A symmetry suppresses the cochlear catastrophe

Christopher A. Shera and George Zweig
Hearing Research Laboratory, Signition, Inc., P.O. Box 1020, Los Alamos, New Mexico 87544

(Received 5 January 1990; accepted for publication 21 November 1990)

When the independent spatial variable is defined appropriately, the empirical finding that the phase of the cochlear input impedance is small [Lynch et al., J. Acoust. Soc. Am. 72, 108–130 (1982)] is shown to imply that the wavelength of the pressure wave in the cochlea changes slowly with position near the stapes. As a result, waves traveling in either direction through the basal turn undergo little reflection, and the transfer of energy between the middle and inner ears remains efficient at low frequencies. The slow variation of the wavelength implies that the series impedance \( Z \) and shunt admittance \( Y \) of the cochlear transmission line are approximately proportional at low frequencies and thus requires that the width of the basilar membrane and the cross-sectional areas of the cochlear sealae taper in opposite directions. Maintenance of the symmetry between \( Z \) and \( Y \) is both necessary and sufficient to ensure that the spatial derivative of the wavelength, and hence the phase of the cochlear input impedance, remains small. Although introduced in another context, the model of Zweig ("Finding the impedance of the organ of Corti," J. Acoust. Soc. Am. 89, 1229–1254 (1991)) manifests the symmetry between \( Z \) and \( Y \). In other transmission-line models of cochlear mechanics, however, that symmetry is absent, and the spatial derivative of the wavelength diverges at low frequencies—the "cochlear catastrophe." Those models therefore contradict the impedance measurements and predict little transfer of energy between the middle and inner ears.

PACS numbers: 43.64.Kc, 43.64.Ha, 43.64.Bt

INTRODUCTION

Measurements of the velocity of the basilar membrane in response to tones of different frequency (e.g., Rhode, 1971; Robles et al., 1986) and the absence of spectral ripples in noninvasive measurements of middle-ear input impedance (Kemp and Chum, 1980; Zwicker and Schloth, 1984) both indicate that little reflection of forward-traveling waves occurs within the cochlea at high sound-pressure levels. Indeed, it is widely believed that the cochlea evolved to suppress such reflection at stimulus levels sufficiently above threshold (Zweig et al., 1976; Zweig, 1976). A number of authors have argued, however, that the cochlea is strikingly asymmetric with respect to wave travel in the two directions along the organ of Corti and that the internal reflection of backward-traveling waves is significant at all sound levels (de Boer and Viergever, 1984; de Boer et al., 1986a,b; Viergever, 1986; Kaernbach et al., 1987). Such reflection, if present, would have important consequences for understanding the nature of otoacoustic emissions and their contribution to auditory signal processing (Kemp, 1978; Kemp, 1979a).

This paper demonstrates, however, that measurements of the cochlear input impedance (Lynch et al., 1982; Nedzel-nitsky 1974a; Nedzel-nitsky, 1980), which indicate that its phase is nearly zero, imply—when the independent spatial variable is appropriately defined—that the wavelength of the traveling pressure wave changes slowly with position near the stapes. Consequently, reflection of waves traveling in either direction through the basal turn must be small. The slow variation of the wavelength implies that the longitudinal impedance \( Z \) of the cochlea and the shunt admittance \( Y \) of the organ of Corti are approximately proportional. Maintenance of that symmetry between \( Z \) and \( Y \) is both necessary and sufficient for transmission-line models to agree with the impedance measurements. If the symmetry is broken, however, the spatial derivative of the wavelength diverges at low frequencies. That divergence, manifest in nearly all models of cochlear mechanics, we call the "cochlear catastrophe." Those models are thus in contradiction with measurements of the cochlear input impedance. Whereas the measured input impedance is essentially real and constant over a wide frequency range, the models predict a nonzero phase and a considerable variation in amplitude arising from the broken symmetry. Another model of cochlear mechanics (Zweig, 1987; Zweig, 1991) enforces the symmetry and so avoids the cochlear catastrophe, remaining approximately consistent with the impedance data.

The rate of change of the wavelength near the stapes is also shown to affect the sensitivity of the ear. Models of cochlear mechanics that exhibit the catastrophe predict a decrease in the transfer of acoustic energy to the cochlea at low frequencies. Suppression of the cochlear catastrophe prevents that dramatic decline in middle-ear efficiency.

Overview. The paper consists of two parts. In the first, the cochlear input impedance is defined, its measurement in the cat reviewed, and an approximate analytic expression for it obtained. Consistency with the measurements of Lynch et al. (1982) is shown to require that the wavelength of the traveling wave change slowly at the basal end of the cochlea. The implications of a slowly changing wavelength for the reflection of traveling waves, for the geometric structure of
the cochlea, and for the sensitivity of hearing are then discussed. The second part parallels the first, illustrating the results in a simple class of cochlear models. Those models fall into two categories differing in the spatial variation of their parameters: those in which the wavelength changes slowly near the stapes (e.g., Zweig, 1987; Zweig, 1991), and those, such as the models used to discuss the reflection of retrograde waves (Viergever, 1986; de Boer et al., 1986a,b; and Kaernbach et al., 1987), that exhibit the cochlear catastrophe. The companion paper (Shera and Zweig, 1991a) explores the consequences of breaking the symmetry between $Z$ and $Y$ for the reflection of traveling waves.

I. THE SYMMETRY

A. The cochlear input impedance

As seen from the basal end of the cochlea, the response at the driving frequency to a pure tone of angular frequency $\omega$ and amplitude $A$ can, if the organ of Corti is essentially incompressible (cf. Shera and Zweig, 1991b), be characterized by the cochlear input impedance, which is defined as the ratio of the pressure difference $P(x,\omega;A)$ across the organ of Corti to the volume velocity $U(x,\omega;A)$ of the cochlear fluids in the scala vestibuli:

$$\tilde{Z}_0(\omega;A) \equiv \frac{P}{U} \bigg|_{x=0; \text{cochlea driven forward}}$$

(1)

The position $x=0$ corresponds to the basal opening of the cochlear spiral, and the diacritical arrow indicates that the cochlea is being driven in the "natural," or forward, direction.

B. Amplitude and frequency range of interest

At moderate intensities nonlinearities in cochlear mechanics make significant contributions to $\tilde{Z}_0(\omega;A)$, which varies strongly with $A$ (Kemp, 1979b). At high intensities, however, the relative amplitude of those nonlinear contributions is always small (Kemp and Chum, 1980; Zwicker and Schloth, 1984), and the function $\tilde{Z}_0(\omega;A)$ becomes independent of the amplitude of the stimulating tone:

$$\tilde{Z}_0(\omega;A) \equiv \tilde{Z}_0(\omega), \quad \text{for } A > A_w.$$  

(2)

In humans, the stimulus amplitude $A_w$ corresponds to roughly 60 dB above threshold at frequencies $\omega/2\pi \sim 1$ kHz.

At the lowest frequencies ($\omega/2\pi \leq 100$ Hz) interpretation of $\tilde{Z}_0(\omega)$ is complicated by viscosity and the effects of the geometry of the apical scalae and helicotrema (Koshigoe et al., 1983; Puria and Allen, 1991). For example, the termination of the organ of Corti at the helicotrema may result, at very low frequencies, in the partial reflection of waves back toward the stapes. Such waves can have significant effects on the cochlear input impedance (Puria and Allen, 1991). By restricting attention to higher frequencies ($\omega/2\pi \gtrsim 100$ Hz), at which stimulus energy is absorbed before reaching the apical end of the cochlea, such complications are avoided and measurements of $Z_0(\omega)$ can be compared with the predictions of models that do not specify cochlear responses to the lowest frequencies.

C. Measurements of $Z_0(\omega)$

Lynch et al. (1982) and Nedzelnitsky (1974a; 1980) have measured the input impedance of the cat inner ear at high stimulus amplitudes. At the lowest frequencies ($\omega/2\pi \leq 80$ Hz) their measurements include effects due to the impedance of the round window, but at higher frequencies the impedance they measure reduces to $Z_0(\omega)$ and is determined solely by the internal mechanics of the cochlea. Their measurements of $Z_0(\omega)$, together with smoothed, minimum-phase fits (Zweig and Konishi, 1987; Konishi and Zweig, 1989) to the data, are shown in Fig. 1. The measurements indicate that the phase $\angle Z_0(\omega)$ of the cochlear input impedance is small over a broad range of frequencies greater than approximately 100 Hz (see also Nedzelnitsky, 1974b):

$$\angle Z_0(\omega) \equiv \tan^{-1} \left( \frac{\text{Im } Z_0(\omega)}{\text{Re } Z_0(\omega)} \right) \lesssim 1 \quad (\omega/2\pi \gtrsim 100 \text{ Hz}),$$

(3)

where Re and Im indicate the real and imaginary parts of their arguments. Note, in addition, that Re $Z_0(\omega)$ is roughly constant.

![Graph](image-url)
The measurement errors are not precisely known, but since driving-point impedances are minimum-phase functions (Bode, 1945), a lower bound on the error is given by the deviations from the minimum-phase fit, which do not exceed ±2 dB in the amplitude and ±10° in the phase. Lynch et al. (1982) provide an upper bound on the error of ±10 dB in the amplitude and roughly ±40° in the phase (Nedzelnitsky, 1974a) but believe those limits substantially overestimate the actual error at frequencies greater than 100 Hz (Lynch et al., 1982; Peake, 1989).

D. Transmission-line models of cochlear mechanics

An approximate analytic form for \( Z_0(\omega) \) can be derived from transmission-line models of cochlear mechanics, enabling one to understand the constraints that measurements of \( Z_0(\omega) \) impose on such models. Those constraints can be expected to take the form of a symmetry principle enforcing the empirical relation \( \angle Z_0(\omega) = 0 \).

At intensities \( I > I_m \) and frequencies \( \omega < \omega_m \) where \( \omega_m \) is the characteristic angular frequency at the beginning of the organ of Corti \( (x = 0) \), the basal turn of the cochlea is analogous to a linear, one-dimensional mechanical transmission line (Zwislocki-Moeicki, 1948; Peterson and Bogert, 1950; Zweig, 1991) with series impedance \( Z(x,\omega) \) and shunt admittance \( Y(x,\omega) \) per unit length. A section of the cochlear transmission line is illustrated schematically in Fig. 2. Application of Kirchoff's circuit laws yields a pair of coupled, first-order transmission-line equations,

\[
\frac{dP}{dx} = -\bar{Z}U \quad (4)
\]

and

\[
\frac{dU}{dx} = -YP \quad (5)
\]

describing the variation of \( P \) and \( U \).

Validity of the simple transmission-line analog used here requires that the cochlear response be linear and that the long-wavelength approximation hold in the basal turn of the cochlea at low frequencies. The motion of the organ of Corti is nonlinear primarily in the region of maximal velocity (Rhode, 1971; Robles et al., 1986), which for angular frequencies \( \omega < \omega_m \) occurs in the more apical turns of the cochlea. In addition, for frequencies \( \omega < \omega_m \) the wavelengths of the waves on the organ of Corti are long relative to the heights of the scalae (Nedzelnitsky, 1980). The pressure then depends only on position along the organ of Corti and not on the two orthogonal directions; the geometry of the basal turn is thus effectively one-dimensional.4

E. A change of coordinates

Solution of the transmission-line equations is simplified by regarding \( P \) and \( U \) as functions of the "spatial" variable \( \chi \)

\[
\chi(x,\omega) = -i \int_0^x \bar{Z}(\xi,\omega) \, d\xi \quad (6)
\]

Two points are then separated by a "distance" equal to \( -i \) times the total series impedance between them. Conventional cochlear models predict that the impedance of the cochlear fluids to motion in the longitudinal direction is predominantly inertial. The series impedance \( \bar{Z}(x,\omega) \) is thus essentially imaginary, and the factor \(-i\), where \( i=\sqrt{-1} \), thus makes \( \chi(x > 0,\omega) \) a positive, real-valued, monotonically increasing function of \( x \). Written in terms of \( \chi \) the transmission-line equations become

\[
\frac{dP}{d\chi} = -iU \quad (7)
\]

and

\[
\frac{dU}{d\chi} = -\frac{i}{\lambda^2} P, \quad (8)
\]

where \( \lambda(\chi,\omega) \) is the characteristic impedance \( Z_c(\chi,\omega) \) of the transmission line:

\[
\lambda(\chi,\omega) \equiv \frac{Z_c(\chi,\omega)}{\bar{Z}(\chi,\omega)} = \left( \frac{\bar{Z}}{Y} \right)^{1/2} \quad (9)
\]

Equations (7) and (8) describe a transmission line with series impedance \( i \) and shunt admittance \( i/\lambda^2 \) per unit length \( d\chi \).

Decoupling Eqs. (7) and (8) yields a wave equation for the pressure difference \( P(\chi,\omega) \) across the scala media:

\[
\frac{d^2P}{d\chi^2} + \frac{1}{\lambda^2} P = 0 \quad (10)
\]

When distance is measured in terms of \( \chi \), \( \lambda(\chi,\omega) \) is just \( 1/2\pi \) times the local wavelength \( \lambda(\chi,\omega) \) of the wave on the basilar membrane (Zweig et al., 1976). Throughout this paper \( \lambda(\chi,\omega) \) is thus referred to as the wavelength (and \( \lambda' \equiv d\lambda/d\chi \) as its spatial derivative). Note, in addition, that the symbols \( \lambda(\chi,\omega) \) and \( Z_c(\chi,\omega) \) are used interchangeably.

F. Theoretical input impedance

If the wavelength \( \lambda(\chi,\omega) \) varies slowly with position \( \chi \), waves traveling down the organ of Corti undergo little reflection. Equation (10) for the pressure can then be solved by expanding \( P \) in an asymptotic WKB series (e.g., Bender and Orszag, 1978), which yields (e.g., Green, 1837; Jeffreys, 1924; Zweig et al., 1976)

\[
P(\chi,\omega) \sim \exp \left( -i \int_0^\chi \frac{d\chi'}{\lambda} + \frac{1}{2} \ln \lambda + \cdots \right) \quad (11)
\]

C. A. Shera and G. Zweig: Symmetry and catastrophe
for the forward-traveling pressure wave. Equation (7) for $U$ then implies that

$$Z_0^{-1}(\omega) = i \frac{d \ln P}{d \chi}$$

$$\sim i \frac{d}{d \chi} \left\{- i \int \frac{d \chi'}{\lambda} \left[ 1 + \frac{1}{2} \ln \lambda + \cdots \right] \right\}_{\chi = 0}. \quad (12)$$

When the wavelength has the form predicted by transmission-line models at frequencies $\omega \ll \omega_o$, truncating the series after the first two terms is optimal and yields

$$Z_0(\omega) \approx \lambda_0 / (1 + i \lambda_0 / 2). \quad (13)$$

The subscripts "0" indicate that the quantities are evaluated at the basal end of the organ of Corti; for example,

$$\lambda_0(\omega) \equiv \lambda(0, \omega). \quad (14)$$

The prime denotes differentiation with respect to $\chi$:

$$\lambda'_0(\omega) \equiv \frac{d \lambda(\chi, \omega)}{d \chi} \bigg|_{\chi = 0}. \quad (15)$$

Note that $\lambda'(\chi, \omega)$ is dimensionless.

Recall that by restricting attention to frequencies $\omega / 2\pi \gtrsim 100$ Hz and stimulus amplitudes $A > A_o$, contributions to the input impedance due to reflection from the helicotrema and the amplification by the "cochlear laser" (Zweig, 1991; Zweig, 1989) of wavelets scattered from mechanical inhomogeneities in the organ of Corti can be assumed small. Reflections from apical regions of the cochlea may, however, be responsible for the fine structure in the measured impedance curves (Puria and Allen, 1991). If reflections are not too large, $Z_0(\omega)$ can be approximated by an expression depending only on the mechanics at the basal end of the cochlea.

G. A limit on the rate of change of the wavelength

The measurements of Lynch et al. (1982) place important constraints on transmission-line models of cochlear mechanics. As shown later in the examples (Sec. II), those models predict that at frequencies much less than the characteristic frequencies near the stapes (i.e., at $\omega \ll \omega_o$), the wavelength $\lambda(\chi, \omega)$ is approximately real and the imaginary part of its spatial derivative $\lambda'(\chi, \omega)$ is small:

$$|\lambda'_0(\omega)| \ll 1, \quad (16)$$

and

$$|\lambda_0'| \ll 1. \quad (17)$$

Since forward-traveling waves have the approximate form

$$(Zweig \ et\ al.,\ 1976) \quad P_+ (\chi, \omega) \simeq A_+ (\omega) \sqrt{\lambda} \exp \left(-i \int \frac{d \chi'}{\lambda} \right), \quad (18)$$

the real nature of the wavelength guarantees that waves of low frequency propagate through the basal turn of the cochlea without substantial change in amplitude. To within the first few waves, in particular, at frequencies $\omega / 2\pi \ll 100$ Hz (cf. Fig. 1) therefore yields

$$\lambda'_0(\omega) \ll 1 \quad (\omega \ll \omega_o). \quad (19)$$

As an immediate consequence, note that the rough constancy of the measured $Z_0(\omega)$ implies

$$\lambda'_0(\omega) \approx \text{const} \quad (\omega \ll \omega_o). \quad (20)$$

Inequality (19), which constitutes the central result upon which this paper elaborates, depends for its validity on the empirical finding that $\Delta Z_0(\omega)$ is small (Lynch et al., 1982) and on inequalities (16) and (17), which follow from basic assumptions underlying models of cochlear mechanics. Should those assumptions prove inapplicable to the real cochlea, the mechanics of hearing must be considerably different from that currently conceived.

H. Relation to cochlear reflection of traveling waves

The inequality

$$|\lambda'_0(\omega)| \ll 1 \quad (\omega \ll \omega_o), \quad (21)$$

which transmission-line models of cochlear mechanics must satisfy if they are to be consistent with the measurements of Lynch et al. (1982), can be interpreted physically in terms of the reflection of waves traveling along the organ of Corti. Inequality (23) is equivalent to the condition that the change in wavelength over distances on the order of a wavelength be less than the wavelength. That statement implies, by analogy with the propagation of light through a medium of variable refractive index (e.g., Born and Wolf, 1959), that waves traveling in either direction along the organ of Corti undergo little reflection. Mathematically, the statement means that the WKB approximation may be used when solving the transmission-line equations, at least within the basal turn of the cochlea (Schroeder, 1973; Zweig et al., 1976). Note that Eq. (23) thus provides ex post facto justification for the WKB expansion of the pressure used to obtain Eq. (13) for $Z_0(\omega)$.

I. A symmetry between $Z$ and $Y$

The limit on the spatial derivative of the wavelength imposed by the measurements,

$$|\lambda'_0| = \left| \frac{d}{d \chi} \left( \frac{Z}{Y} \right) \right| \bigg|_{\chi = 0} \ll 1 \quad (\omega \ll \omega_o), \quad (24)$$

implies that near the basal end of the cochlea the longitudinal impedance $Z(\chi, \omega)$ of the cochlea and the shunt admittance $Y(\chi, \omega)$ of the organ of Corti are constrained to be roughly proportional at low frequencies:

$$(\omega \ll \omega_o), \quad (25)$$

where $\phi(\omega)$ is independent of $\chi$. Conversely, if $Z$ and $Y$ are roughly proportional, the derivative of their ratio will be small. Based on its geometric interpretation in conventional cochlear models (see below), we call the proportionality between $Z$ and $Y$ the "tapering symmetry."

In deriving Eq. (25) we assume that the derivative $\chi' = \lambda(d \ln \lambda / d \chi)$ is small because $\lambda'(\chi, \omega)$ is essentially im-


C. A. Shera and G. Zweig: Symmetry and catastrophe 1279
dependent of $\chi$ (at small $\chi$) and not because the wavelength itself is small. Support for that assumption comes from measurements of the magnitude the cochlear input impedance (Lynch et al., 1982). When combined with Eq. (13) for $Z_o$, those measurements indicate that at low frequencies the wavelength of the pressure wave within the basal turn of the cochlea is long; i.e., that $\lambda_o$ is not small.

Technically, the impedance measurements require only that the symmetry hold at the point of measurement (i.e., at $\chi = 0$). We assume that the approximate symmetry continues to hold at least within the basal turn of the cochlea. An estimate of the length scale over which the symmetry might be expected to hold can be obtained from the Taylor expansion of $\lambda(\chi, \omega)$ about $\chi = 0$:

$$\lambda(\chi, \omega) \approx \lambda_0 + \chi \lambda'_0 + \cdots.$$  \hfill (26)

Thus,

$$\lambda(\chi, \omega) \approx \lambda_0 \left( |\chi| \lambda/\lambda'_0 \right).$$  \hfill (27)

Note that if the symmetry between $\bar{Z}$ and $Y$ is broken, the derivative $\lambda'(\chi, \omega)$ can become large. As shown below, for example, transmission-line models in which such symmetry breaking occurs predict that $\lambda(\chi, \omega)$ is independent of frequency in the basal turn. Since in those models the series impedance $\bar{Z}$, and hence the differential element $dX$, is proportional to $\omega$, the derivative $d\lambda/d\chi$ can be expected to diverge like $1/\omega$ at low frequencies.

The symmetry between $\bar{Z}$ and $Y$ implies a symmetry between $P$ and $U$. When $|\chi'|$ is small—and in the absence of reflections from elsewhere in the cochlea—Eq. (7) for $U$ implies that the ratio of $P$ to $U$ is simply the wavelength, or characteristic impedance, $\lambda(\chi, \omega)$:

$$U \approx P/\lambda.$$  \hfill (28)

The approximate proportionality between $\bar{Z}$ and $Y$ implies that $\lambda$ is nearly constant near the stapes. Consequently,

$$U \approx P/\lambda_0 \left( |\chi| \lambda/\lambda'_0 \right) \approx \omega \lambda(\omega),$$  \hfill (29)

so that $P$ and $U$ are roughly proportional in the basal turn.

The symmetry between $\bar{Z}$ and $Y$ relates two distinct aspects of cochlear mechanics. Whereas the impedance $\bar{Z}$ characterizes the geometry of the scalae and the longitudinal motion of the cochlear fluids, the shunt admittance $Y$ describes the transverse response of an individual section of the organ of Corti to a pressure difference across the scala media. Remarkably, the symmetry imposed by the measurements implies that at low frequencies those functions are roughly proportional in the basal turn of the cochlea.

J. Spatial coordinates revisited

The symmetry between $\bar{Z}$ and $Y$ selects the $\chi$ coordinate system—originally introduced as a mathematical convenience for solving the transmission-line equations—as the most natural for describing the variation of pressure and volume velocity in the basal turn of the cochlea. Since $\bar{Z}$ and $Y$ are approximately proportional, the wavelength $\lambda$ measured in units defined by $\chi$ is nearly constant at frequencies $\omega \ll \omega_0$ near the stapes. Consequently, $P$ can be written as a simple superposition of plane waves of the form

$$e^{\pm i\omega x/\lambda_0} \left( |\chi| \lambda/\lambda'_0 \right) \approx \omega \lambda(\omega).$$  \hfill (30)

The same is not true, however, for the familiar wavelength $\lambda_s$ measured in units of length $x$. The familiar wavelength and its derivative are related to $\lambda$ and $\lambda'$ through the equations

$$\lambda_s = \frac{dx}{d\chi} \approx \frac{i\lambda}{Z},$$  \hfill (31)

and

$$\frac{d\lambda_s}{dx} = \frac{d\chi}{dx} \frac{d\lambda}{d\chi} = \lambda' - \frac{d\ln Z}{d\chi}.$$  \hfill (32)

Recall that $\lambda(\chi, \omega \ll \omega_0)$ is approximately constant in the basal turn [see Eq. (22)]. Since both $\bar{Z}$ and $d\chi/d\lambda$ are, in standard models, proportional to $\omega$, the familiar wavelength $\lambda_s$ and its spatial derivative $d\lambda_s/dx$ thus diverge like $1/\omega$ at low frequencies.

K. Application to conventional cochlear models

Earlier it was shown that consistency with the measurements of Lynch et al. requires that the wavelength change slowly near the stapes and therefore that $\bar{Z}$ and $Y$ be roughly proportional. At low frequencies in the basal turn, conventional cochlear models predict that the series impedance $\bar{Z}$ is determined by the acoustic inertia $\bar{M}(x)$ of the cochlear fluids and the shunt admittance $Y$ is dominated by the compliance $C(x)$ of the organ of Corti and its basilar membrane. $\bar{Z}$ and $Y$ thus have the limiting asymptotic forms

$$\bar{Z} \approx \omega \bar{M}(x) \quad \text{and} \quad Y \approx \omega \bar{C}(x),$$  \hfill (33)

and therefore

$$\lambda_s \approx \frac{(\bar{M}/C)^{1/2}}{\beta \omega}.$$  \hfill (34)

Here, the variable

$$\beta(\chi, \omega) \equiv \omega/\omega_s(\chi),$$  \hfill (35)

where $\omega_s(\chi)$ is the mapping between characteristic frequency and position. Near the stapes the symmetry thus constrains the spatial variation of the effective compliance of the organ of Corti $C(x)$ to be that of the effective inertia of the cochlear fluids $\bar{M}(x)$:

$$C(x) \approx \frac{\phi}{\bar{M}(x)} \frac{\phi}{\bar{M}(x)},$$  \hfill (36)

where $\phi$ is a constant independent of position and frequency. (Note that $\bar{Z}$ and $Y$, shown to be proportional when considered as functions of $\chi$, maintain their proportionality when considered as functions of $x$.)

Calculation of the derivative of the wavelength yields

$$\lambda'_s(\omega) = -\omega_s/\omega \quad \text{for} \omega \ll \omega_0,$$  \hfill (37)

where the frequency scale $\omega_s$ is defined by

$$\omega_s = \frac{1}{\bar{M}_0} \frac{d}{dx} \left( \frac{\bar{M}}{C} \right)^{1/2} \bigg|_{x=0}.$$  \hfill (38)

Thus, when the symmetry between $\bar{M}$ and $C$ is broken,
L. Relation to scaling symmetry

The symmetry between the impedances $Z$ and $Y$ at low frequencies can be obtained as a limiting case of the scaling symmetry (Zweig, 1976) suggested by Rhöde's (1971) measurements of basilar-membrane transfer functions in the squirrel monkey and also found in the pigeon (Gummer et al., 1987). Applied to cochlear transfer functions, scaling symmetry implies (Zweig, 1976) that the envelopes of the response of the basilar membrane to tones of nearby frequency are "shift-similar," that is, one can be made to overlay the other simply by translating its envelope and adjusting its overall height. In the model of Zweig (1987; 1991) the circuit elements $Z(x,\omega)$ and $Y(x,\omega)$, and consequently the transfer functions $Z(x,\omega)$ and $Y(x,\omega)$, and consequently the transfer functions, "scale," that is, they are functions not of $x$ and $\omega$ independently, but only of the single variable $\beta(x,\omega)$ defined by Eq. (35). At small $\beta$ in that model,

$$Z(x,\omega) = i\beta(x,\omega)\omega_o \overline{M}_0$$

and

$$Y(x,\omega) = -i\beta(x,\omega)\omega_o C_o,$$

where $\overline{M}_0$ and $C_o$ are constants. Hence,

$$\overline{M}(x) = \left[\omega_o/\omega_o(x)\right] \overline{M}_0$$

and

$$C(x) = \left[\omega_o/\omega_o(x)\right] C_o,$$

near the stapes, so that the model automatically reproduces the required proportionality between $\overline{M}$ and $C$.

M. Implications for cochlear geometry

The symmetry between $\overline{M}$ and $C$ does not hold in other cochlear models. For example, $C$ is typically assumed to increase exponentially with position, corresponding to the approximate exponential variation in characteristic frequency at the basal end of the cochlea (e.g., von Békésy, 1960; Greenwood, 1961; Eldredge et al., 1981; Liberman, 1982). The series inductance $\overline{M}$, however, is often assumed to be independent of position. An acoustic inductance, $\overline{M}$ is usually taken to have the form

$$\overline{M}(x) \propto \rho_o / S(x),$$

where $\rho_o$ is the density of the cochlear fluids and $S(x)$ represents the effective cross-sectional area of the two scalae. Simple treatments (e.g., Zwislocki, 1965; Dallos, 1973) give

$$S = \overline{S} S, \quad \overline{S} S / (S_v + S_t),$$

where $S_v$ and $S_t$ are, respectively, the cross-sectional areas of the scala vestibuli and the scala tympani. Thus, $\overline{M}$ is constant when the scalae are approximated as boxes of constant cross section (de Boer, 1980; Viergever, 1980). In such models the spatial variation of $\overline{M}$ and $C$ are therefore quite different, breaking the tapering symmetry required by measurements of the cochlear input impedance.

The symmetry deduced from measurements of the input impedance finds support in a consilience with measurements of cochlear anatomy, which indicate that whereas the width, and hence the compliance (von Békésy, 1960), of the basilar membrane increases toward the helicotrema, the cross-sectional areas of the scalae decrease, especially at the basal end of the cochlea where the variation is roughly exponential (Wever, 1949; Fernández, 1952; Zwislocki, 1965). Those opposing tapers tend to make $\overline{M}$ and $C$ proportional, thereby preserving the symmetry between $\overline{Z}$ and $\overline{Y}$.

N. Corroboration from cadavers

Unfortunately, existing anatomical measurements do not permit a definitive quantitative examination of the proportionality between $\overline{M}$ and $C$. For example, the relationship between measured properties of the cochlea—the point stiffness of the basilar membrane (Gummer et al., 1981; Olson, 1990), for example—and the effective impedances appearing in the model equations is not well understood. Even if one were to adopt the correspondences suggested by simple models—such as Eq. (42)—appropriate measurements have yet to be made in a single animal. Comparing measurements across preparations is complicated both by uncertainties in the location of the measurement coordinate system and by differences in the overall size of the cochlea (Bohne and Carr, 1979).

Despite such uncertainties, a qualitative comparison of measurements on human cadavers is suggestive. Figure 3 compares the spatial variation of the effective cross-sectional area $\overline{S}$, computed from Eq. (42) using the measurements of Wever (1949), with that of the reciprocal of the static volume elasticity $E$ of the organ of Corti measured by von Békésy (1960). Since von Békésy's elasticity measurements were made in cadavers, they do not include contributions from physiologically active mechanical elements. Since the

![Figure 3](image-url)
symmetry between $\bar{Z}$ and $Y$ evolved in living ears, there is little reason to expect it to hold after death. The figure indicates, however, that $S$ and $1/E$, and hence—by adopting the naive correspondences $M \propto 1/S$ and $C \propto E$—$M$ and $C$ are indeed proportional near the base of the cochlea. Although the location of the beginning of the organ of Corti is not precisely known and end effects complicate the interpretation near the stapes, the proportionality appears to hold for roughly the first 15% of the distance along the organ of Corti.\[1,11\]

O. Consequences for the sensitivity of hearing

The slow variation of the wavelength has important consequences for the detection of sound. The efficiency of the middle-ear is defined as the fraction of the time-averaged power entering the middle ear that is absorbed by the cochlea (Rosowski et al., 1986):

$$\eta_{me}(\omega) = \frac{\text{Power into cochlea}}{\text{Power into middle ear}} = \frac{\text{Re}\left\{P_{c} U_{c}^{*}\right\}}{\text{Re}\left\{P_{m} U_{m}^{*}\right\}} = \frac{|Z_{c} T_{mc}|^{2}}{Z_{m}}.$$ \[43\]

Here, $P_{c}(\omega)$ and $U_{c}(\omega)$ are the pressure and volume velocity measured in the ear canal at the eardrum. The middle-ear input impedance $Z_{m}^{i}(\omega)$ and transfer function $T_{mc}^{i}(\omega)$ are defined more precisely in the Appendix.

Although cochlear contributions to middle-ear efficiency are complicated, a qualitative understanding of the effect of tapering symmetry on energy transfer to the cochlea at low frequencies can be obtained by examining the factor $\text{Re} Z_{o}$. Since $\lambda_{0}$ and $\lambda_{s}$ are both approximately real at low frequencies,

$$\text{Re} Z_{o} \approx \text{Re}\left\{\frac{\lambda_{0}}{1 + \lambda_{s}^{2}/2}\right\} \approx \frac{\lambda_{0}}{1 + (\lambda_{s}^{2}/2)^{2}} (\omega \ll \omega_{o}).$$ \[44\]

Because $\lambda_{s}(\omega)$ is small at auditory frequencies, $\text{Re} Z_{o}$, and consequently middle-ear efficiency, stays roughly constant. Conversely, for $\eta_{me}(\omega)$ to remain roughly constant at low frequencies—given the measured transfer characteristics of the cat middle ear, the approximate value of $\text{Re} Z_{o}$, and the theoretical result that $\lambda_0$ varies only slowly with frequency—requires that $\lambda_{s}$ be small.

Note, however, that were $\lambda_{s}(\omega)$ to diverge as $\omega \to 0$, as it does in models exhibiting the cochlear catastrophe, $\text{Re} Z_{o}$ would approach zero. In that limit (i.e., the limit $\text{Re} Z_{o} \to 0$), $\eta_{me}$ becomes proportional to $\text{Re} Z_{o}$ (see the Appendix), and the transfer of energy into the cochlea becomes vanishingly small. Thus, in a world differing from ours only in that the wavelength changes rapidly in the basal turn of the cochlea, the sensitivity of hearing would be considerably reduced at low frequencies.

II. THE CATASTROPHE

The remainder of this paper illustrates the comments made above by explicit computations for two categories of models, distinguished by the extent to which they exhibit the cochlear catastrophe. Note that the issues addressed—the cochlear input impedance and middle-ear efficiency—depend only on the form of the model at low frequencies near the stapes. The reflection of retrograde waves discussed in the companion paper (Shera and Zweig, 1991a) depends on more global characteristics of the model cochleas. The following sections also serve to justify by example the statements (i.e., Eqs. (16) and (17)) that $\lambda_{0}$ and $\lambda_{s}$ are approximately real, which were used to derive the limit on the rate of change of the wavelength (i.e., Eq. (21)).

A. Conventional transmission-line models

In many transmission-line models, including those used to investigate reflection of waves in the cochlea (de Boer and Viergever, 1984; Viergever, 1986; de Boer et al., 1986a,b; and Kaernbach et al., 1987), the series impedance $Z(x,\omega)$ and shunt admittance $Y(x,\omega)$ per unit length have the form

$$Z(x,\omega) = \frac{i\omega M(x) + R(x)}{i\omega C(x)} - \frac{1}{i\omega C(x)}.$$ \[45a\]

and

$$Y(x,\omega) = \left[i\omega M(x) + R(x) + 1/i\omega C(x)\right]^{-1},$$ \[45b\]

where $M, M, R,$ and $C$ are real-valued functions of $x$. The wavelength thus becomes

$$\lambda(x,\omega) = \frac{(\bar{M}/C)^{1/2}}{1 - \beta^{2} + i\delta\beta},$$ \[46\]

where $\beta(x,\omega) = \omega/\omega(x)$ in accord with Eq. (35), $\omega(x) \equiv 1/\sqrt{MC}$ is the characteristic angular frequency, and $\delta(x) \equiv \omega(x)/RC$ is the dimensionless damping parameter. For future reference, note that

$$\lambda_{0}(\omega \ll \omega_{o}) \approx \lambda(0,0) = (\bar{M}_{o}/C_{o})^{1/2} \equiv \lambda_{0};$$ \[47\]

that is, $\lambda_{0}(\omega \ll \omega_{o})$ is essentially real, in agreement with Eq. (16).

At the basal end of the cochlea, the derivative $\lambda'(\chi,\omega)$ has the value

$$\lambda'_{0}(\omega \ll \omega_{o}) \approx \frac{1}{4N_{0}} \left[\frac{\omega_{o}}{\omega} d' + \frac{i}{2} \frac{d\ln(\delta/\omega_{o})}{d\zeta} \right] \bigg|_{\zeta = 0}.$$ \[48\]

The dimensionless spatial variable

$$\zeta \equiv \chi/l$$ \[49\]

used here (see footnote 5) is defined in terms of the length scale $l$ over which the characteristic frequency changes by a factor of $e$ in the basal turn (Liberman, 1982):

$$\omega_{e} = \omega_{o} e^{-\zeta}.$$ \[50\]

The dimensionless parameter $N_{0}$ is defined by

$$N_{0} \equiv \left(1/4\right)(\bar{M}_{o}/M_{o})^{1/2}$$ \[51\]

and the real dimensionless function $\gamma(\zeta)$ by

$$\gamma(\zeta) \equiv \lambda_{0}^{-1}(\bar{M}/C)^{1/2}.$$ \[52\]

Note that $\gamma(0) = 1$.

B. The reality and divergence of $\lambda_{s}(\omega)$

Equation (48) for the derivative can now be used to find the conditions under which $\lambda_{s}(\omega)$ becomes large, giving $Z_{o}(\omega)$ a nonzero phase. Comparison of transmission-line models with measured basilar-membrane transfer functions
(e.g., Zweig et al., 1976; de Boer, 1980) suggests that the damping parameter $\delta_0$ is small whereas $N_0$ is relatively large. The values $\delta_0 \sim \delta_0$ and $N_0 \sim 5$ are typical. If $\delta(\zeta)$ is roughly constant (as it is in the models discussed here), then

$$\frac{d \ln(\delta/\omega_0)}{d \zeta} \sim 1.$$  

(54)

Hence, 

$$|\text{Im} \lambda_0| < 1,$$

(55)
in agreement with Eq. (17).

The derivative of the wavelength then becomes, in agreement with Eq. (37),

$$\lambda'_0(\omega) \approx -\omega_0/\omega \quad (\omega \ll \omega_0),$$

(56)

where the frequency scale,

$$\omega_* = -\omega_0 \left(\frac{1}{4N_0} \left. \frac{d \delta}{d \zeta}\right|_{\zeta = 0} \right) = -\frac{1}{\beta_0} \frac{d}{dx} \left(\frac{M_0}{C}\right)^{1/2} \left|_{x = 0},\right.$$  

(57)

indicates the frequency at which $|\lambda'_0| = 1$ and therefore provides a measure of the severity of the cochlear catastrophe. Typically, the dimensionless quantity $-d\gamma/d\zeta$ is of order one, so that

$\omega_* \approx \delta_0 \omega_0$.  

(58)

However, if the circuit elements $Z$ and $Y$ scale, as they do in the model of Zweig (1987; 1991), then $d\gamma/d\zeta$ vanishes and

$\omega_* = 0$.  

(59)

C. Predictions for $Z_0(\omega)$

Reference to Eq. (13) for the input impedance thus yields

$$Z_0(\omega) \approx \lambda_0/(1 - \iota \omega_0/\omega) \quad (\omega \ll \omega_0).$$

(60)

Unless $\omega_0$ is small enough to suppress the divergence and guarantee that $|\lambda_0(\omega)| \ll 1$ in the frequency range of hearing, the model input impedance will contain a substantial imaginary part at low frequencies ($\omega \ll \omega_0$) and, in particular, the phase of $Z_0(\omega)$ will approach 90°.  

Theoretical predictions for the cochlear input impedance computed from Eq. (1) are shown in Figs. 4, 5, and 6 for the models of Viergever (1986), de Boer et al. (1986a,b), and Kaernbach et al. (1987). The parameter values used by de Boer et al. were selected, on the basis of measurements in other animals, to approximate a human cochlea (de Boer, 1980). To compare the model with measurements on cats, the parameter values must be rescaled. Shown are predictions using both the original parameter values and those rescaled by changing the frequency-position map (Liberman, 1982). The parameter values used by Viergever were kept constant at their original values; the model of Zweig (1987; 1991), derived for low SPL at frequencies greater than approximately 3 kHz but here extrapolated to low frequencies and high stimulus levels (parameter values are those of Zweig except that the feedback strength $p = 0$ and the damping constant $\delta > 0$; i.e., only the passive component of the admittance $Y$ of the scala media has been included). The minimum-phase fit from Fig. 1 ($\ldots$) is shown for comparison. The amplitudes of the model impedances are normalized at 7 kHz to the value given by the phenomenological network model of Lynch et al. (1982). The errors on the measurements are estimated on a comparison with the minimum-phase fits. Note that the averaging performed by Lynch et al. has decreased the random errors but revealed systematic errors of the same order as the random errors in cats 18 and 25. Unless measurement errors are substantially greater than the lower bounds shown here, most models of cochlear mechanics—of which those of Viergever and de Boer et al. are but examples—are in disagreement with the measurements.

Unless measurement errors are substantially greater than the lower bounds estimated from the minimum-phase fits, the model predictions disagree significantly with the empirical values. Although they were not developed to address low-frequency reflection phenomena, many other models of cochlear mechanics, as noted by Wickesberg and Geisler (1986), also exhibit such behavior (e.g., Zweig et al., 1976; Allen, 1979; Sondhi, 1978; Neely, 1981; Wickesberg and Geisler, 1986). Shown for comparison is $Z_0(\omega)$ for the model of Zweig (1987; 1991). Introduced in another context, that model was shown to be valid at high frequencies ($\omega/2\pi \approx 3$ kHz) and low sound-pressure levels but has here been extrapolated to lower frequencies and higher intensities. Nevertheless, because it manifests scaling symmetry that model agrees better with the measured impedance functions.
Any disagreement with the empirical values occurs at frequencies $\omega \leq \omega_c$ for which the imaginary part of $Z_o(\omega)$ becomes substantial. The approximate value of $\omega_c$ for each model can be determined from the phase of $Z_o(\omega)$ by using the relation

$$\omega_c \approx 2 \omega \tan \phi Z_o.$$ 

(61)

Table I gives values of $\omega_c$ for the models of cochlear mechanics shown in the figures. Also given in the table are the derivatives,

$$|\lambda_0'(\phi_0(\omega_o))| \approx 40|\omega_c/\omega_o||,$$ 

(62)

evaluated at a fixed value of $\omega_c/\omega_o = \phi_0$ chosen to represent a typical low frequency in the model. For the cat the frequency $\phi_0(\omega_o/2\pi) \approx 1.5$ kHz (Liberman, 1982). Except for the model of Zweig (1987; 1991), which has $\omega_c = 0$ and therefore completely avoids the cochlear catastrophe, all have $\omega_c/2\pi \gg 100$ Hz and $|\lambda_0'(\phi_0(\omega_o))| > 1$.

The measurements of Lynch et al. can be used to estimate the values of $\omega_c$ and $\lambda_0'$ that would bring such models into agreement with their data. Those estimates, computed from parameters of their phenomenological network model (which represent a best fit to their averaged measurements), are given for comparison; as expected, $\omega_c/2\pi \sim 100$ Hz. The estimate is, of course, only approximate; other factors not related to symmetry breaking in the basal turn (and not accounted for in standard models), such as the presence of

<table>
<thead>
<tr>
<th>Table I. Values of $\omega_c$ and $\lambda_0'$ characterizing the cochlear catastrophe.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cochlear models</td>
</tr>
<tr>
<td>de Boer (1980)</td>
</tr>
<tr>
<td>de Boer et al. (1986a)</td>
</tr>
<tr>
<td>de Boer et al. (1986b)</td>
</tr>
<tr>
<td>Kaernbach et al. (1987)</td>
</tr>
<tr>
<td>Zweig (1987; 1991)</td>
</tr>
<tr>
<td>Empirical values</td>
</tr>
</tbody>
</table>

Cochlear models $\omega_c/2\pi$ $|\lambda_0'(\phi_0(\omega_o))|$
reflections from more apical regions of the cochlea (cf. Puria and Allen, 1991), may affect the apparent value of \( \omega_a \).

### D. Middle-ear efficiency

This section illustrates the effects of the cochlear catastrophe on the efficiency \( \eta_{me}(\omega) \) of the middle ear. By using measurements on the cat, it can be shown (see the Appendix) that \( \eta_{me}(\omega) \) has the approximate form

\[
\eta_{me} \approx \alpha \frac{\text{Re} \ Z_o}{(\text{Re} \ Z_o + R_c/3)} \ \ (\omega/2\pi \leq 700 \ \text{Hz}).
\]

Here, \( R_c \) is the cochlear resistance measured by Lynch et al. (1982) and \( \alpha \) is a dimensionless constant of order one determined by middle-ear mechanics. Equation (60) for the model input impedance implies that

\[
\text{Re} \ Z_o \approx \frac{\lambda_0}{[1 + (\omega/2\alpha)^2]^{1/2}}.
\]

Therefore, \( \text{Re} \ Z_o \), and consequently \( \eta_{me}(\omega) \), becomes small at frequencies below \( \frac{1}{2\alpha} \omega_a \).

Figure 7 plots \( \eta_{me}(\omega) \), computed from Eq. (63), based on the models of Viergever (1986) and de Boer et al. (1986a,b) and Kaernbach et al., 1987, rescaled to the cat. Shown for comparison are results based on the model of Zweig (1987; 1991), the averaged measurements of Lynch et al. (1982), and the minimum-phase fit to those measurements from Fig. 1. Although the absolute efficiencies are not reliable because the constant \( \alpha \) was determined by combining measurements from a gallimaufry of cats, the indicated frequency dependence is approximately correct. In addition, it is reassuring to note that the constraint \( 0 \leq \eta_{me} < 1 \) applicable to a passive system is everywhere satisfied. Inclusion of the empirical finding that \( |\lambda'| \ll 1 \) causes \( \eta_{me}(\omega) \) to remain roughly constant throughout the frequency range of the figure. As expected, however, the symmetry breaking exhibited by the models of Viergever (1986) and de Boer et al. (1986a,b) and Kaernbach et al. (1987) significantly decreases middle-ear efficiency at low frequencies.

### III. SUMMARY

Recent theoretical arguments for significant asymmetry in the reflection of cochlear waves (de Boer and Viergever, 1984; de Boer et al., 1986a,b; Viergever, 1986; Kaernbach et al., 1987) are based on models that, unless measurement errors are substantially greater than the lower bounds estimated from minimum-phase fits to the data, disagree with measurements of the cochlear input impedance (Lynch et al., 1982). This paper demonstrates that those measurements require that the wavelength change slowly in the basal turn of the cochlea and hence that waves traveling in either direction undergo little reflection.

More generally, linear, one-dimensional transmission-line models are expected to describe the mechanics of the basal turn of the cochlea at low frequencies and high sound-pressure levels. The cochlear input impedance therefore has the approximate form

\[
Z_o(\omega) \approx \frac{\lambda_0}{[1 + i\lambda'_0/2]} \ (\omega \ll \omega_a).
\]

In that regime transmission-line models predict that both the wavelength \( \lambda(\chi,\omega) \) and its spatial derivative \( \lambda'(\chi,\omega) \) are approximately real. Since Lynch et al.'s (1982) measurements of the cochlear input impedance indicate that the phase of \( Z_o(\omega) \) is small above 100 Hz, those transmission-line models must also satisfy

\[
|\lambda'(\chi,\omega)| \ll 1 \ (|\chi| \ll |\lambda_0/\lambda'_0| \text{ and } \omega \ll \omega_a);
\]

i.e., the wavelength changes slowly at the basal end of the cochlea. That result has the following consequences, the logical interrelations of which are diagramed in Fig. 8.

1. The series impedance \( \tilde{Z}(\chi,\omega) \) and shunt admittance \( Y(\chi,\omega) \) are roughly proportional at low frequencies near the stapes:

\[
Y(\chi,\omega) \approx \phi^2(\omega) \tilde{Z}(\chi,\omega).
\]

For the broad class of cochlear models defined by Eqs. (33), that symmetry between \( \tilde{Z} \) and \( Y \) reduces to a proportionality between the longitudinal inductance \( M \) representing the inertia of the cochlear fluids and the shunt capacitance \( C \) representing the effective compliance of the organ of Corti and its basilar membrane. The width of the basilar membrane and the cross-sectional areas of the scalae taper in opposite directions, providing independent support for that proportionality.

2. The WKB approximation can be used when solving the cochlear transmission-line equations, at least in the basal turn of the cochlea. Little internal reflection of waves travel-
ing in either direction along the organ of Corti can therefore be expected. The absence of waves traveling in two directions presumably simplifies the analysis of sound.

(3) The efficiency of the middle ear at transferring acoustic power into the cochlea remains roughly constant below 700 Hz. The rate of change of the wavelength near the stapes is thus an important determinant of the sensitivity of the ear at low frequencies.

ACKNOWLEDGMENTS

This work was supported by DARPA and AFOSR contract N00014-86-C0399.

APPENDIX: ESTIMATING MIDDLE-EAR EFFICIENCY

The efficiency $\eta_{me}(\omega)$ of the middle ear at transferring acoustic power to the cochlea depends both on the characteristics of the middle ear and on the cochlear input impedance $Z_o(\omega)$. By combining measurements on the cat to estimate and separate out the contribution made by the middle ear, this appendix derives an expression for middle-ear efficiency as an explicit function of $\text{Re } Z_o$. The appendix thus finds an expression $\eta_{me}(\omega;\text{Re } Z_o)$ that enables one to estimate—by imagining different cochlear models connected to a fixed, empirically characterized middle ear—the middle-ear efficiency associated with each model.

As in Rosowski et al. (1986), the middle-ear efficiency $\eta_{me}(\omega)$ is defined to be the fraction of the time-averaged power entering the middle ear that is absorbed by the cochlea:

$$\eta_{me} \equiv \frac{\text{Re} \{P_o U_e^*\}}{\text{Re} \{P_e U_o^*\}} = |Z_c T_{me}|^2 \frac{\text{Re } Z_o}{\text{Re } Z_c}. \quad (A1)$$

Here, $P_o$ and $U_e$ are the pressure and volume velocity measured in the ear canal at the eardrum and

$$Z_c(\omega) \equiv \frac{P_e}{U_e} \text{middle ear driven forward} \quad (A2)$$

is the middle-ear input impedance. The transfer function $T_{me}$ is defined by

$$T_{me}(\omega) \equiv \frac{U_o}{P_e} \text{middle ear driven forward}. \quad (A3)$$

Of the two quantities $|Z_c T_{me}|^2$ and $\text{Re } Z_c$, that depend on the middle ear in Eq. (A1), the following discussion first considers $|Z_c T_{me}|^2$ and shows that at low frequencies it is nearly independent of the cochlear input impedance $Z_o(\omega)$. An expression for $\text{Re } Z_c$, valid in the same frequency range, is then found as a function of $\text{Re } Z_o$.

Measurements on the cat (Guinan and Peake, 1967; Lynch, 1981; Allen, 1986) indicate that for frequencies less than approximately 700 Hz, $Z_c$ and $T_{me}$ have the form

$$Z_c \approx 1/\omega C_c \quad \text{and} \quad T_{me} \approx \omega C_{me}. \quad (A4)$$

Models of the cat middle ear (e.g., Lynch, 1981; Carr and Zweig, 1984) suggest that the constants $C_c$ and $C_{me}$ are proportional to the combined compliances of such middle-ear structures as the eardrum, cavities, and ossicular joints and are thus essentially independent of $Z_o$.

Allen (1986) explicitly demonstrated that independence for $Z_c$ by measuring $|Z_c(\omega)|$ both before and after setting $Z_o = 0$ by removing the basilar membrane and draining the cochlear fluids. The implications of that experiment can be understood most readily by noting that

$$Z_c = (aZ_o + b)/(cZ_o + d), \quad (A5)$$

where $(a, b, c, d)$ are the elements of the transfer matrix $T$ of the middle ear (Shera and Zweig, 1991b), defined by

$$\begin{pmatrix} P_c \\ U_c \end{pmatrix} = T \begin{pmatrix} P_o \\ U_o \end{pmatrix}. \quad (A6)$$

When the basilar membrane is removed and the cochlear fluids drained,

$$|Z_c|_{Z_o = 0} = |b/d|. \quad (A7)$$

Removing the cochlear load had a negligible effect on $|Z_c|$ below approximately 700 Hz. Hence,

$$\left|aZ_o + b\right|/\left|cZ_o + d\right| \approx \left|b/d\right| (\omega/2\pi \leq 700 \text{ Hz}), \quad (A8)$$

so that

$$\left|aZ_o \right| \ll \left|b\right|, \quad \left|cZ_o \right| \ll \left|d\right|, \quad (A9)$$

and

$$Z_c \approx b/d. \quad (A10)$$

Thus, since

$$T_{me} \approx 1/(aZ_o + b) \approx 1/b, \quad (A11)$$

the structure of the middle and inner ears are such that

$$|Z_c T_{me}| \approx |1/d| \approx |C_{me}/C_c| \quad (A12)$$

and so depends only on the middle ear below 700 Hz.

To estimate middle-ear contributions to $\text{Re } Z_c$, note that at low frequencies models of the cat middle ear (e.g., Lynch, 1981; Carr and Zweig, 1984) predict that the matrix...
elements $a$ and $d$ are both approximately positive real, whereas $b$ and $c$ are, respectively, negative imaginary and positive imaginary. In addition, they suggest that $|bc| < |ad|$. Thus, by Eq. (A5),

$$Re Z_e \approx k \left( Re Z_o + R_{me} \right), \quad (A13)$$

where

$$k \approx a/d \quad \text{and} \quad R_{me} \approx Re(b/d) \quad (A14)$$

are constants.

Allen (1986) has measured $Re Z_e$ while varying the cochlear load, and those measurements can be used to estimate the value of the resistance $R_{me}$. According to Allen’s measurements, removing the cochlear load decreases $Re Z_e$ by approximately 10–15 dB (or roughly a factor of 4) below 700 Hz. Hence,

$$R_{me} \equiv Re Z_e \bigg|_{Z_o = 0} \approx \frac{k R_C}{3} \quad (A15)$$

where $R_C$ represents the resistance of the cochlea. Equation (A15) gives the approximate value of $R_{me}$, determined by middle-ear mechanics, in terms of the known cochlear resistance. Thus,

$$Re Z_e \approx k \left( Re Z_o + R_C / 3 \right) \quad (A16)$$

Using Eqs. (A12) and (A16) in Eq. (A1) for $\eta_{me}(\omega)$ yields the expression, namely Eq. (63), used in the text:

$$\eta_{me}(\omega; Re Z_o) \approx \frac{\alpha Re Z_o}{Re Z_o + R_C / 3} \quad (\omega/2\pi \leq 700 \text{ Hz}), \quad \alpha \equiv \left( 1/k \right) \left( C_{me}/C_e \right)^2 \quad (A17)$$

The measurements of Guinan and Peake (1967) indicate that $C_{me} \approx 2.5 \times 10^{-6} \text{ cm}^2/\text{dyn}$ and Lynch (1981) provides the average value $C_e \approx 2.36 \times 10^{-7} \text{ cm}^2/\text{dyn}$. Combining the measurements of Allen (1986) with Lynch et al.’s (1982) determination of $R_C$ and Shaw’s (1974) measurements of the cross-sectional area of the ear canal yields the estimate $k \approx 1/85^3$. Consequently, $\alpha \approx 0.8$. Note that the value relies on measurements from many cats and thus provides only a rough estimate of its value in any individual. Nonetheless, Eq. (A17) can be used, when combined with model predictions of $Re Z_o(\omega)$, to explore the predicted frequency variation of middle-ear efficiency.

The cochlear catastrophe takes its name by analogy with the apparent divergence at low photon energy in the scattering cross section of an electron, the so-called “infrared catastrophe” of quantum electrodynamics (Bloch and Nordsieck, 1937; Feynman, 1961). The word “catastrophe” comes from the Greek “ kata
trophe” meaning “to turn down” and describes the ironic reversal in fortune characteristic of the dénouement of a classical tragedy. Appropriately, models of cochlear mechanics exhibiting the catastrophe display a pronounced decrease in the magnitude of the cochlear input impedance and a sharp fall-off in energy transfer to the cochlea at low frequencies.

The situation in nonmammals may be more complex (e.g., Rosowski et al., 1984).

Lynch et al. (1982) measure the ratio $P_o/U$, where $P_o$ is the pressure in the scala vestibuli. As defined by Eq. (1), however, the cochlear input impedance $Z_G(\omega)$ is the ratio of the pressure difference

$$P = P_o - P_i \quad (A10)$$

between the scala vestibuli and scala tympani to the fluid volume velocity $U$ in the scala vestibuli. The measurements of Nedzelnitsky (1980) indicate, however, that

$$P_o \geq P_i \quad (\omega/2\pi \geq 100 \text{ Hz}), \quad (A11)$$

so that $P \approx P_i$ at frequencies greater than 100 Hz in the basal turn of the cat cochlea. Lynch et al. (1982) refer to $Z_o$ as the “input impedance across the cochlear partition” and denote it by $Z_e$.

Sondhi (1978) has shown, for example, that the input impedance of a two-dimensional cochlear model is essentially identical with the one-dimensional result. However, the effects of the vestibule have yet to be carefully investigated.

Three related spatial variables $(x, \chi, \zeta)$ are used in this paper. The first, with dimensions

$$[x] = \text{length},$$

represents distance along the organ of Corti. The second, with dimensions of acoustic impedance,

$$[\chi] = \text{mass/length}^2/\text{time},$$

is used to transform the transmission-line equations (4) and (5) into a form [namely Eq. (10) for $P$] without explicit first derivatives of the dependent variable. The coordinate $\chi$ will later be shown to be the most natural for a description of wave propagation in the cochlea. The third spatial variable, $\zeta$, represents length measured in units of the distance over which the characteristic frequency changes by about an octave in the basal turn and is introduced to simplify expressions involving the dependence of model parameters on position.

Throughout this paper when a function, say $Z(x, \omega)$, is written as a function of another spatial variable, say $\chi$, we adopt the notational convention that

$$Z(x, \omega) \equiv Z(x(\chi, \omega), \omega).$$

Viergever and de Boer (1987) obtained a similar approximate form [to which Eq. (13) reduces when the series impedance $Z$ is independent of position] for the “matching impedance” of a nonuniform transmission line and found it to be in excellent agreement with numerical calculations.

The traditional accent of the ecstacy of catastrophe.

The least frequencies $Z$ may acquire a real part arising from viscous effects. That contribution should be small in the basal turn if the ratio $\epsilon$, of the viscous boundary layer thickness to the radius of the scala vestibuli (or tympani) satisfies

$$\epsilon = \sqrt{\pi} / \eta \langle S \rangle \ll 1.$$ 

Here, $\rho$ and $\eta$ are, respectively, the density and coefficient of viscosity of the cochlear fluids, and $S$ is the cross-sectional area of the scala. The values $\rho = 1g/cm^3$, $\eta = 0.02g/cm\cdot s$ (von Békésy, 1960), and $S = 0.01cm^2$ (e.g., Wever, 1949; Dallos, 1970) indicate that the inequality is satisfied at frequencies

$$\omega/2\pi \geq 3 \text{ Hz}.$$

The predictions of scaling symmetry are consistent with Greenwood’s (1961) demonstration that von Békésy’s post-mortem measurements of the static volume elasticity $E(x)$ of the organ of Corti obey the approximate scaling relation

$$E(x) \approx \left( \omega_0/\omega \right) E_0 \quad (A19)$$

in a variety of animals, from mice to elephants.

Although a typical mammalian cochlea consists of a coiled tube containing three chambers (the scala vestibuli, the scala media, and the scala tympani), simple models of cochlear mechanics approximate the structure by two chambers (the scala vestibuli and scala tympani) separated by the organ of Corti with its basilar membrane. In that simplified view, the quantity $S_0$ appearing in Eq. (42) does not represent the true area of the scala vestibuli but should include some fraction of the area $S_{me}$ of the scala media. Since $S_0 \ll S$, at the basal end of the cochlea, however, that correction is small.

Similar results are obtained in guinea pigs by combining the anatomical measurements of Fernández (1952) with the basilar membrane stiffness measurements of Guimer et al. (1981). The analysis, however, is not definitive, both because Guiner et al.’s estimate of the slope of the stiffness variation is uncertain (their measurements are confined to only a small patch of the basilar membrane) and because the relationship between the point stiffness they measure and the effective volume compliance $C$ appearing in the equations is not well understood.
The Appendix of the companion paper (Shera and Zweig, 1991a) shows
that Eq. (60) for \( Z_0(\omega) \) captures the leading-order behavior of the cochlear
input impedance, even in models that exhibit the cochlear catastrophe.

\[
Z_0 \approx (i\omega L_0) \left[ R_0 + i\omega C_0 \right] \quad (\omega \ll \omega_c),
\]

where
\[
R_0 = \frac{\lambda_0}{\omega}, \quad \text{and} \quad L_0 = 2\omega_0/\omega_c.
\]

Note that Lynch et al. (1982) represented their averaged measurements with a phenomenological network model, which reduces, at frequencies greater than approximately 100 Hz, to a resistance \( R_c \) in parallel with an inductance \( M_c \) (their notation). Like Dallos (1970), Lynch et al. (1982) speculate that the inductive term arises from effects at the apical end of the cochlea. As shown here and in Allen (1979) and Puria and Allen (1991), inductive effects can arise from the spatial variation of the wavelength near the stapes.

The companion paper (Shera and Zweig, 1991a) shows that Eq. (60) for \( Z_0(\omega) \) reduces, at frequencies greater than approximately 100 Hz, to a resistance \( R_c \) in parallel with an inductance \( M_c \) (their notation). Like Dallos (1970), Lynch et al. (1982) speculate that the inductive term arises from effects at the apical end of the cochlea. As shown here and in Allen (1979) and Puria and Allen (1991), inductive effects can arise from the spatial variation of the wavelength near the stapes.

\[
Z_0(\omega) \approx \frac{1}{\omega} \left[ R_0 \pm \frac{\omega L_0}{\omega_c} \right] \quad (\omega \ll \omega_c),
\]

where
\[
R_0 = \frac{\lambda_0}{\omega}, \quad \text{and} \quad L_0 = 2\omega_0/\omega_c.
\]

Note that Lynch et al. (1982) represented their averaged measurements with a phenomenological network model, which reduces, at frequencies greater than approximately 100 Hz, to a resistance \( R_c \) in parallel with an inductance \( M_c \) (their notation). Like Dallos (1970), Lynch et al. (1982) speculate that the inductive term arises from effects at the apical end of the cochlea. As shown here and in Allen (1979) and Puria and Allen (1991), inductive effects can arise from the spatial variation of the wavelength near the stapes.

The companion paper (Shera and Zweig, 1991a) shows that Eq. (60) for \( Z_0(\omega) \) reduces, at frequencies greater than approximately 100 Hz, to a resistance \( R_c \) in parallel with an inductance \( M_c \) (their notation). Like Dallos (1970), Lynch et al. (1982) speculate that the inductive term arises from effects at the apical end of the cochlea. As shown here and in Allen (1979) and Puria and Allen (1991), inductive effects can arise from the spatial variation of the wavelength near the stapes.

\[
Z_0(\omega) \approx \frac{1}{\omega} \left[ R_0 \pm \frac{\omega L_0}{\omega_c} \right] \quad (\omega \ll \omega_c),
\]

where
\[
R_0 = \frac{\lambda_0}{\omega}, \quad \text{and} \quad L_0 = 2\omega_0/\omega_c.
\]

Note that Lynch et al. (1982) represented their averaged measurements with a phenomenological network model, which reduces, at frequencies greater than approximately 100 Hz, to a resistance \( R_c \) in parallel with an inductance \( M_c \) (their notation). Like Dallos (1970), Lynch et al. (1982) speculate that the inductive term arises from effects at the apical end of the cochlea. As shown here and in Allen (1979) and Puria and Allen (1991), inductive effects can arise from the spatial variation of the wavelength near the stapes.

The companion paper (Shera and Zweig, 1991a) shows that Eq. (60) for \( Z_0(\omega) \) reduces, at frequencies greater than approximately 100 Hz, to a resistance \( R_c \) in parallel with an inductance \( M_c \) (their notation). Like Dallos (1970), Lynch et al. (1982) speculate that the inductive term arises from effects at the apical end of the cochlea. As shown here and in Allen (1979) and Puria and Allen (1991), inductive effects can arise from the spatial variation of the wavelength near the stapes.

\[
Z_0(\omega) \approx \frac{1}{\omega} \left[ R_0 \pm \frac{\omega L_0}{\omega_c} \right] \quad (\omega \ll \omega_c),
\]

where
\[
R_0 = \frac{\lambda_0}{\omega}, \quad \text{and} \quad L_0 = 2\omega_0/\omega_c.
\]

Note that Lynch et al. (1982) represented their averaged measurements with a phenomenological network model, which reduces, at frequencies greater than approximately 100 Hz, to a resistance \( R_c \) in parallel with an inductance \( M_c \) (their notation). Like Dallos (1970), Lynch et al. (1982) speculate that the inductive term arises from effects at the apical end of the cochlea. As shown here and in Allen (1979) and Puria and Allen (1991), inductive effects can arise from the spatial variation of the wavelength near the stapes.


