + \rho u_p b = 0 \qquad (2.11)$$

Equation 2.11 relates the velocity q_v of fluid in the scala vestibuli with the velocity u_p of the cochlear partition. The analogous equation coupling the motion of the tympanic fluid to that of the partition is (Dallos 1973, p. 141)

$$S_t \frac{\partial p}{\partial t} + \frac{\partial}{\partial x}(\rho q_t) - \rho u_p b = 0 \qquad (2.12)$$

The negative sign appears in equation 2.12 because the velocity u_p of the partition is directed toward the scala tympani.

If the cochlear fluid is homogeneous and incompressible, then ρ is constant and equations 2.11 and 2.12 may be combined to give the following expression for volume velocity per unit length of the cochlear partition:

$$u_p b = - \frac{\partial q_v}{\partial x} = \frac{\partial q_t}{\partial x} \qquad (2.13)$$

3. Equation of motion of the cochlear partition

The complex volume velocity of the cochlear partition is related to the complex pressure difference $P_v - P_t$ across the partition by the acoustic impedance of the partition (Zwislocki 1965). From equation 2.10 and Figure 4, the volume velocity of the partition is $u_p b \Delta x$. Therefore, using equation 2.13, the equation of motion of the cochlear partition is

written as

$$(P_v - P_t) \; Y_p \;\; = \;\; \frac{dQ_t}{dx} \;\; = \;\; - \; \frac{dQ_v}{dx} \tag{2.14}$$

where Y_p is the acoustic admittance of the partition per unit length.

4. Transmission line analogy.

Equations 2.5, 2.8, and 2.14 are the differential equations describing the element of the transmission line shown in Figure 5 (Zweig et al. 1976). It is the choice of the parameters Z_v, Z_t, and Y_p, especially the manner in which they change with the distance x, that determines how well the model of Figure 5 describes the mechanics of the cochlea. The results of various transmission line models will be discussed below, but first, a summarization of the assumptions inherent in the model is given.

5. Summary

The assumptions made in the derivation of the transmission line analogy are summarized as follows:

1. Gravitational forces are neglected.

2. Forces due to convection of fluid are neglected. This is true if the fluid velocity is small and changes slowly with respect to x, y, and z (Bird et al. 1960).

3. In each scala, the cross sectional area S changes much more slowly with x than does the average pressure p. Hence,

$$\frac{1}{S} \frac{\partial S}{\partial x} \;\; << \;\; \frac{1}{p} \frac{\partial p}{\partial x}$$

4. The viscous force in the fluids are

    a. neglected $(R_v = R_t = 0)$, or
    b. assumed proportional to the volume rate of flow of fluid; the ratio of proportion is R_v or R_t.

$$Q_v(x) \xrightarrow{\hspace{1cm}}$$

Impedance
$Z_v \Delta x$

$$Q_v(x+\Delta x) \xrightarrow{\hspace{1cm}}$$

Admittance
$Y_p \Delta x$

$P_v(x) - P_t(x)$

$P_v(x+\Delta x) - P_t(x+\Delta x)$

Impedance
$Z_t \Delta x$

$$Q_t(x) \xrightarrow{\hspace{1cm}}$$

$$Q_t(x+\Delta x) \xrightarrow{\hspace{1cm}}$$
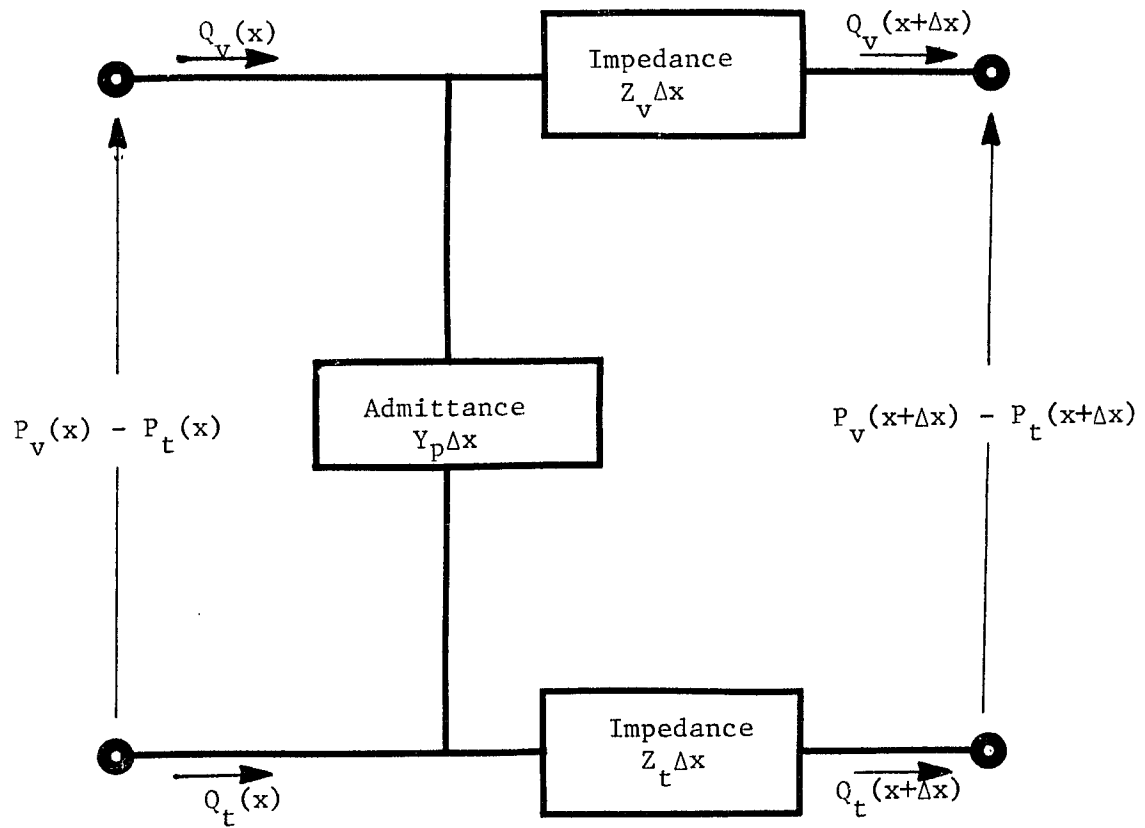
Figure 5. Basic transmission line analog for a segment of the cochlea of
length Δx.

5. The cochlear fluid is homogeneous and incompressible ($D\rho/Dt = 0$ in the notation of Bird et al. 1960, p. 73).

6. The pressure difference across the partition at x is approximated by the difference between average pressures p_v and p_t.

With few exceptions, each of the model studies reported here utilizes all six basic assumptions. In addition, the functions $Z_v(x)$, $Z_t(x)$, and $Y_p(x)$ must be specified and appropriate boundary conditions must be assumed. The results of some of the studies will now be reviewed.

C. Previous Studies

The transmission line model was first proposed in the late 1940's (Zwislocki 1948, 1953; Peterson and Bogert 1950; Ranke 1950). The model was developed to explain observations of traveling waves in the vibration pattern of the basilar membrane. However, in a transmission line, waves may travel in either direction, but waves in the cochlea were known to travel only from the stapes toward the helicotrema (von Bekesy 1960).

Ranke (1950) is credited with obtaining an analytical solution for the pressure difference across the cochlear partition. His solution represents a wave which travels only in one direction, toward the helicotrema. Ranke's contribution to the transmission line model is the statement of conditions on $Y_p(x)$, $Z_v(x)$, and $Z_t(x)$ such that reflections of the traveling wave are suppressed. According to Ranke, a condition sufficient for suppressing wave travel toward the stapes is the following: The product of the admittance per unit length, $Y_p(x)$, and the impedance per unit length, $Z_v(x) + Z_t(x)$, remains approximately constant over a given range of x. The details of the proof are available in the literature (Zweig et al. 1976; Mathews and Walker 1964, Chapter 1).

If the vibration of the stapes produces a sinusoidal pressure wave, the vibration of the basilar membrane depends upon the frequency (von Bekesy 1960). The amplitude of vibration of the basilar membrane increases steadily with increasing distance from the stapes until a resonant place is reached where the amplitude is maximum. Beyond the resonant location, the vibration is highly damped. The point of resonance is close to the stapes for high frequencies, close to the helicotrema for low frequencies. This relationship between place and frequency is caused primarily by an increase in width of the basilar membrane from stapes to helicotrema (von Bekesy 1960, p. 473). The range of resonant frequencies on the basilar membrane covers the entire audio range.

Peterson and Bogert (1950) were among the first to model the frequency selectivity of the cochlea. They characterized the acoustic admittance per unit length as the series combination of three terms. Hence,

$$Y_p^{-1}(x) = (j\omega m(x) + r(x) + \kappa(x)/j\omega) / b \qquad (2.15)$$

where m, r, and κ are respectively the mass, damping, and stiffness per unit surface area of the partition. By assuming κ changes with x in a manner similar to the changes of stiffness of the basilar membrane (von Bekesy 1960, pp. 466-469), they were able to obtain a frequency selectivity in their model qualitatively (but not quantitatively) similar to that observed on the basilar membrane.

Many attempts have been made to obtain quantitative agreement between frequency selectivities of the model and the basilar membrane. Bogert (1951) included the damping term $r(x)$ which Peterson and Bogert (1950) neglected. Fletcher (1951) and Zwislocki (1948) tried different

stiffness functions $\kappa(x)$. Zwislocki (1965) included resistances in the series branches of the model to represent viscous damping in the fluids.

Not long after quantitative agreement was obtained by Zwislocki (1965), new observations of basilar membrane motion were obtained. These observations, obtained with the Mössbauer technique (Johnstone and Taylor 1970; Rhode 1971), indicated that the agreement was not as good as previously thought. The vibration of a point on the basilar membrane exhibited a higher resonance when measured with the Mössbauer technique than when observed visually. However, more recent observations of membrane velocity, obtained with a capacitance probe, have shown a more broadly-tuned response than that obtained with the Mössbauer technique (Wilson and Johnstone 1973, 1975).

All of the above models are linear. In other words, each section of the transmission line analog shown in Figure 5 consists of elements which are independent of pressure and velocity. Some data, however, indicates that the amplitude of vibration of the basilar membrane might not be a linear function of stapes vibration amplitude (von Bekesy 1960, p. 464; Rhode 1971; Rhode and Robles 1974). Geisler (1976) reports that similar nonlinear results may be obtained in the transmission line model by including a nonlinear partition resistance, r(x) in equation 2.15.

The combination tones discussed in Chapter I are generated as the consequence of some nonlinearity. Considerable evidence supports the hypothesis that this nonlinearity is mechanical in nature, and that the resulting combination tone (CT) components are detected in auditory nerve fibers just as if the CTs were introduced as an acoustical stimulus

(Goldstein 1967, 1970; Rose 1970; Smoorenburg 1974; Abbas and Sachs 1976; Abbas 1978; Buunen and Rhode 1978; Goldstein et al. 1978; Zurek and Sachs 1979). Since 95% of all afferent cochlear nerve fibers each inner-vate a single receptor cell along the cochlear partition, it is assumed that each nerve fiber is stimulated in some way by the motion of the partition at the site innervated by the fiber (Spoendlin 1970, 1975). Therefore, the above hypothesis states that if a nerve fiber responds to a CT, the partition vibrates at the frequency of the CT at the point innervated by the fiber.

As mentioned in Chapter I, combination tones have been observed at frequencies $f_1 - n(f_2 - f_1)$, where f_1 and f_2 are the frequencies of a two-sinusoid acoustical stimulus. The CT corresponding to $n=1$ is the loudest. The amplitudes of the others decrease with increasing n and with increas-ing frequency difference $f_2 - f_1$ (Goldstein 1967, 1970).

Hall (1974) recognized that the loudest CT, at $2f_1 - f_2$, would be generated if a cubic nonlinearity were present in the auditory system.[1] He introduced a cubic nonlinearity into the transmission line model of Figure 5 by assuming the resistive component of the partition impedance ($r(x)$ in equation 2.15) has a component proportional to the partition velocity squared. In other words, the pressure difference across the partition was assumed to include a component proportional to the parti-tion velocity raised to the third power.

---

[1]If a function consisting of two sinusoids of frequencies f_1 and f_2 is raised to the third power, the result consists of sinusoids of fre-quencies $3f_2$, $3f_1$, $f_2 + (f_2 - f_1)$, f_2, f_1, and $f_1 - (f_2 - f_1)$.

Hall observed that if the pressure difference at the stapes consists of two sinusoids ($f_2>f_1$), the traveling wave propagates along the partition away from the stapes. As predicted by linear models, there are two locations where the displacement of the partition has a local maximum, corresponding to the two frequencies f_2 and f_1.

At the point of resonance closest to the stapes, the f_2 place, the displacement of the partition consists of both frequencies. The amplitude of the f_1 component depends upon the difference f_2-f_1. Hall observed that, due to the cubic nonlinearity, the displacement also has components at frequencies $f_2+(f_2-f_1)$ and $f_1-(f_2-f_1)$. (Presumably the lowpass characteristics of the partition at the f_2 place attenuate the $3f_1$ and $3f_2$ components to a negligible level.) The amplitudes of the distortion components depend upon the amplitudes and the frequency separation of the two-frequency stimulus (Hall 1974).

Additionally, Hall found that the component at frequency $f_2+(f_2-f_1)$, although larger in frequency than the resonant frequency, has its largest amplitude at or near the f_2 place. The component at frequency $f_1-(f_2-f_1)$, on the other hand, being lower in frequency than f_2, is propagated along the partition as a traveling wave until it reaches the location tuned to its frequency.

Thus, Hall showed that with a cubic nonlinearity a significant CT of frequency $f_1-(f_2-f_1)$ is produced, but the CT of frequency $f_2+(f_2-f_1)$ is not significant. Although Hall did not report the existence of components at $f_1-n(f_2-f_1)$ for n other than one, one can presume that the $f_1-(f_2-f_1)$ component interacts with the f_1 component at the f_1 place,

producing components at $f_1-2(f_2-f_1)$ and $f_1+(f_2-f_1) = f_2$. The latter is damped out, and the former is propagated to its point of resonance. In a similar manner, all components at frequencies $f_1-n(f_2-f_1)$ are generated.

The psychophysical observations of CTs (Goldstein 1967; Smoorenburg 1974; Zurek and Sachs 1979) and the observations of cochlear nerve fiber responses to CTs (Goldstein and Kiang 1968; Rose et al. 1969; Goldstein 1970) are all explained, qualitatively at least, by Hall's nonlinear resistance model. However, no basilar membrane vibrations have been observed at the frequencies associated with CTs (Wilson and Johnstone 1973; Rhode 1977a). This failure to observe CTs is, however, insufficient evidence to discount their presence (Rhode 1977b; Greenwood 1977).

The studies reviewed in this chapter have been concerned with three characteristics of basilar membrane vibration. First, waves travel only in one direction in the cochlea. Second, each site along the basilar membrane has a unique frequency of resonance. Third, the existence of combination tones indicates nonlinear cochlear mechanics.

For each of the three characteristics, sufficient, but not necessary, conditions have been specified to ensure the same characteristics in the transmission line model. First, the electrical parameters Y_p, Z_v, and Z_t "change slowly" along the length of the line. These parameters are analogous to physical properties of the cochlea which do "change slowly" with distance. Second, the capacitive component of Y_p increases monotonically from base to apex. The capacitance is analogous to the compliance (the reciprocal of the stiffness) of the basilar membrane, which exhibits a similar increase. Third, the resistive component of Y_p is nonlinear.

The resistance is analogous to damping, but there is no evidence of non-linear damping in the cochlea. The resistance is merely a "fudge factor," adjusted to obtain better agreement between characteristics of the cochlea and the transmission line model.

III. METHODS

The cochlea has been modeled by an electrical transmission line, as described in Chapter II. The element of the model shown in Figure 5 consists of two parts. One part, the admittance $Y_p \Delta x$, describes the response of the cochlear partition to a pressure difference across it. The other part, consisting of impedances $Z_v \Delta x$ and $Z_t \Delta x$, describes the motion of fluid within the two fluid-filled compartments.

In the next two chapters, the two components are considered in detail. First, the equations of motion of fluids, which include convective and viscous effects, are shown to be linear under normal operation. Next, the equation of motion of the cochlear partition is shown to be nonlinear.

Existing nonlinear models of cochlear mechanics assume nonlinear damping within the cochlear partition. This dissertation attempts to prove this assumption invalid. Any damping within the partition is negligible compared to viscous damping of the cochlear fluids. The latter is represented by linear terms in the equations of motion.

Existing nonlinear models assume partition damping is the only significant nonlinearity within the cochlea. However, the results of the next two chapters show that the compliance of the partition represents the only significant nonlinearity.

The nonlinear compliance is manifested by a cubic term in the equations of motion. Qualitative comparisons will be made between the "nonlinear compliance" model and Hall's (1974) model, which includes a cubic damping term.

Quantitative comparisons between the CT responses of the cochlea and models may lead to false conclusions. The only quantitative information about CTs in the auditory system comes from cancellation tone experiments (Goldstein 1967, 1970; Goldstein and Kiang 1968; Rose et al. 1969; Smoorenburg 1974; Zurek and Sachs 1979) and from cochlear microphonic measurements (Dallos 1970, 1973).

In the cancellation tone experiments an additional sinusoidal component is introduced into the acoustical stimulus. Its frequency is adjusted to match that of the CT component. Its amplitude and relative phase are then adjusted to cancel the CT response. Since the additional stimulus, the cancellation tone, is subject to the same nonlinear process as the primary stimuli, cancellation tone experiments give no information about the nonlinear process.

Measurements of cochlear potentials, called cochlear microphonics, have shown significant CT components (Dallos 1970, 1973). Since the precise origin of these potentials is unknown, a quantitative comparison to any model is meaningless.

IV. MOTION OF THE COCHLEAR FLUIDS

A. Introduction

In the transmission line model of Chapter II, the volume velocity of the cochlear fluids is the ratio of the pressure gradient to the impedance per unit length. Peterson and Bogert (1950) assumed that the impedance is analogous to an electrical inductance. Similar assumptions have been made by Bogert (1951) and Fletcher (1951) and more recently by Hubbard and Geisler (1972) and Hall (1974). Zwislocki (1965) assumed the impedance includes a resistor in series with the inductor, the former representing viscous losses.

In this chapter it is shown that the simple series combination of an inductor and resistor is not an adequate model for the cochlear fluid. Viscous forces, while linear, cannot be represented by a single element. Convective forces are nonlinear but negligible under normal conditions. Gravitational forces are neglected.

B. Viscous Effects

The equation of motion in the x direction for a volume element of fluid is given in Chapter II, equation 2.1, as

$$\rho \frac{\partial v_x}{\partial t} = f_c + f_v - \frac{\partial p}{\partial x} \tag{4.1}$$

where f_c is the sum of the convective forces per unit volume and f_v is the sum of the forces per unit volume due to fluid viscosity. For a Newtonian fluid of constant viscosity μ, the viscous force per unit volume is given by (Bird et al. 1960, p. 84)

$$f_v = \mu \left(\frac{\partial^2 v_x}{\partial x^2} + \frac{\partial^2 v_x}{\partial y^2} + \frac{\partial^2 v_x}{\partial z^2} \right) \tag{4.2}$$

Averaging over the cross sectional area of the scala vestibuli gives

$$S_v^{-1} \int_{S_v} f_v \, dS = (\mu/S_v) \frac{\partial^2 q_v}{\partial x^2} + f_{wv} \tag{4.3}$$

where

$$f_{wv} = (\mu/S_v) \int_{S_v} \left(\frac{\partial^2 v_x}{\partial y^2} + \frac{\partial^2 v_x}{\partial z^2} \right) dS \tag{4.4}$$

Since the integral in equation 4.4 is over the area S_v, it is evaluated at the perimeter. Equivalently, f_{wv} is the shear stress at the wall (hence the subscript w), integrated around the perimeter L_v, then divided by the area S_v. The shear stress at the wall, in turn, is the viscosity μ multiplied by the velocity gradient perpendicular to the wall (Bird et al. 1960, Chapter 1). Hence,

$$f_{wv} = -(\mu/S_v) \int_{L_v} \frac{\partial v_x}{\partial n} \bigg|_{L_v} dL \tag{4.5}$$

where $(\partial v_x/\partial n)\big|_{L_v}$ is the longitudinal velocity v_x evaluated an infinitesimal distance Δn away from the wall of the scala vestibuli, divided by Δn.

Because equation 4.5 involves differentiation and integration in directions perpendicular to x, it is difficult to include the wall drag force per unit volume in the one-dimensional transmission line model of Chapter II. To eliminate this difficulty, f_{wv} is generally assumed proportional to the volume rate of flow (Zwislocki 1965; Dallos 1973, p. 142). Hence,

$$f_{wv} = -R_v q_v \tag{4.6}$$

The proportionality constant R_v depends upon the cross sectional area, and is therefore a function of x.

Neglecting convection, equations 4.1, 4.3, and 4.6 may be combined to give the one-dimensional equation of fluid motion with damping,

$$\frac{\partial p_v}{\partial x} = - (\rho/S_v) \frac{\partial q_v}{\partial t} - R_v q_v + (\mu/S_v) \frac{\partial^2 q_v}{\partial x^2} \qquad (4.7)$$

A similar expression for the scala tympani is given by

$$\frac{\partial p_t}{\partial x} = - (\rho/S_t) \frac{\partial q_t}{\partial t} - R_t q_t + (\mu/S_t) \frac{\partial^2 q_t}{\partial x^2} \qquad (4.8)$$

These equations, along with equation 2.14 of Chapter II, define the transmission line element shown in Figure 6. As shown in the figure, the last terms of 4.7 and 4.8, representing viscous losses within the cochlear fluids, are equivalent to the shunt conductances $S_v \Delta x/\mu$ and $S_t \Delta x/\mu$, respectively. The drag forces at the walls are modeled by the longitudinal resistances $R_v \Delta x$ and $R_t \Delta x$.

In the above discussion, viscous forces are assumed only in the x direction. This assumption is valid throughout the fluid-filled compartments where the instantaneous velocity is primarily in the x direction. In a small layer close to the cochlear partition, however, transverse motion of the fluids become significant. Since this boundary layer is small compared to the entire scala, viscous losses in the boundary layer are neglected.

C.   Convection

The convective terms in equation 4.1 are given by (Bird et al. 1960, p. 84)
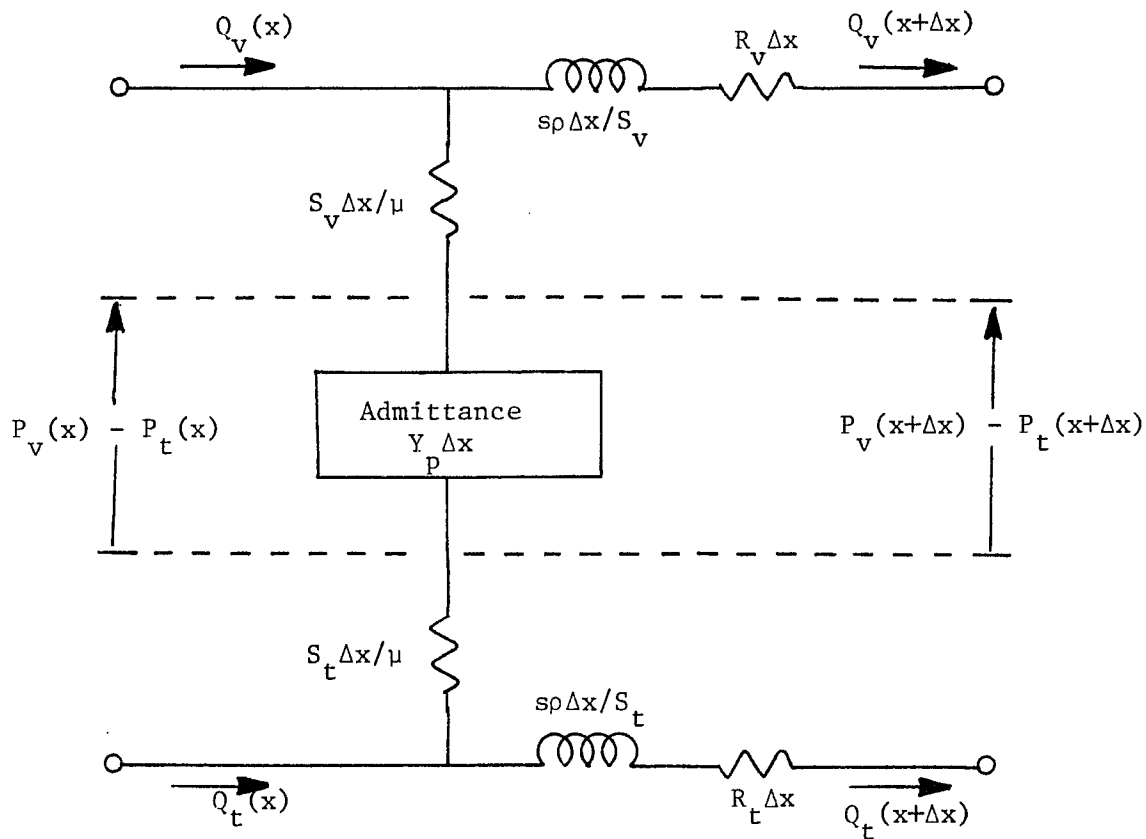
Figure 6. Transmission line analog for a segment of the cochlea of length
Δx. [Fluid inertia is modeled by the inductors. The series
resistances represent viscous losses along the walls of the
cochlear duct, while the shunt conductances represent losses
within the fluid compartments.]

$$f_c = -\rho \left(v_x \frac{\partial v_x}{\partial x} + v_y \frac{\partial v_x}{\partial y} + v_z \frac{\partial v_x}{\partial z} \right) \tag{4.9}$$

These components have heretofore been neglected, based on the assumption that fluid velocity is small.

In cases where the fluid velocity components are not small, the nonlinear convective terms cannot be ignored. If the acoustical stimulus consists of two sinusoids of frequencies f_1 and f_2, a "difference tone" corresponding to the frequency $f_2 - f_1$ is observed if the amplitude of the stimulus is large (Goldstein 1967; Dallos 1970). Perhaps it is the second-order convection terms which are responsible for this phenomenon.[1] At normal sound levels, however, the velocity components are small enough that the convective force is negligible compared to the inertial force $\rho(\partial v_x/\partial t)$ in equation 4.1.

---

[1]When a function consisting of two sinusoids of frequencies f_1 and f_2 is multiplied by another function consisting of two sinusoids of the same two frequencies, the resulting function is a sum of sinusoids with frequencies $2f_2$, $f_2 + f_1$, $2f_1$, and $f_2 - f_1$.

V. MOTION OF THE COCHLEAR PARTITION

A. Introduction

The velocity of the cochlear partition at x is assumed to be the product of the pressure difference across the partition times the partition admittance at that location. This assumption implies that adjacent regions of the partition are not mechanically coupled together. Models which couple adjacent sections do not exhibit the high frequency selectivity of the basilar membrane (Zweig et al. 1976).

Peterson and Bogert (1950) were among the first to model the partition admittance in terms of an electrical analog. They assumed the series combination of an inductor and capacitor adequately models the inertia and compliance of the partition over a given region.

To include damping, Bogert (1951) introduced a resistive element in series with the inductor and capacitor. While no direct physical correlate of the damping element has been shown, it has been used to "tune" the characteristics of the model to fit the behavior of the cochlea (Zwislocki 1965).

Combination tones have been introduced into the model by using a nonlinear resistive element (Hubbard and Geisler 1972; Hall 1974). Hall showed that with a cubic nonlinearity the combination tone response is similar to that of the cochlea.

In this chapter the equation of motion of the cochlear partition is given. Each term of the equation has a direct physical analog. The physical model also has an electrical analog, but the capacitive element, not the resistive element, is nonlinear.

First, the cochlear partition is modeled as a thin elastic plate. Mechanical coupling among adjacent sections is assumed negligible. In other words, the elastic plate is assumed to act as a series of beams of width Δx stretched across the cochlea. The length of a beam at x is the width $b(x)$ of the cochlear partition at that site. The thickness $\tau(x)$ of the cochlear partition is taken as the thickness of the beam.

It is shown that for small deflections the pressure difference across the partition produces a proportional volume displacement of the partition. For larger deflections, however, the pressure is approximately proportional to $Y+kY^3$, where Y is the volume displacement, and k is a constant.

In a later section, the cochlear partition is modeled as an elastic membrane. This model is obtained from the elastic plate model by setting the flexural rigidity of the plate equal to zero. Since mechanical coupling from adjacent sections is assumed negligible, the membrane is analogous to a set of strings stretched across the cochlea. The strings are spaced Δx apart and have lengths equal to $b(x)$. With the membrane model the pressure is proportional to $Y+kY^3$. The cubic term becomes especially prominent if the lateral tension in the membrane is small.

B. Elastic Plate Model

Forces on an elastic plate having the same configuration as the cochlear partition shown in Figure 4 are considered. Mechanical coupling between regions of width Δx is assumed negligible. The plate is therefore analogous to a series of beams of length $b(x)$, width Δx, and thickness $\tau(x)$, stretched across the cochlea.

Consider a static pressure p(x) applied to one side of the plate causing a displacement of the plate in the positive y direction. If the edges of the plate (the ends of the beams) are simply supported, and if the maximum displacement of the plate is small compared to the thickness τ, the displacement at any point (x,z) is given by (Timoshenko 1958a, p. 141; 1958b, pp. 76-77)

$$y(x,z) = p \ (b^3 z - 2bz^3 + z^4) \ / \ 24 \ D \tag{5.1}$$

where

$$D = E\tau^3 \ / \ 12(1 - \nu^2) \tag{5.2}$$

is the flexural rigidity of the plate, E is Young's modulus of elasticity, and ν is Poisson's ratio.

The volume displacement is found by integrating 5.1 over the length of the beam and multiplying by the width Δx. Hence,

$$\Delta Y(x) = (\textstyle\int_0^b y(x,z) \ dz \ ) \ \Delta x \tag{5.3}$$

For the plate of equation 5.1

$$\Delta Y(x) = p(x) \ b^5(x) \ \Delta x \ / \ 120 \ D \tag{5.4}$$

Equation 5.4 describes the response of the plate to a static pressure difference. In the dynamic situation, p is a function both of x and t. From Newtons's second law, the inertial force must also be included in the equation of motion, giving

$$p(x,t) = (\rho_p/\Delta x) \ \frac{\partial^2}{\partial t^2}(\Delta Y) + (120 \ D \ / \ b^5 \ \Delta x) \ \Delta Y \tag{5.5}$$

where ρ_p is the mass per unit volume of the plate.

1. Stretching of the elastic plate

If the displacement y(x,z) of the plate is not small compared to the thickness τ, internal tensile stresses must be considered. In each beam

these stresses act to restore the beam toward its rest position, much like tension on a string tends to keep the string straight. At any cross section of a beam, the tensile stress is equivalent to a force ΔF distributed over the cross sectional area $\tau \Delta x$.

The displacement of the plate due to a static pressure difference $p(x)$ is now given by (Timoshenko 1958b, p. 42)

$$y(x,z) = \frac{p}{fa^2} \left(\frac{\cosh a(b/2 - z)}{\cosh ab/2} - 1 \right) + \frac{p}{2f} (b - z) z \qquad (5.6)$$

where $a^2 = f/D$, and $f = \Delta F/\Delta x$ is the tensile force per unit length.

Since the edges of the plate ($z=0$ and $z=b(x)$) are immobile, the plate bulges as the pressure increases. Let $s(x)$ represent the length following the path $y(x,z)$ from $z=0$ to $z=b$. For small slopes $\partial y/\partial z$, the length $s(x)$ is given by (Timoshenko 1958a, p. 178)

$$s(x) = b + \tfrac{1}{2} \int_0^b \left(\frac{\partial y}{\partial z} \right)^2 dz \qquad (5.7)$$

Substitution of 5.6 into 5.7 gives an expression in terms of the pressure and tensile force for the length s, given by

$$s = b + (p^2 b^7 / 256 D^2) A(\lambda) \qquad (5.8)$$

where

$$A(\lambda) = (2\lambda^3/3 + 5 \tanh \lambda - 4 \lambda - \lambda \operatorname{sech}^2 \lambda) / \lambda^7 \qquad (5.9)$$

In equations 5.8 and 5.9, the tensile force per unit length f is replaced by the dimensionless quantity λ^2, where

$$\lambda^2 = b^2 f / 4 D \qquad (5.10)$$

2. Hooke's law

The length $s(x)$ is equal to the width $b(x)$ of the plate if the pressure is zero. As the pressure difference increases, either positive

or negative, the plate bulges according to equations 5.7 through 5.10. Since the bulge increases the length s(x), a corresponding increase in the lateral tension must occur. The tensile force per unit length f is related to the elongation by Hooke's generalized law of elasticity (Young 1972, p. 127).

Assume for the moment that f=0 when p=0. From Hooke's law the stress is given by (Timoshenko 1958b, p. 77)

$$f/\tau \;=\; E\,(s - b)\,/\,b\,(1 - \nu^2)$$

where (s-b)/b is the lateral elongation of the plate.

For completeness, the case f>0 when p=0 is also considered. This is the case when the elastic plate is stretched from some resting width b' to the actual width b>b'. According to Hooke's law, the tensile stress is now given by

$$f/\tau \;=\; E\,(s - b')\,/\,b'\,(1 - \nu^2) \tag{5.11}$$

Let f_0 denote the value of f when p=0. Setting s=b and solving equation 5.11 for b' gives

$$b' \;=\; b\,/\,(1 + f_0(1 - \nu^2)/\tau E) \tag{5.12}$$

Substituting equation 5.12 into 5.11 and solving for the length s gives

$$s \;=\; b\,(E\tau + f(1-\nu^2))\,/\,(E\tau + f_0(1-\nu^2)) \tag{5.13}$$

3. Relationship between pressure and tensile stress

Equating 5.13 and 5.8 gives a relationship between pressure and tensile force per unit length. Representing the latter by the dimensionless quantity λ^2 defined in equation 5.10 and the former by the dimensionless pressure, defined by

$$\Pi = (3 b^8 / 256 D^2 \tau^2)^{\frac{1}{2}} p \qquad (5.14)$$

gives

$$\Pi^2 = (\lambda^2 - \lambda_0^2) / A(\lambda) (1 + \lambda_0^2 \tau^2 / 3 b^2) \qquad (5.15)$$

where $\lambda_0^2 = \lambda(f_0) = b^2 f_0 / 4D$.

The effect of nonzero resting tension ($\lambda_0^2 > 0$) depends upon the ratio of thickness τ to width b, as shown in equation 5.15. The curves in Figure 7 are based on the assumption that $\lambda_0 \tau / b$ is small compared to unity.

4. Volume displacement per unit length

The volume displacement per unit length $\partial Y / \partial x$ of the elastic plate is obtained by dividing equation 5.3 by Δx and taking the limit as Δx approaches zero. Using equation 5.6 for $y(x,z)$ gives

$$\frac{\partial Y}{\partial x} = (4b^2 \tau^2 / 675)^{\frac{1}{2}} (3b^8 / 256 D^2 \tau^2)^{\frac{1}{2}} p \, \Gamma(\lambda) \qquad (5.16)$$

where

$$\Gamma(\lambda) = 7.5 (\tanh \lambda - \lambda + \lambda^3 / 3) / \lambda^5 \qquad (5.17)$$

It is convenient to define a dimensionless volume displacement per unit length as

$$\psi = \Gamma(\lambda) \, \Pi(\lambda, \lambda_0) = (675 / 4b^2 \tau^2)^{\frac{1}{2}} \frac{\partial Y}{\partial x} \qquad (5.18)$$

Since acoustical compliance is defined as the ratio of volume displacement to pressure, the function $\Gamma(\lambda)$ is called the "dimensionless compliance per unit length" of the cochlear partition. It is plotted in Figure 8. Elimination of λ from Figures 7 and 8 results in the plot of Figure 9 of volume displacement per unit length versus pressure.

DIMENSIONLESS
TENSILE FORCE
PER UNIT LENGTH λ^2

$\lambda_0^2 = 2$

DIMENSIONLESS PRESSURE Π
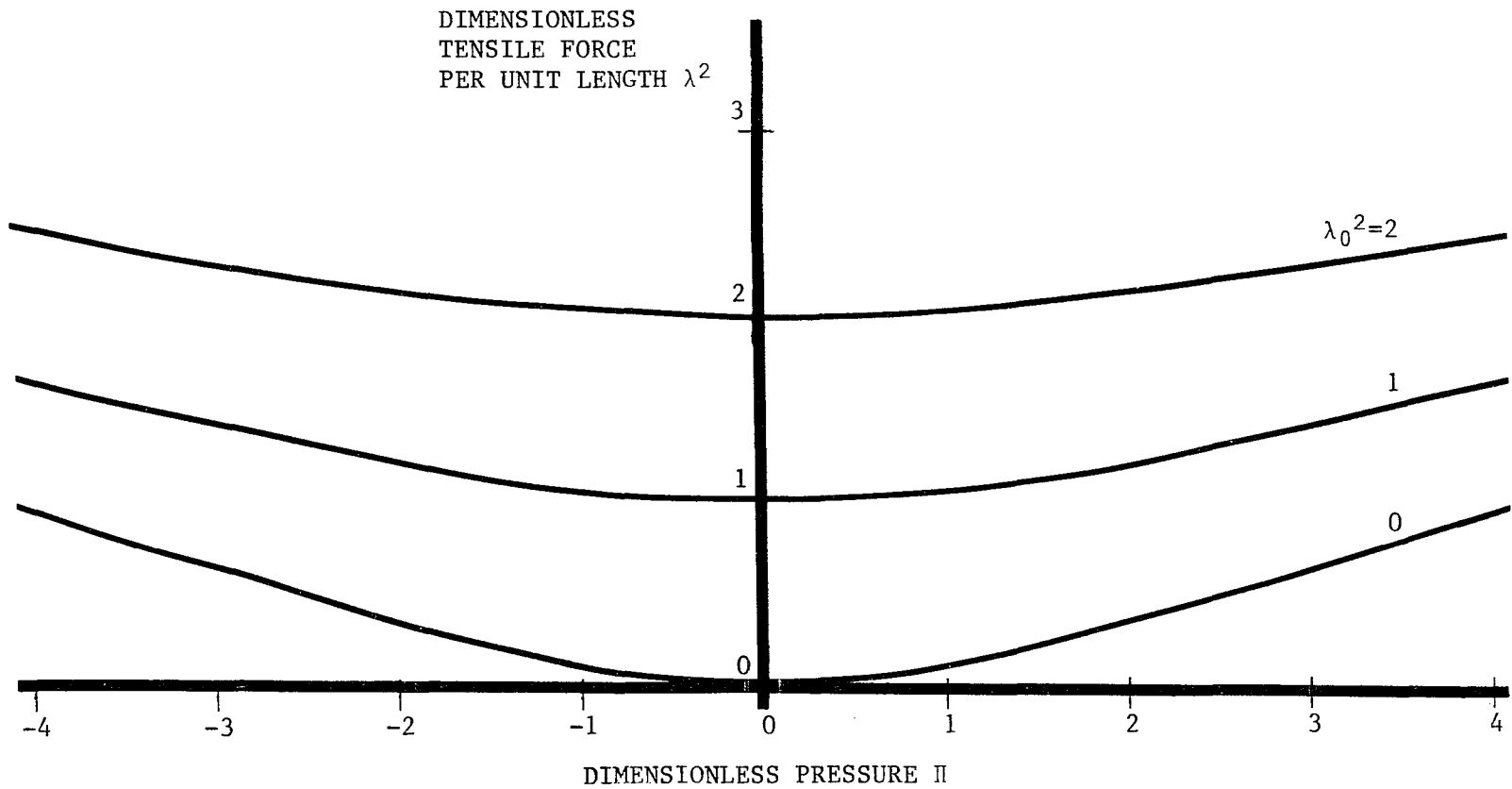
Figure 7. Relationship between dimensionless pressure Π and dimensionless tensile force per unit length λ^2 in an elastic plate.
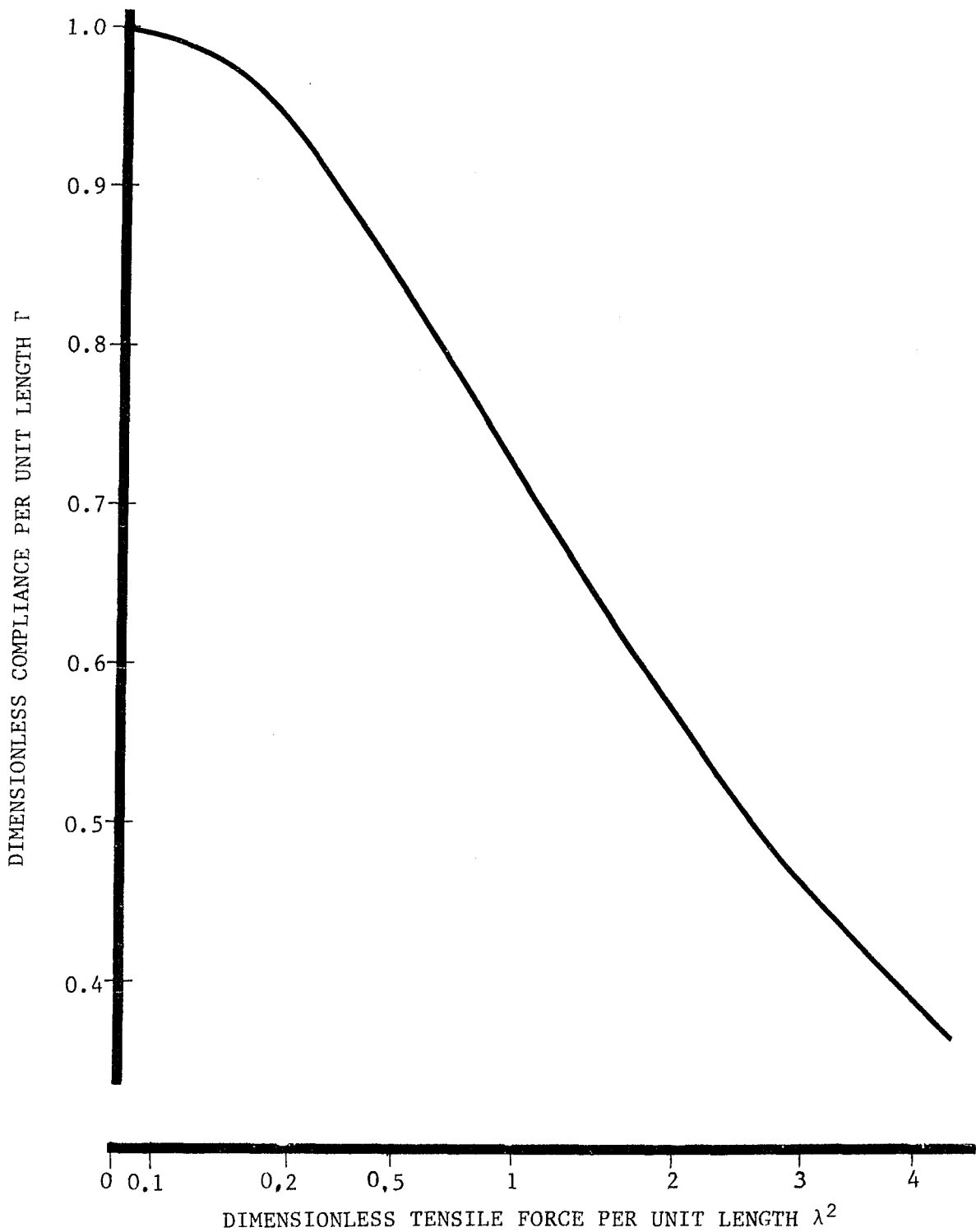
Figure 8. Relationship between dimensionless compliance per unit length Γ
and tensile force per unit length λ^2 in an elastic plate. [The
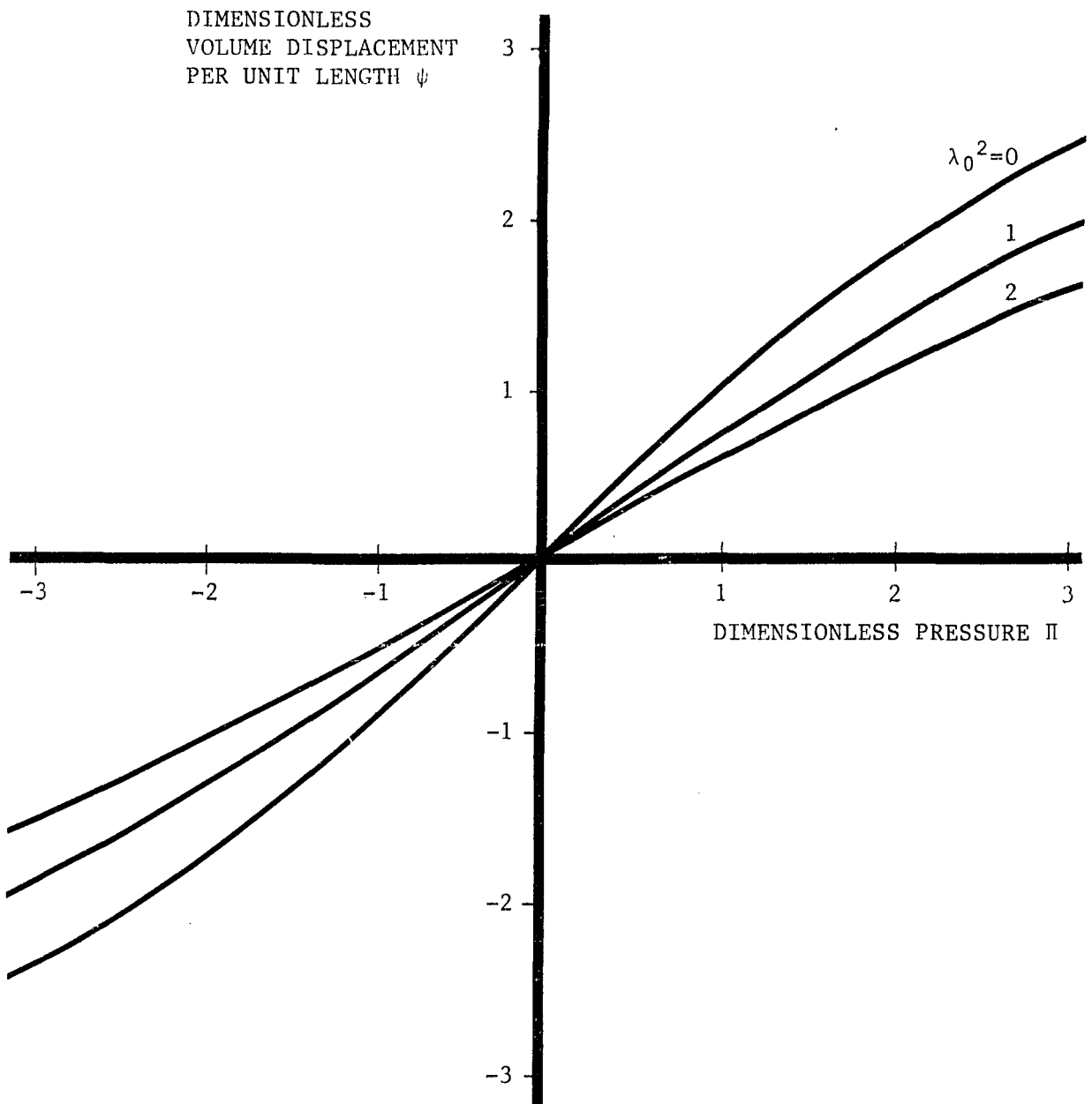abscissa is linear in λ, rather than λ^2.]

Figure 9. Relationship between dimensionless volume displacement per unit length ψ and dimensionless pressure Π for an elastic plate.

5. Maclaurin series expansion for pressure

Equation 5.18 relates the static volume displacement per unit length ψ to a static pressure difference Π. When writing the equation of motion, it is convenient to express the pressure in terms of the volume displacement as

$$\Pi = \Gamma^{-1} \psi \tag{5.19}$$

The Maclaurin series expansion of $\Pi(\psi)$ is

$$\Pi(\psi) = \Pi(0) + \psi \frac{d\Pi}{d\psi}(0) + \frac{\psi^2}{2!} \frac{d^2\Pi}{d\psi^2}(0) + \frac{\psi^3}{3!} \frac{d^3\Pi}{d\psi^3}(0) + \ldots \tag{5.20}$$

From equations 5.15 through 5.18, Π is an odd function of ψ. In other words $\Pi(-\psi) = -\Pi(\psi)$. Therefore, in equation 5.20 the coefficients of even-order terms in ψ must all be zero. Hence,

$$\Pi(\psi) = \psi \frac{d\Pi}{d\psi}(0) + \frac{\psi^3}{3!} \frac{d^3\Pi}{d\psi^3}(0) + \frac{\psi^5}{5!} \frac{d^5\Pi}{d\psi^5}(0) + \ldots \tag{5.21}$$

The first coefficient, found by differentiating equation 5.19, is given by

$$\frac{d\Pi}{d\psi} = \left(\Gamma + \Pi \frac{d\Gamma}{d\Pi} \right)^{-1} \tag{5.22}$$

Since $\lambda = \lambda_0$ and $\Pi = 0$ when $\psi = 0$, $\frac{d\Pi}{d\psi}(0) = \Gamma^{-1}(\lambda_0)$. This coefficient, equal to the reciprocal of the compliance at rest, is denoted by k_0.

Successive differentiations of equation 5.22 give

$$\frac{d^2\Pi}{d\psi^2} = - \left(\frac{d\Pi}{d\psi} \right)^3 \left(\Pi \frac{d^2\Gamma}{d\Pi^2} + 2 \frac{d\Gamma}{d\Pi} \right) \tag{5.23}$$

and

$$\frac{d^3\Pi}{d\psi^3} = - \left(\frac{d\Pi}{d\psi} \right)^4 \left(3 \frac{d^2\Gamma}{d\Pi^2} + \Pi \frac{d^3\Gamma}{d\Pi^3} \right) - 3 \frac{d^2\Pi}{d\psi^2} \left(\frac{d\Pi}{d\psi} \right)^2 \left(\Pi \frac{d^2\Gamma}{d\Pi^2} + 2 \frac{d\Gamma}{d\Pi} \right) \tag{5.24}$$

From equations 5.15 and 5.17, $d\Gamma/d\Pi$ is zero when $\psi=0$. Since $\Pi(0)$ is also zero, the second derivative $d^2\Pi/d\psi^2$ is zero at $\psi=0$. This result is consistent with the discussion above that $\Pi(\psi)$ is an odd function.

For $\psi=0$ equation 5.24 reduces to

$$\frac{d^3\Pi}{d\psi^3} = -\left(\frac{d\Pi}{d\psi}\right)^4\left(3\frac{d^2\Gamma}{d\Pi^2}\right) = -3 k_0^4 \frac{d^2\Gamma}{d\Pi^2} \tag{5.25}$$

The derivative $d^2\Gamma/d\Pi^2$ can be evaluated from equations 5.15 and 5.17 by elimination of λ. For λ_0 and ψ both equal to zero, the derivative is given by

$$\frac{d^2\Gamma}{d\Pi^2}(\lambda_0=0) = -(2/15)(17/21)^2 \tag{5.26}$$

Substituting 5.25 and 5.26 into 5.21 gives the following third order approximation if $\lambda_0=0$:

$$\Pi(\psi) \simeq \psi + ((17/21)^2/15)\,\psi^3 \tag{5.27}$$

The value of the constant k_0 is one in this case. If the resting tension is nonzero ($\lambda_0^2 > 0$), then

$$\Pi(\psi) \simeq \psi\,k_0 - \tfrac{1}{2}\,\psi^3\,k_0^4\,\frac{d^2\Gamma}{d\Pi^2}(\lambda_0) \tag{5.28}$$

6. Summary

The static pressure difference across an elastic plate is described as the sum of terms of volume displacement per unit length raised to odd integer powers. If the volume displacement is small, terms of fifth order and higher can be neglected, resulting in equation 5.28. If the pressure is a function of time, an inertial term is also included, giving

$$p(x,t) = \rho_p \frac{\partial^2}{\partial t^2}\left(\frac{\partial Y}{\partial x}\right) + \kappa_0 \frac{\partial Y}{\partial x} + \kappa_1\left(\frac{\partial Y}{\partial x}\right)^3 \tag{5.29}$$

where κ_0 and κ_1 are constants determined from equation 5.28.

C. Elastic Membrane Model

Forces on an elastic membrane having the same shape as the cochlear partition of Figure 4 are considered. As in the previous section, the membrane is sectioned into many strips of width Δx and length $b(x)$. Mechanical coupling between adjacent strips is assumed negligible.

The displacement $y(x,z)$ due to a pressure difference $p(x)$ is given by (Fung 1965, pp. 170-172)

$$\frac{\partial^2 y}{\partial t^2} = p/f \qquad (5.30)$$

where f is the tension ΔF in each strip, divided by the width Δx. Integrating 5.30 twice with respect to z while applying the boundary conditions $(\partial y/\partial z)=0$ at the middle $(z=b/2)$ and $y=0$ at the ends $(z=0$ and $z=b)$ gives the equation for static deflection of the membrane

$$y = (p/2f)\, z\, (b - z) \qquad (5.31)$$

It is noted that equation 5.31 can be obtained directly from 5.6, the displacement of an elastic plate, by setting the flexural rigidity D=0.

1. Stretching of the membrane

The displacement of the membrane is zero when the pressure difference is zero. But when the pressure is nonzero, the membrane bulges in a direction opposing the pressure difference, stretching the membrane. From equation 5.7 the length $s(x)$ following the path $y(x,z)$ from $z=0$ to $z=b$ is approximated by

$$s(x) = b\,(1 + p^2 b^2/24 f^2) \qquad (5.32)$$

2. Hooke's law

For most problems involving membranes it is convenient to assume that the tensile force is constant. However, if f is zero[1], equation 5.31 is indeterminate. Here the assumption is made that the membrane is elastic. In other words, if the membrane is stretched, a proportional increase in the restoring tension f is produced. From Hooke's law

$$f = e \, (s - b') \, / \, b' \qquad (5.33)$$

where e is a constant which depends upon the material and $b' \leqq b$ is the width that the membrane would have if released from its attachment at z=0 and z=b.

Let f_0 denote the value of f when p=0 (i.e. when s=b). In terms of the tension f, the length s is given by

$$s = b \, (e + f) \, / \, (e + f_0) \qquad (5.34)$$

3. Relationship between pressure and tension

If equations 5.32 and 5.34 are equated, a relationship is obtained between the tension f and the pressure p, given by

$$p^2 = 24 \, f^2 \, (f - f_0) \, / \, b^2 \, (e + f_0) \qquad (5.35)$$

As with the displacement $y(x,z)$, the expression 5.35 is also obtained from the corresponding expression for an elastic plate (equation 5.15) by setting the flexural rigidity equal to zero.

4. Volume displacement per unit length

From equations 5.3 and 5.31, the volume displacement per unit length of the membrane is given by

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[1] There is some evidence that there is no resting tension in the basilar membrane. (See von Bekesy 1960, pp. 472-473.)

$$\frac{\partial Y}{\partial x} = b^3 p / 12 f \qquad (5.36)$$

If the parameter f could be eliminated from equations 5.35 and 5.36 the volume displacement could be stated explicitly as a function of the pressure p. However, it is convenient to do the opposite. An explicit expression for pressure in terms of $\partial Y/\partial x$ is sought.

5. Membrane nonlinearity

Since the membrane equations are special cases of the equations for an elastic plate, an expression of the form of equation 5.28 is sought. The equation is of the form

$$p = k_0 \frac{\partial Y}{\partial x} + k_1 \left(\frac{\partial Y}{\partial x} \right)^3 \qquad (5.37)$$

where k_0 and k_1 are constants.

Substitution of 5.36 into 5.37 and division by p gives

$$1 = k_0 b^3 / 12f + k_1 (b^3/12f)^3 p^2$$

which, if solved for p^2, gives

$$p^2 = f^2 (f - k_0 b^3) / k_1 (b^3/12)^3 \qquad (5.38)$$

If

$$k_0 = f_0 / b^3$$

and if

$$k_1 = 72 (e + f_0) / b^7$$

then equation 5.38 is identical to equation 5.35.

6. Summary

The static pressure difference across a membrane is given by

$$p = (f_0/b^3) \frac{\partial Y}{\partial x} + (72(e+f_0)/b^7) \left(\frac{\partial Y}{\partial x} \right)^3 \qquad (5.39)$$

where $\partial Y/\partial x$ is the static volume displacement per unit length. Note that if the membrane tension f_0 is small the cubic term is not negligible even for small $\partial Y/\partial x$. If the pressure is a function of time, the inertial term is added to the right side of 5.39, giving

$$p(x,t) = \rho_p \frac{\partial^2}{\partial t^2}\left(\frac{\partial Y}{\partial x}\right) + \frac{f_0}{b^3}\frac{\partial Y}{\partial x} + \frac{72\,(e + f_0)}{b^7}\left(\frac{\partial Y}{\partial x}\right)^3 \qquad (5.40)$$

D. Discussion

In the last two sections, two different hypothetical models of the cochlear partition are described. For the first model the equation of motion is given by 5.29. Equation 5.40 is the corresponding equation for the membrane model. Each of these equations is analogous to an electrical impedance consisting of an inductance $\rho_p/\Delta x$ in series with a nonlinear capacitance.

Neither of these models includes a damping term because the partition is assumed elastic. If the partition is truly elastic, there is no loss of energy within it due to motion (Caro et al. 1978, Chapter 7). Even if there is internal damping, it is considered small compared to the viscous damping of the fluids. Therefore, the partition resistance is neglected.

It is not clear whether the cochlear partition is better modeled by an elastic plate or by an elastic membrane. Bekesy described the basilar membrane as an "unstressed, gelatinous, elastic plate" (von Bekesy 1960, p. 465). Also, since the cochlear partition includes the organ of Corti and its supporting structures in addition to the basilar membrane, the effective thickness of the partition is not negligible. This would seem to indicate that the plate is the better model. However, since the two

models are similar (compare equation 5.40 with equation 5.29), the question

of which is better is not important.

VI. RESULTS

The results of the study of motion of cochlear fluids (see Chapter IV) are depicted in Figure 6. Inductances $\rho\Delta x/S_v$ and $\rho\Delta x/S_t$ represent the inertia of the fluids. Viscous damping is represented by the resistances $R_v\Delta x$ and $R_t\Delta x$ and the shunt conductances $S_v\Delta x/\mu$ and $S_t\Delta x/\mu$. The resistances $R_v\Delta x$ and $R_t\Delta x$ depend upon the geometry of the scalae vestibuli and tympani, respectively.

The study of the cochlear partition (Chapter V) also results in an electrical model. A series combination of inductance $\rho_p/\Delta x$ and nonlinear capacitance $c\Delta x$, shown in Figure 10, is analogous to the inertia and compliance, respectively, of the partition if

$$c = \{ k_0 + k_1 (\frac{\partial Y}{\partial x})^2 \}^{-1} \qquad (6.1)$$

If the partition is an elastic membrane, then (from equation 5.40 of Chapter V)

$$k_0(x) = f_0 / b^3(x)$$

and

$$k_1(x) = 72 (e + f_0) / b^7(x)$$

where $b(x)$ is the width of the cochlear partition, f_0 is the tension of the cochlear partition when at rest, and e is the spring constant per unit length of membrane. Since f_0 is small, the nonlinear term predominates. If the partition is more rigid, as in the case of an elastic plate, the constants k_0 and k_1 have different values, but the form of equation 6.1 is the same.

The compliance per unit length c is the ratio of the volume displacement per unit length $\partial Y/\partial x$ to the pressure p. Combining equations 5.14
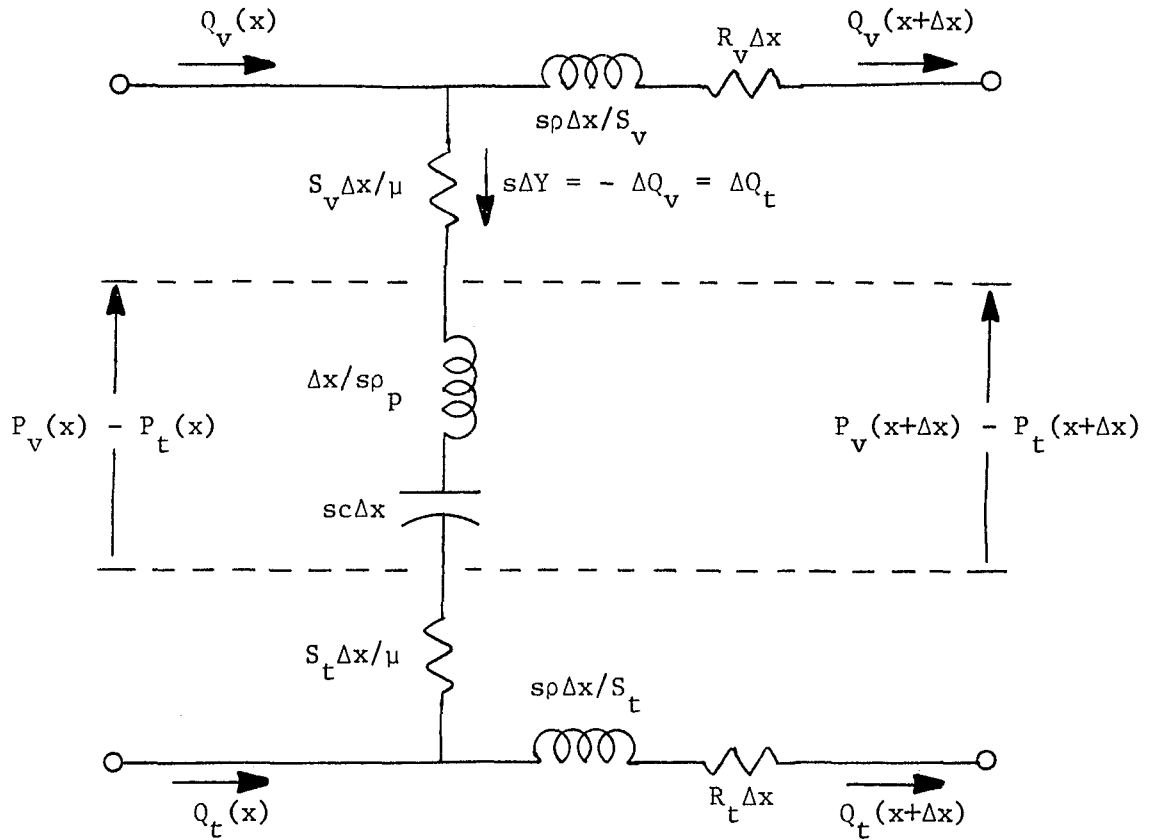
Figure 10. Detailed transmission line analog for a segment of the cochlea of length Δx. [The elements between the dotted lines represent the cochlear partition. The vestibular fluid is modeled by the elements above the upper dotted line. The elements below the lower dotted line model the tympanic fluid. Effects of fluid convection have been neglected.]

and 5.18 of Chapter V gives a relationship between c and its dimensionless equivalent Γ. This relationship, valid for thin, rigid plates, is given by

$$c = (b^5 / 120 D) \Gamma \qquad (6.2)$$

The dimensionless compliance per unit length Γ is plotted against the dimensionless volume displacement per unit length $\psi = (675/4b^2\tau^2)^{\frac{1}{2}} (\partial Y/\partial x)$ in Figure 11. Compliance is maximum when the resting tension $f_0 = \lambda_0^2 (4D/b^2)$ is zero. Compliance is reduced by increased displacements.

To summarize, the equations of motion in the cochlear model are

$$\frac{\partial p_v}{\partial x} = - (\rho/S_v) \frac{\partial q_v}{\partial t} - R_v q_v + (\mu/S_v) \frac{\partial^2 q_v}{\partial x^2} \qquad (6.3)$$

$$\frac{\partial p_t}{\partial x} = - (\rho/S_t) \frac{\partial q_t}{\partial t} - R_t q_t + (\mu/S_t) \frac{\partial^2 q_t}{\partial x^2} \qquad (6.4)$$

and

$$p_v - p_t = \rho_p \frac{\partial^2}{\partial t^2}(\frac{\partial Y}{\partial x}) + c^{-1} \frac{\partial Y}{\partial x} \qquad (6.5)$$

where

$$\frac{\partial}{\partial t}(\frac{\partial Y}{\partial x}) = - \frac{\partial q_v}{\partial x} = \frac{\partial q_t}{\partial x} \qquad (6.6)$$

These equations are also the circuit equations for a transmission line, one element of which is shown in Figure 10.

The dependent variables in the equations are pressures p_v and p_t, volume velocities q_v and q_t, and the volume displacement per unit length $\partial Y/\partial x$. The independent variables are time t and position x. Although the coefficients are functions of position x, equations 6.3 and 6.4 are linear differential equations. Equation 6.5 is nonlinear because the
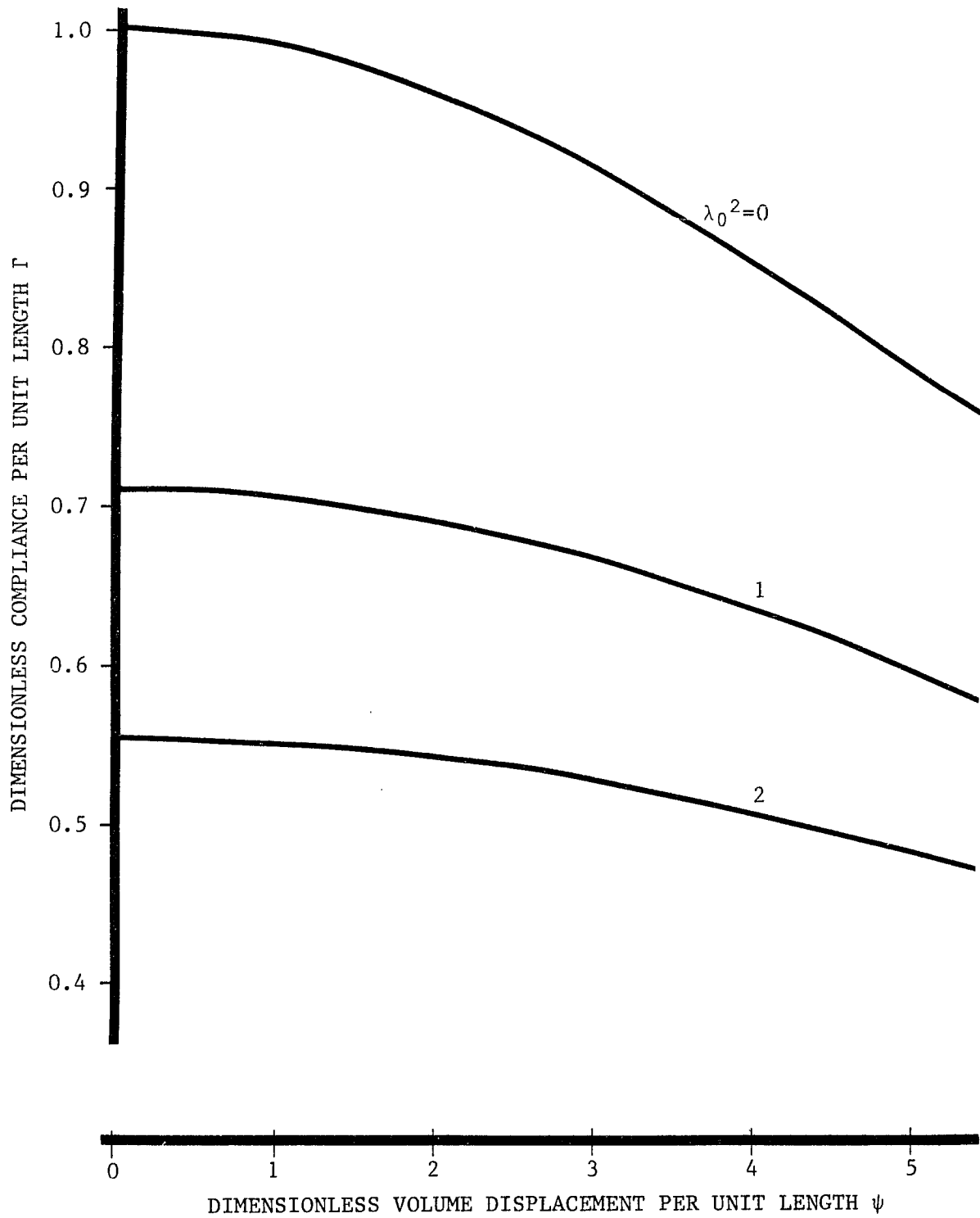
Figure 11. Relationship between dimensionless compliance per unit length
Γ and dimensionless volume displacement per unit length ψ of
an elastic plate.

compliance of the partition is a function of volume displacement (see

equation 6.1) as well as position x.

VII. CONCLUSIONS

Three major conclusions are drawn from this investigation of cochlear mechanics. First, the premise of nonlinear damping made by several previous investigators has no foundation in Newtonian mechanics. Second, contrary to previous assumptions, the compliance of the partition does not remain constant as the partition vibrates. Third, the nonlinearity of the nonconstant-compliance model is consistent with the combination tone response of the cochlea.

Damping in previous models of cochlear mechanics represents losses associated with movement of the cochlear partition (Hubbard and Geisler 1972; Hall 1974; Schroeder 1975). These losses may be within the partition or within the fluids of the scalae vestibuli and tympani. However, if the partition is elastic no energy is lost within it. A perfectly elastic material of course does not exist, but the cochlear partition is known to have elastic properties (von Bekesy 1960). Therefore, losses within the partition are small compared to viscous losses within the fluids. The viscous force on an element of an incompressible Newtonian fluid is proportional to the Laplacian of the velocity vector. Since the Laplacian is a linear operator, the viscous force is linear. Nonlinear damping is therefore inconsistent with Newtonian mechanics.

The primary physical justification for the frequency-vs-place principle of basilar membrane motion is the variation of partition compliance along the length of the cochlea (von Bekesy 1960, p. 473). The compliance at any location, however, has been assumed constant by all of the investigators whose models are reviewed in Chapter II. The results

of Chapter V show the compliance to be constant only if the partition is so rigid that its displacement is small compared to its thickness. Bekesy's observations, however, indicate that such rigidity is not present in the cochlea (von Bekesy 1960, pp. 464-476).

The compliance of an elastic partition depends upon displacement. As the partition bulges in response to a pressure differential, the tension within the partition increases. This increased tension causes the partition to become stiffer (less compliant) as it is stretched from its resting position. Therefore, compliance depends upon the instantaneous displacement of the partition.

The final conclusion is obtained by comparing the nonconstant-compliance model to previous nonlinear models of cochlear mechanics. The general form of the transmission line analog of the cochlea is shown in Figure 12. The shunt conductance $G\Delta x$ includes the combined effects of partition damping and viscous losses within the cochlear fluids. If the electrical inductances, capacitance, and resistances are constant, the model is linear. Wave motion in the cochlea and the frequency response characteristics of the basilar membrane have been matched by such linear models.

Odd-order distortion products, such as the $2f_1-f_2$ combination tone have been produced in the transmission line model by assuming a nonlinear shunt resistance of the form (Hall 1974; Schroeder 1975)

$$G^{-1}(x) = R_0(x) (1 + \alpha \{ \frac{\partial}{\partial t}(\frac{\partial Y}{\partial x}) \}^2) \tag{7.1}$$

where α is a constant. Equation 7.1 simply states that the resistance includes a constant term plus a term proportional to the square of the
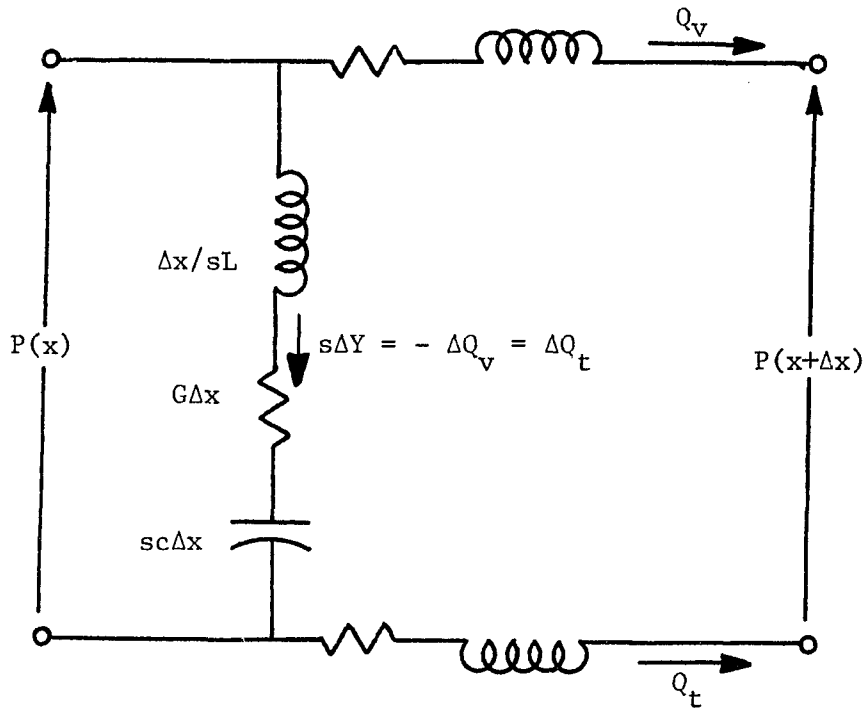
Figure 12. General form of the transmission line analog for a section of the cochlea of length Δx. [Series inductances are analogous to fluid inertia, series resistances to viscous drag along the cochlear walls, shunt inductance to partition inertia, and shunt capacitance to compliance of the partition. Shunt conductance includes the combined effects of partition damping and viscous losses within the cochlear fluids. Therefore, the pressure difference $P(x)$ does not represent the pressure difference across the partition.]

partition velocity. Such an assumption results in a cubic term in the expression for p(x) (see Figure 12), given by

$$p(x) = L(x) \frac{\partial^2}{\partial t^2}(\frac{\partial Y}{\partial x}) + R_0(x) \frac{\partial}{\partial t}(\frac{\partial Y}{\partial x}) + \alpha R_0(x)\{\frac{\partial}{\partial t}(\frac{\partial Y}{\partial x})\}^3 + c^{-1} \frac{\partial Y}{\partial x}$$

$$(7.2)$$

Hall demonstrated that the cubic nonlinearity creates odd-order distortion consistent with the combination tone response of the cochlea. He also recognized that a similar nonlinear inductance or capacitance produces the same odd-order distortion effects.

Figure 12 represents the nonconstant-compliance model of Figure 10 if $G^{-1}=(S_v+S_t)/\mu$ and $L=\rho_p$. The partition compliance, given by equation (1) of Chapter VI. is represented by a cubic term in the expression for p(x), given by

$$p(x) = L(x) \frac{\partial^2}{\partial t^2}(\frac{\partial Y}{\partial x}) + \frac{\partial}{\partial t}(\frac{\partial Y}{\partial x})/G(x) + k_0(x) \frac{\partial Y}{\partial x} + k_1(x) (\frac{\partial Y}{\partial x})^3 \quad (7.3)$$

Because of the similarity of equations 7.2 and 7.3, the distortion effects of the two models are similar. Therefore, the odd-order distortion of the nonlinear-compliance model is consistent with the combination tone response of the cochlea.

In summary, a nonconstant partition compliance was hypothesized. This hypothesis has been proved in a simplified model of the cochlea.

It was further hypothesized that nonconstant partition compliance is responsible for generating combination tones. It has been concluded that (1) the nonlinearity due to the compliance of the cochlear partition is significant, and (2) this is the only significant nonlinearity in the cochlear model. Therefore, combination tones are a direct result of the

nonlinear partition compliance. The combination tone response of the nonlinear cochlear model is consistent with that of the cochlea.

With today's technology, an electrode array can be placed within the cochlea to stimulate the auditory nerve directly. One reason these prostheses have only limited success is lack of knowledge of what constitutes a normal stimulus to the nerve fibers. It is known that the mechanical properties of the basilar membrane affect the response of nerve fibers. This dissertation provides evidence for a mechanical nonlinearity. Whether this nonlinearity is necessary for intelligibility of speech remains to be determined. If so, it can be incorporated into the signal processing circuitry of cochlear prostheses.

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