Human middle-ear model with compound eardrum and airway branching in mastoid air cells

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An acoustical/mechanical model of normal adult human middle-ear function is described for forward and reverse transmission. The eardrum model included one component bound along the manubrium and another bound by the tympanic cleft. Eardrum components were coupled by a time-delayed impedance. The acoustics of the middle-ear cleft was represented by an acoustical transmission-line model for the tympanic cavity, aditus, antrum, and mastoid air cell system with variable amounts of excess viscothermal loss. Model parameters were fitted to published measurements of energy reflectance (0.25–13 kHz), equivalent input impedance at the eardrum (0.25–11 kHz), temporal-bone pressure in scala vestibuli and scala tympani (0.1–11 kHz), and reverse middle-ear impedance (0.25–8 kHz). Inner-ear fluid motion included cochlear and physiological third-window pathways. The two-component eardrum with time delay helped fit intracochlear pressure responses. A multi-modal representation of the eardrum and high-frequency modeling of the middle-ear cleft helped fit ear-canal responses. Input reactance at the eardrum was small at high frequencies due to multiple modal resonances. The model predicted the middle-ear efficiency between ear canal and cochlea, and the cochlear pressures at threshold.

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Pages: 2698–2725

NOMENCLATURE

Below are abbreviations and often used symbols not otherwise referenced in Figs. 1 and 2 or Table I.

ER	Energy reflectance
FEM	Finite element model
MAP	Minimum audible pressure
ME	Middle ear
MEE	Middle-ear efficiency
MACS	Mastoid air cell system
OAE	Otoacoustic emission
RMS	Root mean squared
SFOAE	Stimulus frequency OAE
ST	Scala tympani
SV	Scala vestibuli
TM	Tympanic membrane
VEMP	Vestibular evoked myogenic potential
$\hat{A}_F$	Effective area for force
$\hat{A}_V$	Effective area for velocity
$\hat{N}_P$	Effective transformer ratio for pressure
$\hat{N}_U$	Effective transformer ratio for volume velocity
N_1	Transformer ratio for single-piston eardrum
N_2	Transformer ratio for ossicular-bound component of two-component eardrum
ΔP_{co}^{MA}	Cochlear pressure difference at the MAP
$\mathcal{R}_v^R$	Reverse middle-ear pressure reflectance
S_e	Area of ear canal
S_f	Area of free component of two-component eardrum

S_o	Area of ossicular-bound component of two-component eardrum
S_{TM}	Total area of TM
V_{st}	Stapes velocity
V_u	Umbo velocity
W_c	Acoustical power absorbed by the cochlea
W_e	Acoustical power absorbed by the middle ear
$Z_{c,e}$	Characteristic impedance of ear canal
Z_{co}	Cochlear input impedance
Z_{in}^R	Reverse middle-ear impedance
ΔZ_{co}	Differential cochlear impedance

I. INTRODUCTION

This study formulates a lumped-element circuit model of adult human middle-ear mechanics based on comparisons with measured air-conduction data. The middle-ear model is novel in three respects. First, the tympanic membrane (TM) has two components, which allows relative motion between a component bound to the manubrium and a freely moving component (termed free component) that drives an acoustic motion within the tympanic cleft. These components are coupled via a time-delayed impedance. The free component includes multiple modes of oscillation with varying resonance frequencies. Second, the model includes the acoustical effects of the tympanic cavity, aditus, and antrum terminated by the impedance of a branching airway model of the mastoid air cell system, which are calculated using the model in Keefe (2015). Three, fluid motion within the inner ear is directed into the cochlea, but may have alternate sound paths, termed physiological third windows, for motions in such structures as the “neurovascular channels, vestibular

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aqueduct, cochlear aqueduct, etc.” (Stieger *et al.*, 2013). The present model includes such third-window effects.

The range of transfer function measurements related to middle-ear function is extensive (Puria, 2003). For forward transmission of a sound from ear canal to cochlea, these include input, or single-point, transfer functions measured in the ear canal such as impedance and reflectance, and transmission, or two-point, transfer functions such as the ratio of the stapes velocity, or of the pressure at the oval or round window, to the ear-canal pressure. For reverse transmission of a source of vibration at the round window or a pressure source within the cochlea, these include input response functions measured in the cochlea at the oval window such as impedance and reflectance, and transmission functions such as the ratio of ear-canal pressure to stapes velocity or to pressure at the oval window. Acoustic transfer functions can be defined at pairs of locations within the tympanic cleft or inner ear. This report describes model predictions for all of these types of transfer functions, in which a subset of measurements is used to calculate the unknown model parameters while other measurements are used to evaluate the generalizability of the model.

Model parameters were fitted based on forward-transmission acoustical transfer functions measured in the ear canal from Margolis *et al.* (1999) of the equivalent input impedance at the TM and the energy reflectance over frequencies from 0.25 to 11 kHz, and on data from Stinson (1990) of energy reflectance up to 13 kHz. The equivalent input impedance at the TM was based on measurements of input impedance at the probe tip within the ear canal using an acoustic transmission line model of the ear canal, which was assumed to have a cylindrical geometry specified by the measured cross-sectional area of the ear canal at the probe tip and the estimated canal length. The procedures by which the equivalent input impedance at the TM were calculated were described in Margolis *et al.* (1999).

Parameters were also fitted based on data from Nakajima *et al.* (2008) of pressure transfer functions from the ear canal to scala vestibuli (SV) or scala tympani (ST). These data were obtained in human temporal bones between the ear canal and cochlea over frequencies from 0.1 to 11 kHz. Last, parameters were fitted to the reverse middle-ear impedance data from Puria (2003) for frequencies from 0.25 to 8 kHz.

Previous middle-ear models of direct relevance to the present study are briefly described. A two-piston model of the eardrum was formulated (Shaw, 1977; Shaw and Stinson, 1981) to represent the parts of the eardrum coupled and uncoupled to the ossicular chain, and further analyzed in models (Shera and Zweig, 1991a; Goode *et al.*, 1994). Stinson (1990) applied the 1981 two-piston model to predict energy reflectance in the ear canal, but these predictions differed from measured data above 8 kHz. A problem was that the predicted energy reflectance approached one at high frequencies due to the large input reactance of the middle ear at high frequencies, whereas high-frequency measurements of energy reflectance had smaller values.

Puria and Allen (1998) reported experimental evidence for the presence of time delay in the cat eardrum by modeling the eardrum as a distributed parameter transmission line. The human middle-ear model of O'Connor and Puria (2008)

included such an eardrum transmission line with a time delay of 46 μ s. Parent and Allen (2010) described a human middle-ear model that included a time-domain wave model of the eardrum, and reported agreement with experimental results up to 5 kHz, but discrepancies at higher frequencies. Limitations of these eardrum models with time delay included: (1) the mechanical-acoustical interactions of the eardrum with the air enclosed within the structures of the tympanic cleft were not described and (2) observed eardrum motions with modal standing waves (de La Rouchefoucauld *et al.*, 2010; Cheng *et al.*, 2010) were not described.

In the middle-ear circuit model of Zwislocki (1962), the impedance of the tympanic cleft was placed in series with the circuit representing the eardrum, ossicular chain, and cochlea. This circuit topology lacks the property that the oval and round windows are also boundaries of the tympanic cleft with respect to the fluids within the cochlea. To predict intracochlear pressures within cochlear fluid, it is necessary to describe the boundary conditions between the tympanic cleft at each of the eardrum, oval, and round windows (Peake *et al.*, 1992; Shera and Zweig, 1992). A model that adequately represented these boundary conditions was that of Shera and Zweig (1992), which modified the middle-ear model of Kringlebotn (1988). This model represented the eardrum as a single piston.

The oval and round windows are boundaries through which middle-ear vibrations couple to acoustical volume velocities in the inner-ear fluids. Stieger *et al.* (2013) reported evidence for an additional “third window” for inner-ear fluid motion in normal human temporal bones based on simultaneous measurements of stapes footplate velocity and pressures in SV and ST. These data were interpreted using a lumped-element circuit model adapted from Merchant and Rosowski (2008).

The present model incorporates these additional shunt pathways for inner-ear fluid. The middle-ear model includes a two-compartment eardrum model with time delay in which the compartment with a boundary on the tympanic cleft has multiple modal resonances. However, the model does not include bone-conduction effects.

This introduction concludes with a brief description of finite element models (FEMs) of human middle-ear function, and a contrast of differences with the lumped-element and one-dimensional transmission line approaches used in the present model. Funnell *et al.* (2013) reviewed FEMs of the human and other mammalian middle ears. A FEM model of human middle ear mechanics and the passive mechanics of the cochlea (Gan *et al.*, 2007; Zhang and Gan, 2011) was extended to predict the absorbance in the ear canal of adults (Zhang and Gan, 2013). A FEM model of the ear canal and middle ear was used to analyze the role of the human mastoid cavity on sound transmission (Lee *et al.*, 2010). Recent FEMs of human middle-ear function used realistic, three-dimensional, descriptions of middle-ear anatomy and required fitting of a larger number of model parameters. Parameter values were selected based on some combination of level-and frequency-dependent measurements of the biological tissues comprising the middle ear, and by constraining the FEM to accurately predict one or more middle-ear

transfer functions. FEMs are a powerful tool to predict tympanometric responses and nonlinearities in middle-ear function and model the three-dimensional dynamics associated with the translations and rotations of the ossicular chain. FEMs have not included realistic descriptions of the airway branching of the mastoid air cell system (MACS), possibly due to the absence of detailed anatomical data describing the connectivity of the airways. Their acoustical effects have been subsumed in some FEMs as a part of the volume of the mastoid cavity.

Lumped-element and one-dimensional transmission line models of middle-ear function have advantages as well. These models can easily be generalized to include ear-canal and cochlear models, and their computational complexity is much less than for a FEM. Many experimental studies have reported findings in terms of one-dimensional acoustical/mechanical transfer functions. Their measurements in some parts of the middle or inner ear were represented using a lumped-element circuit or transmission line whose equivalent circuit and parameter values may be directly incorporated into a more complete model of middle-ear function. Such an approach validates the sub-section of the model using such an equivalent circuit. This appears to be a simpler validation approach than is possible with a FEM.

The present study used this approach for several transfer functions described below. This ensured that the resulting model was accurate for those aspects of middle-ear function for which there were explicit data. The present model was analyzed with respect to a more diverse set of middle-ear measurements than has been used previously with other models.

II. MODEL FORMULATION

A. Framework

Middle-ear mechanics and acoustical transmission in the ear canal and cochlear are assumed to have linear dynamics, and to be based on a one-dimensional model. The latter is a strong assumption inasmuch as the mechanical dynamics of each ossicle have additional translational and rotational degrees of freedom. The validity of this assumption is assessed in the present study by the degree to which the model predictions are in accord with experimental measurements in the ear canal and within the cochlear fluids.

The overall framework is represented using a one-dimensional model (Shera and Zweig, 1991a, 1992). This section summarizes the transfer-function framework introduced by Shera and Zweig and extends it to include shunt motions in inner-ear fluids. All variables (except where otherwise stated) are functions of frequency f or radian frequency $\omega = 2\pi f$ with time dependence $e^{j\omega t}$ using $j = \sqrt{-1}$. A transfer matrix $\mathbf{T}$ relates pairs of generalized forces and velocities in a two-port network, in which each pair of generalized force and velocity is represented by a column vector with two elements. The transfer matrix is a 2×2 complex matrix that describes the frequency response of a linear system. It has a unit determinant in a linear system due to reciprocity, as is applicable to transfer matrices used to model the middle ear and ear canal.

As shown in Fig. 1, a transfer function $e^{\hat{\mathbf{T}}_u}$ from ear canal to umbo relates the mechanical force F_u and velocity V_u at the umbo to the acoustical pressure P_e and volume velocity U_e within the ear canal just in front of the eardrum by

FIG. 1. Transfer matrix framework for middle-ear models. The names of the dynamical variables are listed on the figure. The inner-ear circuit includes elements for the cochlea and for third-window shunt pathways at SV and ST.

$$\begin{pmatrix} P_e - P_{tc} \\ U_e \end{pmatrix} = {}^e\hat{\mathbf{T}}_u \begin{pmatrix} F_u \\ V_u \end{pmatrix}. \quad (1)$$

The hat above ${}^e\hat{\mathbf{T}}_u$ denotes that the ear-canal pressure P_e is with respect to the pressure P_{tc} in the tympanic cavity on the inner side of the eardrum. The characteristic impedance $Z_{c,e}$ of the ear canal is expressed in terms of the equilibrium air density ρ , phase velocity of sound c , and cross-sectional area S_e of the ear canal by

$$Z_{c,e} = \rho c / S_e. \quad (2)$$

Following [Shera and Zweig \(1991a\)](#), the matrix elements of ${}^e\hat{\mathbf{T}}_u$ are expressed in terms of effective areas for force $\hat{A}_F$ and velocity $\hat{A}_V$, and an eardrum transfer impedance $\hat{Z}_e$ and eardrum transfer admittance $\hat{Y}_e$ by

$${}^e\hat{\mathbf{T}}_u = \begin{pmatrix} \hat{A}_F^{-1} & \hat{Z}_e \\ \hat{Y}_e & \hat{A}_V \end{pmatrix}. \quad (3)$$

Each effective area has the physical dimensions of area. With the malleus held fixed ($V_u = 0$), $\hat{A}_F$ represents the area by which the pressure difference $P_e - P_{tc}$ must be multiplied to equal the umbo force F_u . With the ossicular load removed ($F_u = 0$), $\hat{A}_V$ represents the area by which the umbo velocity V_u must be multiplied to equal the volume velocity U_e . Expressed for forward transmission as the ratio of an output umbo variable to an input acoustical variable in the ear canal, these relations are

$$\begin{aligned} \hat{A}_F &= \left. \frac{F_u}{(P_e - P_{tc})} \right|_{V_u=0}, \\ \hat{A}_V^{-1} &= \left. \frac{V_u}{U_e} \right|_{F_u=0}. \end{aligned} \quad (4)$$

Each effective area would equal the eardrum area if the eardrum were a rigid piston, but each varies with frequency in the two-component eardrum model.

Again expressed for forward transmission as the ratio of an output umbo variable to an input acoustical variable in the ear canal, the eardrum transfer impedance and transfer admittance satisfy a free and blocked boundary condition, respectively, on umbo variables as follows:

$$\begin{aligned} \hat{Z}_e^{-1} &= \left. \frac{V_u}{(P_e - P_{tc})} \right|_{F_u=0}, \\ \hat{Y}_e^{-1} &= \left. \frac{F_u}{U_e} \right|_{V_u=0}. \end{aligned} \quad (5)$$

The right-hand side of the top relation converges to the measured transfer function between umbo velocity and ear-canal pressure in front of the TM in the limit that F_u and P_{tc} approach zero.

The transfer function ${}^u\hat{\mathbf{T}}_{ow}$ from umbo to oval window relates the acoustical pressure P_{ow} and volume velocity U_{ow} just inside the cochlear at SV to the mechanical force and velocity at the umbo by

$$\begin{pmatrix} F_u \\ V_u \end{pmatrix} = {}^u\hat{\mathbf{T}}_{ow} \begin{pmatrix} P_{ow} - P_{tc} \\ U_{ow} \end{pmatrix}. \quad (6)$$

The hat above ${}^u\hat{\mathbf{T}}_{ow}$ denotes that the SV pressure P_{ow} is evaluated with respect to the pressure P_{tc} (see Fig. 1).

The pressure P_{tc} within the tympanic cleft at the approximate midpoint of the TM is assumed equal in a long-wave approximation to the pressures within the tympanic cleft acting over the oval and round windows. This approximation was previously used by [Shera and Zweig \(1992\)](#), and is adopted in the present study to model the tympanic cleft using a one-dimensional model.² The input impedance Z_{cav} of the middle-ear cleft at this location in the tympanic cavity is related to the volume velocities out of the TM and into each of the oval and round windows by

$$P_{tc} = Z_{cav}(U_e - U_{ow} - U_{rw}). \quad (7)$$

As shown in Fig. 1, the volume velocity of the round window is U_{rw} . The cochlear fluids and internal structures are assumed to be incompressible.

The cascade of a pair of sections of the transmission line is represented by matrix multiplication of the transfer matrices. Thus, the acoustical variables in the ear canal and oval window are related by³

$$\begin{pmatrix} P_e - P_{tc} \\ U_e \end{pmatrix} = {}^e\hat{\mathbf{T}}_u {}^u\hat{\mathbf{T}}_{ow} \begin{pmatrix} P_{ow} - P_{tc} \\ U_{ow} \end{pmatrix}. \quad (8)$$

An eardrum-to-oval window transfer matrix ${}^e\hat{\mathbf{T}}_{ow}$ is defined for the matrix product in the above equation, and parameterized in terms of complex transfer coefficients $\hat{N}_P^{-1}$, $\hat{Z}$, $\hat{Y}$, and $\hat{N}_U$ by

$${}^e\hat{\mathbf{T}}_{ow} = {}^e\hat{\mathbf{T}}_u {}^u\hat{\mathbf{T}}_{ow} = \begin{pmatrix} \hat{N}_P^{-1} & \hat{Z} \\ \hat{Y} & \hat{N}_U \end{pmatrix}. \quad (9)$$

As described by [Shera and Zweig \(1992\)](#), $\hat{N}_P$ is an effective transformer ratio for pressure and $\hat{N}_U$ is an effective transformer ratio for volume velocity.

The circuit in Fig. 1 also includes a model of sound transmission in the inner ear that includes a differential cochlear impedance ΔZ_{co} , shunt admittance Y_{3v} for a third window in SV, and shunt admittance Y_{3t} for a third window in ST. The circuit relations Y_{3v} and Y_{3t} implicit in Fig. 1 are those of [Stieger et al. \(2013\)](#). Viewed from the port through which U_{ow} exits, the volume velocity through the vestibular pathway is $Y_{3v}P_{ow}$, so that the volume velocity U_{co} through the cochlea is

$$U_{co} = U_{ow} - Y_{3v}P_{ow}. \quad (10)$$

The differential cochlear impedance ΔZ_{co} relates the volume velocity through it to the pressure difference $\Delta P_{co} = P_{ow} - P_{rw}$ across it,

$$\Delta P_{co} = P_{ow} - P_{rw} = \Delta Z_{co} U_{co}. \quad (11)$$

The name differential cochlear impedance derives from the finding that it is the pressure difference between the oval and

round windows that generates the cochlear traveling wave in the normal ear (Békésy, 1960). This contrasts with a definition of the cochlear input impedance Z_{co} as the ratio of the pressure difference $P_{ow} - P_{tc}$ across the oval window to the volume velocity U_{ow} swept out by the stapes footplate,

$$Z_{co} = (P_{ow} - P_{tc})/U_{ow} = \Delta Z_{co} + Z_{rw}. \quad (12)$$

This cochlear input impedance is equal to the sum of the differential cochlear impedance and the impedance of the round window. In the limit that $P_{tc} = 0$, Z_{co} is the ratio of pressure in the vestibule to the volume velocity swept out by the stapes windows. Equation (12) only holds if there are no third windows (i.e., if $Y_{3v} = Y_{3t} = 0$), and is used only in the Discussion. It is ΔZ_{co} in Eq. (11) rather than Z_{co} that is used to formulate the present model.

The volume velocity through the third window in ST is expressed in terms of the pressure P_{rw} at the round window by $Y_{3t}P_{rw}$, so that the volume velocity through the impedance Z_{rw} is $U_{co} - Y_{3t}P_{rw} = U_{ow} - Y_{3v}P_{ow} - Y_{3t}P_{rw}$. The pressure difference $P_{rw} - P_{tc}$ is related to this volume velocity by

$$P_{rw} - P_{tc} = Z_{rw}(U_{ow} - Y_{3v}P_{ow} - Y_{3t}P_{rw}). \quad (13)$$

As shown in Fig. 1, the volume velocity through Z_{rw} is U_{rw} . It follows from this observation and Eq. (13) that

$$U_{rw} = -U_{ow} + Y_{3v}P_{ow} + Y_{3t}P_{rw}. \quad (14)$$

The U_{ow} and U_{rw} are equal and opposite in the absence of third-window effects ($Y_{3v} = Y_{3t} = 0$).

A particular middle-ear model is generated with this framework by specifying all matrix elements of ${}^e\hat{T}_u$ and ${}^o\hat{T}_{ow}$, the impedances Z_{cav} , Z_{rw} , and ΔZ_{co} , and the shunt admittances Y_{3v} and Y_{3t} (see Fig. 1). Reverse middle-ear models also require specification of the impedance of the ear-canal termination. Individual parts of this model are described below.

B. Tympanic membrane

To construct the two-component TM model, the mechanical TM displacement (from equilibrium) is considered in the time domain in terms of the displacement $x_f(t)$ of the larger part of the TM that is free of the umbo, and the displacement $x_o(t)$ of the smaller part of the TM that is attached to the umbo (with subscripts f for free and o for ossicular-bound, respectively). The free component is driven over its area S_f by the pressure difference $P_e - P_{tc}$ between the ear canal and tympanic cavity. The component attached to the ossicular chain at the umbo is driven by the difference in force between this pressure difference acting over the area S_o of the attachment and the force acting on the umbo $F_u(t)$, i.e., $S_o[P_e(t) - P_{tc}(t)] - F_u(t)$. The free part of the TM has a much larger area than that bound to the umbo, i.e., $S_f \gg S_o$, with a total eardrum area S_{TM} given by

$$S_{TM} = S_f + S_o. \quad (15)$$

The coupling between components is represented by a mechanical compliance C_{mC} , with a net force proportional to

the difference in the displacement of the component at time t and the other component at an earlier time $t - \tau$.

The time τ represents an internal travel time on the TM between the components. It is assumed that this internal travel time arises between some unspecified type of wave motion on the TM. In the absence of modeling the TM as a continuous medium, the presence of such a wave motion is represented in this lumped, two-component eardrum model as an internal delay.

The coupled time-delayed oscillator equations take the form

$$\begin{aligned} M_f \frac{d^2 x_f(t)}{dt^2} &= S_f [P_e(t) - P_{tc}(t)] - R_{mf} \frac{dx_f(t)}{dt} - C_{mf}^{-1} x_f(t) \\ &\quad - C_{mC}^{-1} [x_f(t) - x_o(t - \tau)], \\ M_o \frac{d^2 x_o(t)}{dt^2} &= (S_o [P_e(t) - P_{tc}(t)] - F_u) \\ &\quad - R_{mo} \frac{dx_o(t)}{dt} - C_{mo}^{-1} x_o(t) \\ &\quad - C_{mC}^{-1} [x_o(t) - x_f(t - \tau)], \end{aligned} \quad (16)$$

with M for mass, R_{mf} (R_{mo}) for mechanical resistance, and C_{mf} (C_{mo}) for mechanical compliance, i.e., inverse stiffness, of the free (ossicular-coupled) component. Throughout this report, an initial subscript m present on any impedance parameter denotes that it is a mechanical impedance parameter; any other initial letter signifies an acoustical impedance parameter. This pair of equations reduces for $\tau = 0$ to a “two-piston model” (Shaw, 1977; Shaw and Stinson, 1981), i.e., a pair of coupled oscillators.

It is convenient to transform this mechanical system into an equivalent acoustical system in the frequency domain in terms of the corresponding acoustical impedances Z_f , Z_o , and Z_C defined by

$$\begin{aligned} Z_f &= [j(\omega M_f - C_{mf}^{-1}/\omega) + R_{mf}]/S_f^2, \\ Z_o &= [j(\omega M_o - C_{mo}^{-1}/\omega) + R_{mo}]/S_o^2, \\ Z_C &= (j\omega C_{mC})^{-1}/S_f^2. \end{aligned} \quad (17)$$

The frequency dependence of any variable is omitted whenever its meaning is clear. The mechanical system is represented in terms of displacements $x_f(t)$ and $x_o(t)$ of the two components of the TM, which have Fourier transforms $X_f(f)$ and $X_o(f)$, respectively. For time-delayed variables, the Fourier transform of $x_f(t - \tau)$ is $X_f e^{-j\omega\tau}$, and the transform of $x_o(t - \tau)$ is $X_o e^{-j\omega\tau}$. The equivalent acoustical system is expressed in terms of the volume velocities of the free component $U_f = j\omega X_f$ and the ossicular-bound component $U_o = j\omega X_o$. The equation of continuity for the total volume velocity U_e in the ear canal just in front of the TM and the volume velocity swept out by the TM is

$$U_e = U_f + U_o. \quad (18)$$

The dimensionless ratio κ of the area of the free component of the TM to the area of the ossicular-bound component is defined by

TABLE I. Middle-ear model parameters. A blank entry for the unit of any parameter indicates a dimensionless value. A value in column Code is blank when estimated from published experimental values, O when estimated in the main optimization, M when estimated in the optimization to determine the MACS geometry, and L for the low-loss condition of ξ_V and ξ_T . The source of each fixed parameter value is referenced in some cases in terms of the report of the measurement and in other cases from modeling papers or books. Sources of parameters include: L_e in reverse transmission (Puria, 2003), S_{TM} and k_2 (Kringelbotn, 1988), κ (Shera and Zweig, 1991a), m_s (Merchant *et al.*, 1996), S_s (Békésy, 1960), ΔZ_{co} and round window parameters C_{rw} , I_{rw0} , and R_{rw0} (Nakajima *et al.*, 2008), tympanic cleft parameters (Singh, 2007) adjusted to the geometry of connected rectangular-side cavities, and thermodynamic air constants evaluated at a body temperature of 37°C (Benade, 1968). The annular ligament compliance C_{mal} was estimated as the value with m_s that results in a resonance frequency of 3 kHz. This is the measured resonance frequency for the series combination of the cochlear impedance and the stapes impedance [expressed as an equivalent acoustical impedance as in Eq. (40)] for the condition in which the cochlear fluid was drained (Merchant *et al.*, 1996). The mechanical resistance R_{mal} of the annular ligament was selected such that its equivalent acoustical resistance was 10 G Ω . This is the same value used in the model of O'Connor and Puria (2008), and slightly larger than the model-derived estimate of 5.7 G Ω by Merchant *et al.* (1996), which was based on their measured data.

Section	Code	Parameter	Value	Units (SI)
Ear canal		S_e	0.503×10^{-4}	m^2
		L_e	0.2×10^{-2}	m
Eardrum		S_{TM}	0.60×10^{-4}	m^2
		κ	9	
	O	I_1	11.2×10^3	kg m^{-4}
	O	C_1	2.39×10^{-12}	$\text{kg}^{-1} \text{m}^4 \text{s}^2$
	O	R_1	17.8×10^6	$\text{kg m}^{-4} \text{s}^{-1}$
	O	I_2	0.583×10^3	kg m^{-4}
	O	C_2	5.98×10^{-12}	$\text{kg}^{-1} \text{m}^4 \text{s}^2$
	O	R_2	20.7×10^6	$\text{kg m}^{-4} \text{s}^{-1}$
	O	I_3	0.0535×10^3	kg m^{-4}
	O	C_3	1.53×10^{-12}	$\text{kg}^{-1} \text{m}^4 \text{s}^2$
	O	R_3	0.497×10^6	$\text{kg m}^{-4} \text{s}^{-1}$
	O	C_C	6.60×10^{-12}	$\text{kg}^{-1} \text{m}^4 \text{s}^2$
	O	τ	30.2×10^{-6}	s
Ossicular chain		k_2	1.30	
	O	m_m	5.38×10^{-6}	kg
	O	C_{mm}	100	$\text{kg}^{-1} \text{s}^2$
	O	R_{mm}	14.4×10^{-3}	kg s^{-1}
	O	C_{mmi}	0.161×10^{-3}	$\text{kg}^{-1} \text{s}^2$
	O	R_{mmi}	0.0317×10^{-3}	kg s^{-1}
	O	m_i	4.35×10^{-6}	kg
	O	C_{mis}	0.344×10^{-3}	$\text{kg}^{-1} \text{s}^2$
	O	R_{mis}	184×10^{-3}	kg s^{-1}
		C_{mal}	0.899×10^{-3}	$\text{kg}^{-1} \text{s}^2$
		R_{mal}	0.102	kg s^{-1}
		m_s	4.60×10^{-6}	kg
		S_s	0.032×10^{-4}	m^2
Cochlea		ΔZ_{co}	21.1×10^9	$\text{kg m}^{-4} \text{s}^{-1}$
Round window		C_{rw}	9×10^{-14}	$\text{kg}^{-1} \text{m}^4 \text{s}^2$
		I_{rw0}	4.62×10^7	kg m^{-4}
		R_{rw0}	2.34×10^8	$\text{kg m}^{-4} \text{s}^{-1}$
	O	ξ_V (high-loss)	19.8	
	O	ξ_T (high-loss)	8.79	
	L	ξ_V (low-loss)	2.88	
	L	ξ_T (low-loss)	1.78	
Air constants		ρ	1.1369	kg m^{-3}
		B_a	1.4173×10^5	$\text{kg m}^{-1} \text{s}^{-2}$
		η	1.8928×10^{-5}	$\text{kg m}^{-1} \text{s}^{-1}$
		γ	1.4014	
		ν	0.8393	
Shunt pathway admittances		Y_{3t}	0	$(\text{kg m}^{-4} \text{s}^{-1})^{-1}$
		Y_{3v}	$0.35/\Delta Z_{co}$	$(\text{kg m}^{-4} \text{s}^{-1})^{-1}$

$$\kappa = S_f/S_o. \quad (19)$$

This ratio, with value specified in Table I, satisfies $\kappa \gg 1$ inasmuch as most of the TM is freely moving (Shera and Zweig, 1991a). It follows from Eqs. (15) and (19) that

$$S_f = S_{TM} \frac{\kappa}{\kappa + 1}, \quad (20)$$

$$S_o = \frac{S_{TM}}{\kappa + 1}.$$

On combining Eqs. (16)–(19), the coupled, time-delayed oscillator system is expressed as an equivalent acoustical system by

$${}^e\hat{\mathbf{T}}_u = 1/[Z_f + (1 + \kappa e^{-j\omega\tau})Z_C] \begin{pmatrix} Z_f + Z_C & Z_o(Z_f + Z_C) + \kappa^2 Z_C[Z_f + Z_C(1 - e^{-2j\omega\tau})] \\ 1 & Z_o + Z_f + Z_C[(1 + \kappa e^{-j\omega\tau})^2 + \kappa^2(1 - e^{-2j\omega\tau})] \end{pmatrix} \begin{pmatrix} k_1^{-1} & 0 \\ 0 & k_1 \end{pmatrix}, \quad (22)$$

with

$$k_1 = S_o. \quad (23)$$

The transformer ratio k_1 is defined as equal to the area of the part of the eardrum that is bound to the ossicular chain. The right-most matrix in Eq. (22) converts mechanical variables in the ossicular chain into acoustical variables. It is verified analytically that the determinant of ${}^e\hat{\mathbf{T}}_u$ is equal to 1, so that reciprocity is satisfied in this two-component eardrum model with time-delayed coupling.

With specified acoustical impedances Z_f , Z_o , and Z_C , Eqs. (1) and (22) are a detailed model for the two-component TM with time delay between its components. This ${}^e\hat{\mathbf{T}}_u$ reduces to the form of the two-piston model in Shera and Zweig (1991a) when $\tau = 0$. Shera and Zweig considered a “strong coupling limit” between the mechanics of the two pistons in which the two-piston model was expressed in terms of an equivalent single-piston model. The present two-component eardrum model with non-zero time delay does not reduce to an equivalent single-piston model.

Whereas the particular expressions for the impedances in Eq. (17) were used to formulate the eardrum model in Eq. (22), this representation of ${}^e\hat{\mathbf{T}}_u$ may also be applied with any other choices of impedances. This is important because preliminary analyses showed that the impedance models in Eq. (17), especially for Z_f , did not adequately fit the experimental data for any parameter values.

The final optimized model replaces the acoustical impedance Z_f in Eqs. (17) and (22) by a compound oscillator with three modal resonances. This impedance Z_f is re-defined in terms of acoustical inertances I_n , acoustical compliances C_n , and acoustical resistances R_n (with $n = 1, 2, 3$) as follows:⁴

$$Z_f = \left(\sum_{n=1}^3 \{j[\omega I_n - 1/(\omega C_n)] + R_n\}^{-1} \right)^{-1}. \quad (24)$$

$$P_e - P_{tc} = Z_f U_f + Z_C[U_f - \kappa e^{-j\omega\tau} U_o],$$

$$P_e - P_{tc} = S_o^{-1} F_u + Z_o U_o + Z_C \kappa [\kappa U_o - e^{-j\omega\tau} U_f],$$

$$U_o = S_o V_u. \quad (21)$$

The equation of continuity in the bottom row equates the volume velocity U_o of the ossicular-bound component of the TM to the product of its area S_o and the umbo velocity V_u . It follows that $V_u/(j\omega)$ is the Fourier transform of $x_o(t)$ in Eq. (16). The U_f is eliminated from Eq. (21) using Eq. (18), and these equations are recast in terms of the eardrum transfer matrix ${}^e\hat{\mathbf{T}}_u$ in Eq. (1) into the following form:

Regarding the acoustical impedance Z_o of the ossicular-bound component of the TM, its inertance and resistance elements in Eq. (17) are omitted in the final model, because their effects are included in the mechanical parameters m_m and R_{mm} , respectively, which represent the attachment of the eardrum to the umbo [these are introduced below in Eq. (28)]. The re-defined Z_o is expressed in terms of an acoustical compliance C_o by

$$Z_o = (j\omega C_o)^{-1}. \quad (25)$$

Equation (24) for Z_f approaches a compliance-dominated impedance $[j\omega(C_1 + C_2 + C_3)]^{-1}$ as the frequency is reduced towards zero. The compliance of the ossicular-bound component of the TM is assumed to equal the compliance of the freely moving component of the TM at low frequencies, as the material properties of the TM are assumed similar in each compartment. Thus, C_o in Eq. (25) is

$$C_o = C_1 + C_2 + C_3. \quad (26)$$

Multiple modal resonances are not present on the ossicular-bound component of the TM as it is constrained to move with the manubrium. It is assumed that no mechanical resonance exists within the manubrium or in any other ossicle.

Following Eq. (17), the acoustical coupling impedance Z_C is expressed in terms of a compliance C_C by

$$Z_C = (j\omega C_C)^{-1}. \quad (27)$$

The time delay is represented already in Eqs. (21) and (22).

This eardrum model with time-delayed coupling between displacements of two components was formulated based on the finding of TM delay in the cat (Puria and Allen, 1998). One goal was to evaluate the need for such delay in predicting a diverse set of transfer functions. The present

model of TM delay differs from previous models (O'Connor and Puria, 2008; Parent and Allen, 2010) in that the TM is assumed to have multiple compartments coupled by a time-delayed compliance. The multiple modal resonances in the umbo-free component of the TM approximate the types of eardrum motions with modal standing waves that have been observed in gerbil (de La Rouchefoucauld *et al.*, 2010) and human temporal bone with widely open tympanic cleft (Cheng *et al.*, 2010; Cheng *et al.*, 2013). Standing waves are described in terms of Z_f in Eq. (24) with multiple modal resonances.

The model omits description of a local sound field in the ear canal near the TM. This local region near the TM extends along axial distances within a distance on the order of the ear-canal radius away from the TM. Inhomogeneous motions on the TM are coupled to this localized sound field but only its spatially averaged motion over the TM contributes to the propagating acoustic mode within the ear canal [as represented by Eq. (18)]. An additional kinetic energy density associated with the remainder of the local sound field (acting via a sum over the evanescent mode responses) would be described in a long-wavelength approximation by an additional small inertance (Keefe and Benade, 1981). This inertance would be placed in series between the ear-canal transmission line and the forward input impedance at the TM, but this small inertance is neglected in the present model. The input impedance and its accompanying pressure reflectance are defined over the entire cross-sectional area of the ear canal.

C. Ossicular chain

The ossicular model for ${}^u\hat{\mathbf{T}}_{ow}$ in Eq. (6) is based on a one-dimensional model of vibration transmission. It has the same form as previous ossicular models (Hudde and Engel, 1998; O'Connor and Puria, 2008), although with different parameter values. This transfer matrix is evaluated by concatenating seven transfer matrices of its constituent parts from left to right in the circuit shown in Fig. 2 as follows:

$$\begin{aligned} {}^u\hat{\mathbf{T}}_{ow} = & \begin{pmatrix} 1 & j\omega m_m + (j\omega C_{mm})^{-1} + R_{mm} \\ 0 & 1 \end{pmatrix} \\ & \times \begin{pmatrix} k_2^{-1} & 0 \\ 0 & k_2 \end{pmatrix} \begin{pmatrix} 1 & 0 \\ [(j\omega C_{mmi})^{-1} + R_{mmi}]^{-1} & 1 \end{pmatrix} \\ & \times \begin{pmatrix} 1 & j\omega m_i \\ 0 & 1 \end{pmatrix} \begin{pmatrix} 1 & 0 \\ [(j\omega C_{mis})^{-1} + R_{mis}]^{-1} & 1 \end{pmatrix} \\ & \times \begin{pmatrix} 1 & j\omega m_s + (j\omega C_{mal})^{-1} + R_{mal} \\ 0 & 1 \end{pmatrix} \\ & \times \begin{pmatrix} k_3^{-1} & 0 \\ 0 & k_3 \end{pmatrix}. \end{aligned} \quad (28)$$

The first matrix contains a series mechanical oscillator impedance to represent the malleus attached to the TM with malleus mass m_m , mechanical compliance C_{mm} , and mechanical resistance R_{mm} . The second matrix is a transformer with

transformer ratio k_2 , which is interpreted as an ossicular lever ratio between malleus and incus (Kringelbotn, 1988). The third matrix contains a shunt admittance composed of the series combination of a mechanical compliance C_{mmi} and resistance R_{mmi} to represent the mechanics of the malleolar-incudo joint. The fourth matrix represents the impedance for the incus mass m_i . The fifth matrix contains a shunt admittance composed of the series combination of a mechanical compliance C_{mis} and resistance R_{mis} to represent the mechanics of the incudo-stapedial joint. The sixth matrix is a series mechanical oscillator with elements m_s to represent stapes mass, and a mechanical compliance C_{mal} and resistance R_{mal} to represent the annular ligament. The seventh matrix is a transformer from force variables back to acoustical variables within the cochlear fluid with transformer ratio k_3 defined by

$$k_3 = S_s^{-1}, \quad (29)$$

i.e., k_3 is the inverse of the stapes footplate area S_s (Kringelbotn, 1988).

D. Round-window and differential cochlear impedances

The model round-window impedance Z_{rw} in Eq. (13) is adopted from human temporal-bone measurements. The Z_{rw} is expressed in terms of constant acoustic compliance C_{rw} , inertance I_{rw0} , and resistance R_{rw0} elements (see Table I) by (Nakajima *et al.*, 2008)

$$\begin{aligned} Z_{rw} = & (j\omega C_{rw})^{-1} \\ & + \left[\sum_{i=1}^6 (10^{(i-1)/2} R_{rw0} + 10^{-(i-1)/2} j\omega I_{rw0})^{-1} \right]^{-1}. \end{aligned} \quad (30)$$

The summed resistance increases approximately as the square root of frequency.

For data recorded over a bandwidth from 0.1 up to 20 kHz, Nakajima *et al.* (2008) reported that the acoustical differential cochlear impedance ΔZ_{co} of the cochlea measured in human temporal bone “was generally resistive.” Below 1 kHz, its phase was near zero and its magnitude was “nearly independent of frequency.” Its mean magnitude at higher frequencies fluctuated approximately by a factor of 2 above and below its magnitude below 1 kHz, with larger variability in magnitude and phase above 4 kHz. For purposes of this model, ΔZ_{co} was assumed to have a real constant value as listed in Table I. This value is close to the average measured values.

E. Closed middle-ear cavity

It remains to represent Z_{cav} , which occurs in Eq. (7), in the model specification for the intact middle-ear cavity. As introduced in the paragraph above that equation, Z_{cav} is the input impedance in the tympanic cavity at the TM.

Keefe (2015) described an acoustical transmission-line model of the middle-ear cavities and MACS for the adult human middle ear with normal function. The air-filled

Model of Ossicular Chain

FIG. 2. Transfer matrix model of middle ear for eardrum and ossicular chain. Boundary conditions are represented at the tympanic cleft for the eardrum, and oval and round windows.

cavities included the tympanic cavity, aditus, antrum, and the MACS. A morphometric model of the MACS was first constructed as a binary, symmetrical airway branching model between the entryway into the MACS at the antrum to the smallest generation of air cells that terminated the MACS. Each airway in the MACS was modeled as a cylindrical tube having a given length and radius, such that these airway dimensions scaled in a manner similar to that of other airways and blood vessels in mammalian organs. Using an optimization procedure, the number of generations of branching and the parameters scaling the airway dimensions in each generation of branching were calculated so that the total volume and surface area of the MACS model matched the average total volume and surface area of adult human temporal bones. The resulting morphology had 11 generations of binary branching airways, with equal airway dimensions within each generation. The more distal generations from the antrum had airways with smaller lengths and radii.

Using this morphometric model, an acoustical transmission-line model of the MACS was constructed that included viscothermal losses within the airways. This viscothermal loss model was based on an ideal model of linearized acoustics in a rigid-walled tube whose inner wall was maintained at a constant biologically maintained temperature, but was augmented through the use of a viscous loss parameter ζ_V and thermal loss parameter ζ_T . Each parameter was dimensionless and equal to a real, positive constant bounded below by the value of one that corresponded to the ideal model. Each parameter value was assumed to be a constant that did not vary with frequency or with the generation

of airway within the morphometric model. Larger values of either parameter allowed for losses in biological airways larger than predicted by the ideal viscothermal model. The acoustical MACS model predicted the input impedance Z_{MACS} of the MACS for this morphology as a function of frequency for each selected value of ζ_V and ζ_T .

The acoustical model for sound propagation from the interior side of the tympanic membrane into the tympanic cavity, aditus and antrum was constructed as a transmission line in which the termination impedance of the antrum was Z_{MACS} . Using this model, the impedance Z_{cav} was calculated as a function of frequency for each selected value of ζ_V and ζ_T that influenced Z_{MACS} .

Viscothermal losses in the MACS are possibly increased relative to the ideal model by the presence of a mucoidal layer, in which gas exchange occurs between the blood capillaries within the mucoidal layer and the air within the MACS. The middle-ear cleft included the tympanic cavity, aditus, antrum, MACS, as well as the Eustachian tube that was assumed closed in the present model. While the surfaces of all these cavities as well as of the tympanic membrane and round window also contain mucoidal layers adjacent to the air within the middle-ear cleft, the integrated viscothermal loss is dominated by the much smaller airways in the MACS, which include the largest surface area of contact with enclosed air. Gas exchange within the middle-ear cleft is thus dominated by gas exchange in the MACS. For these reasons, the additional viscothermal losses in the acoustical model were only considered in the MACS, while viscothermal losses in the other cavities of the middle-ear cleft were described by the ideal model.

Numerical results for Z_{MACS} and Z_{cav} were calculated for higher and lower values of ξ_V and ξ_T in Keefe (2015). These same values are listed in Table I of the present report as the parameter values of the high-loss and low-loss conditions, respectively. The low-loss value of ξ_V was defined such that $\xi_V - 1$ was one-tenth of the value of ξ_V in the high-loss condition. The low-loss value of ξ_T was defined in a similar manner relative to the high-loss value of ξ_T . However, Keefe (2015) did not describe how the high-loss values of ξ_V and ξ_T were defined. In fact, these values were defined based on the results of the present overall model optimization as described below, in which ξ_V and ξ_T , among other variables, were allowed to vary within each iteration of the optimization.

F. Open middle-ear cavity

In many experimental studies of middle-ear mechanics using temporal bones, the middle-ear cavities are surgically opened prior to measuring the transfer functions. The impedance Z_{cav} for this open-cavity condition was calculated in the model as an acoustical radiation impedance, which differed from its value for the closed-cavity condition just described. The back side of the tympanic membrane was assumed to radiate in a manner similar to that of a piston of the same area mounted in a flat baffle. While the actual boundary of the TM in the surgically opened condition would differ significantly from that of a flat baffle, the assumption of a flat baffle was adopted because it was more accurate than assuming a radiation impedance of zero (as used in some middle-ear studies), and because its solution is available.

This radiation impedance $Z_{rad}(k, a)$ is a function of the acoustical wavenumber $k = \omega/c$, in which c is the free-space phase velocity of sound in air. It also varies with the piston radius a , which is taken to be equal to the equivalent radius of the freely moving compartment of the tympanic membrane area $S_f = \pi a^2$ in Eq. (20).

The radiation impedance $Z_{rad}(k, a)$ is given in terms of the Bessel function J_1 and Struve function H_1 of first order by (Pierce, 1989)

$$Z_{rad}(k, a) = \frac{\rho c}{\pi a^2} \left\{ 1 - \frac{2J_1(2ka)}{2ka} + j \frac{2H_1(2ka)}{2ka} \right\}. \quad (31)$$

An approximate relation for the Struve function (Aarts and Janssen, 2003) was used in model calculations. The model for the open-cavity condition used $Z_{cav} = Z_{rad}(k, a)$ in Eq. (7). This model described the expected form of the radiation impedance associated with the radiating back of the tympanic membrane, but is of limited accuracy as the detailed geometry of the tympanic cavity after it is surgically opened is not adequately described.

G. Third window pathways in inner-ear fluid

This section defines the transfer function described in Stieger *et al.* (2013) for third-window effects acting near the oval window and near the round window. Their inner-ear fluid model is shown in the inner-ear portion of the circuit in Fig. 1 and represented by Eqs. (10)–(14).

Stieger *et al.* (2013) measured a transfer function H_{sc} for forward and reverse transmission between stapes velocity and pressure difference across the cochlea, which is defined as

$$H_{sc} = \frac{V_{st}}{P_{ow} - P_{rw}}, \quad (32)$$

in which the stapes velocity V_{st} is calculated using Eq. (29) as

$$V_{st} = U_{co}/S_s = k_3 U_{co}. \quad (33)$$

In the absence of all third window effects ($Y_{3v} = Y_{3t} = 0$), this transfer function is equal in forward and reverse transmission, and calculated using a re-arrangement of Eq. (11) as

$$H_{sc} = k_3 / \Delta Z_{co}. \quad (34)$$

Measurements of $|H_{sc}|$ were slightly larger in forward than reverse transmission, which Stieger *et al.* interpreted as evidence for the presence of fluid motion in a third window in SV, i.e., with $Y_{3v} \neq 0$. Because forward transmission was only slightly affected by the presence of the leak, they reasoned that $|1/Y_{3v}|$ in Fig. 1 was much smaller than the magnitude of the cochlear input impedance $|Z_{co}|$ in Eq. (12), but comparable to or larger than the reverse input impedance of the middle ear (as defined below).

H. Numerical methods

An error function was defined based on the squared magnitude differences of predicted and measured transfer functions across frequency. The unknown values of model parameters were calculated through an optimization procedure that minimized the error function, thus obtaining the best possible match between the model and data. The transfer functions selected for use in the optimizations were mainly those for forward transmission with respect to a volume-velocity sound source U_e in the ear canal just in front of the eardrum. These forward transfer functions included the middle-ear impedance Z_e and energy reflectance (ER) at the eardrum defined by

$$\begin{aligned} Z_e &= P_e / U_e, \\ \mathcal{R}_e &= (Z_e - Z_{c,e}) / (Z_e + Z_{c,e}), \\ ER &= |\mathcal{R}_e|^2, \end{aligned} \quad (35)$$

in which $\mathcal{R}_e$ is the pressure reflectance at the eardrum and $Z_{c,e}$ is the characteristic impedance of the ear canal [see Eq. (2)]. The forward transmission functions were the pressure transfer function H_{ev}^F from ear canal to SV and the pressure transfer function H_{et}^F from ear canal to ST. These are defined by

$$\begin{aligned} H_{ev}^F &= P_{ow} / P_e, \\ H_{et}^F &= P_{rw} / P_e. \end{aligned} \quad (36)$$

Based on preliminary analyses of models obtained by optimizing the forward-transmission transfer functions, the reverse middle-ear impedance Z_{me}^R was added to the

FIG. 3. (Color online) Equivalent input impedance at the TM represented by its reactance and resistance (top) and energy reflectance (bottom). These are plotted for the model predictions, the measurements of [Margolis et al. \(1999\)](#), and the energy reflectance measurements of [Stinson \(1990\)](#). Resistance curves are plotted in thicker lines than reactance curves. The *in vivo*, or middle-ear (ME) cavity closed, prediction is shown for this impedance and energy reflectance. The temporal-bone, or ME cavity open, prediction is also shown for energy reflectance.

optimization procedure in order to improve predictions of reverse transmission. The details of the optimization procedure are described in the Appendix. The 21 model parameters listed in Table I with the code letter *O* denote that their values were determined through this optimization. Once all model parameters were fixed, all other forward-and reverse-transmission transfer functions were calculated using numerical methods described in the Appendix.

In particular, the high-loss values of ξ_V and ξ_T with code letter *O* in Table I were calculated by the model optimization. Except for Fig. 4 showing results for both low-loss and high-loss conditions, the modeling results in Figs. 3 and 5–13 were all obtained for the high-loss condition.

III. RESULTS

A. Middle-ear impedance and energy reflectance

In forward sound transmission from the ear canal to the cochlea, the middle-ear impedance is the ear-canal impedance estimated at the eardrum. Figure 3 (top panel) compares the resistance and reactance parts of the equivalent input impedance at the TM from model predictions and measurements ([Margolis et al., 1999](#)). This model prediction was for the middle-ear cavities closed, which was appropriate for comparison with data measured in the ears of adult subjects. A notable property of the measured data was that

the mean reactance was not substantially inertance dominated at high frequencies, i.e., its value fluctuated close to $0 \text{ M}\Omega$ between 1 and 11.3 kHz. The predicted reactance was also not inertance-dominated at high frequencies. The predicted and the measured mean resistance declined from approximately $50 \text{ M}\Omega$ at low frequencies down to values close to zero at high frequencies. The root mean squared (RMS) differences between the model and the mean data over frequencies from 0.25 to 10.7 kHz were $11 \text{ M}\Omega$ for the resistance and $19 \text{ M}\Omega$ for the reactance.

The energy reflectance measurements included data from [Margolis et al. \(1999\)](#) at frequencies from 0.25 to 11.3 kHz, and data from [Stinson \(1990\)](#) at frequencies from 11.3 to 13 kHz. After interpolating each dataset to the same frequency range, the energy reflectance data were compared over the common frequency region from 5 to 11.3 kHz over which each dataset had at least five test ears at each frequency. The average RMS difference in these measurements of mean energy reflectance over this common frequency range was 0.048 (see also the mean data plotted in the bottom panel of Fig. 3). This similarity in means gave confidence in adding the higher frequency data from [Stinson \(1990\)](#) up to 13 kHz to better constrain the estimates of the model parameters.

The mean energy reflectance data from both studies are plotted in the bottom panel of Fig. 3 along with two model predictions, one with middle-ear cavities open and the other with middle-ear cavities closed. The closed-cavity condition in the model was that fitted to the measured energy reflectance in the ears of adult subjects. Other results reported in this section present model outputs for both closed-and open-cavity conditions; the closed-cavity condition was the *in vivo* condition and the open-cavity condition was compared with measurements in temporal bones with middle-ear cavities opened. The predicted energy reflectance was slightly larger in the closed-than the open-cavity condition at frequencies from 0.9 up to 9 kHz. The model described the local minimum in the mean data near 1 kHz, and the local maximum near 8 kHz. The RMS difference in energy reflectance between the model and the [Margolis et al.](#) mean data from 0.25 to 10.7 kHz was 0.099. This RMS difference decreased to 0.064 for an upper averaging log frequency of 8 kHz and increased to 0.136 for an upper frequency of 12.7 kHz. The standard errors of the mean energy reflectance for the [Margolis et al.](#) dataset were plotted in [Margolis et al. \(2001\)](#) and were of order 0.05 across frequency, i.e., slightly smaller than the RMS differences between the model and mean data.

It was possible to obtain better agreement between measured and predicted energy at high frequencies up to 13 kHz by allowing worse agreement in other transfer functions in the calibration set (see also the Appendix). Because the goal was to fit many different kinds of transfer functions, there were some unavoidable tradeoffs in accuracy that would be less likely to arise in modeling studies predicting a smaller set of transfer functions.

The multiple modal resonances in the free component of the eardrum [see Eq. (24)] were an important element in the model in controlling the reactance at high frequencies. In a

FIG. 4. (Color online) Comparison of energy reflectance in normal middle ear (middle-ear cavity closed) with high-loss (thin solid line) and low-loss (thick solid line) MACS models, and in a middle ear with a zero mastoid impedance $Z_{MACS}=0$ and with the antrum blocked just after the aditus ad antrum. The energy reflectance for the normal middle ear in the high-loss MACS model is repeated from Fig. 3.

simple-oscillator model of the eardrum, the reactance would be negative below the resonance frequency and positive above (with slope proportional to frequency). With multiple modal resonances, the reactance was influenced by the compliance-dominated responses of the higher-frequency resonances and the inertance-dominated responses of the lower-frequency resonances. The nine fitted model parameters describing the free component of the eardrum response contributed to the adequate fit of the model to the measured mean reactance. The tympanic-cavity impedance Z_{cav} was also important in attaining this fit.

Voss *et al.* (2008) measured ER in three human temporal bones in a normal condition with intact MACS in comparison to one condition with the mastoid widely open to approximate a large airspace, and another condition with the mastoid closed off at the aditus ad antrum. These abnormal conditions were simulated in the model to compare predicted and experimental results.

The experimental condition with the mastoid widely opened was simulated by calculating Z_{cav} with $Z_{MACS}=0$ in the model of Keefe (2015). While the mastoid widely open case would result in a non-zero radiation impedance that would depend on the unknown details of the canal-wall-up mastoidectomy that was performed, the most straightforward case to model was $Z_{MACS}=0$. The experimental condition with the mastoid closed off at the aditus ad antrum was simulated by calculating Z_{cav} with a blocked entryway at the antrum. This was accomplished by setting the flow into the antrum equal to zero in the middle-ear cleft model of Keefe (2015) that was used to calculate Z_{cav} .

The ER was calculated in this middle-ear cleft model using both the high-loss and low-loss values of the viscothermal coefficients ξ_V and ξ_T in Table I. The predicted ER in Fig. 4 for the mastoid open condition (dotted line) was slightly smaller than the normal low-loss condition (thick solid line) with middle-ear cavities closed between 0.25 and 1.1 kHz, much smaller between 1.3 and 2.3 kHz, and slightly larger between 2.4 and 3.5 kHz. The two responses were

nearly identical above 4.5 kHz except for a slightly larger ER for the mastoid open condition at about 9 kHz. One temporal-bone measurement was influenced by a measurement error, so that the present comparison focused on the other two temporal-bone measurements of Voss *et al.* (2008). The measured ER (not shown) for the mastoid open condition was much smaller than the normal low-loss condition at all lower frequencies up to 2.5 to 3.5 kHz, and generally larger at higher frequencies up to 6 kHz. The predicted changes were qualitatively similar to the measured changes, especially between 1 and 2 kHz, although the magnitude of the change in ER was larger in the measurements. Thus, the model using $Z_{MACS}=0$ to simulate a canal-wall-up mastoidectomy was partially validated.

The predicted ER for the antrum sealed condition in Fig. 4 was increased relative to the normal low-loss condition at frequencies up to 6 kHz with a maximum increase of about 0.24 near 1 kHz, and another large increase above 9 kHz. The measured ER for the antrum sealed condition (Voss *et al.*, 2008) was also increased relative to this normal condition at frequencies ranging up to 1–1.5 kHz and usually decreased at higher frequencies up to 6 kHz. The maximum measured change at low frequencies was more than 0.24 in one ear and less in the other. The antrum-sealed ear is the limiting case of an ear with a very small MACS, as would be the case for the ear of a young child, in whom the MACS develops post-natally, or a child with a history of otitis media.

The normal ER measurements in the temporal bones tended to be larger than the predicted ER in the low-loss condition. A local maximum in ER was also present in the pair of temporal-bone measurements of Voss *et al.* (2008), although at a slightly higher frequency near 2.8 kHz.

The predicted ER for the normal ear in the high-loss condition is also shown (thin solid line) in Fig. 4, and is identical to the ER curve in Fig. 3 for the “Model ME Cav. Closed” condition. The predicted ER was smaller in the low-loss than the high-loss condition (thin line) near 1 kHz, and larger near 2 kHz. That is, the ER fine structure had a larger amplitude of fluctuations in the low-loss condition between about 0.9 and 4 kHz. This fine-structure difference is consistent with fluctuations in the fine structure of the predicted Z_{cav} that occurred between 0.5 and 4 kHz (Keefe, 2015). Inasmuch as fine-structure changes in ER are a transformation of fine-structure changes in the input impedance, this model confirms the statement in Stepp and Voss (2005) that individual variations in the fine structure of Z_{cav} can introduce fine structure into the input impedance.

B. Forward transfer functions

The forward pressure transfer functions H_{ev}^F and H_{et}^F are the ratios of SV pressure P_{ow} and ST pressure P_{rw} , respectively, to the ear-canal pressure generated by a sound source in the ear canal [see Eq. (36)]. Figure 5 shows mean H_{ev}^F data of Nakajima *et al.* (2008) in the left column for the magnitude and phase, and their mean H_{et}^F data in the right column. The prediction with open middle-ear cavities was compared with these experimental measurements.

FIG. 5. (Color online) Forward pressure transfer functions for pressure at SV (left column) and at ST (right column) are plotted relative to the pressure just in front of eardrum for model with middle-ear cavities open (solid line) and closed (dashed-dotted line). These are compared to measurements (dashed line) (Nakajima *et al.*, 2008). The transfer-function level responses are plotted in the top row and phase responses in bottom row. The horizontal dotted lines in the top rows show the ideal transformer ratios N_1 and N_2 (as levels in dB).

Over a log frequency range from 0.1 to 10.9 kHz, the RMS differences between the data and the model with ME cavities open were 2.9 dB in H_{ev}^F level and 1.8 dB in H_{et}^F level; the RMS differences were 13° in H_{ev}^F phase and 19° in H_{et}^F phase. The RMS differences tended to be larger above 7 kHz than at lower frequencies. Among the model parameters in Table I contributing to the goodness of fit in phase, the time delay associated with the coupling between the free and ossicular-bound components of the TM was $\tau = 30.2 \mu\text{s}$. This is within the range of TM delays (17.6 to 75.5 μs) reported by O'Connor and Puria (2008) using a single-piston model of TM delay.

A classical definition of the transformer ratio (N_1) of the middle ear is the dimensionless product of eardrum area S_{TM} , lever ratio k_2 , and k_3 as inverse stapes footplate area (Kringelbotn, 1988), i.e.,

$$N_1 = S_{TM} k_2 k_3. \quad (37)$$

This has the value $N_1 = 24$ (or 28 dB) based on the parameters in Table I. If the eardrum were modeled as a rigid piston, then each effective transformer ratio would be equal to N_1 in Eq. (37), i.e., $\hat{N}_P = \hat{N}_U = N_1$ (Shera and Zweig, 1992).

The maximum magnitude of the SV pressure ratio $|H_{ev}^F|$ was less than N_1 in Eq. (37) at all frequencies (see Fig. 5). For the two-compartment eardrum model used in the present model, a new definition of total transformer ratio N_2 is

$$N_2 = k_1 k_2 k_3 = 2.4, \quad (38)$$

or 7.7 dB in level. This reduction by a factor of 10 from N_1 arises because k_1 is based on the area S_o of the ossicular-bound component of the eardrum rather than its total area S_{TM} [see also Eqs. (23) and (20)]. The N_2 was in the mid-range of values of $|H_{ev}^F|$ across frequency, and was larger

than the maximum value of $|H_{et}^F|$ (see Fig. 5). Thus, N_2 approximated the average forward transmission magnitude to SV across frequency.

Whether the tympanic cavity was open or closed had only modest effects on the predicted pressure transfer to the cochlea for both H_{ev}^F and H_{et}^F . This result suggests that experimental measurements with open middle-ear cavities are generalizable to estimating the forward pressure transfer functions *in vivo*. This conclusion is otherwise difficult to assess experimentally because forward pressure transfer has not been directly measured *in vivo*.

For forward sound transmission, the inner-ear pressure difference between SV and ST is the input pressure generating the cochlear traveling wave (Nakajima *et al.*, 2008). Their measurements of this pressure difference relative to the ear-canal pressure are shown in the left panels of Fig. 6 with model predictions for open-and closed-cavity conditions. The magnitude (plotted as a level) and the phase of this transfer function agreed well with measured values except that the model differed by about 10 dB above 8 kHz. The standard error in the measured magnitude level also increased at these frequencies.

It is relevant to compare this high-frequency difference between model and data to the difference between measurements reported in different studies. The top row of Fig. 7 shows measurements of H_{ev}^F by Puria (2003) and Nakajima *et al.* (2008) in relation to model predictions repeated from Fig. 5. The predicted level above 6 kHz lies between the levels measured in these two studies. The mean measurement differences between studies can exceed the level differences between a particular mean measurement and the model to which it is fitted.

Another important forward transfer function is the ratio of stapes velocity to ear-canal pressure, which is shown in

FIG. 6. (Color online) The forward SV-ST pressure-difference transfer function relative to the pressure just in front of the eardrum is shown (left column) for the model with middle-ear cavities open (solid line) and closed (dashed-dotted line) compared to measurements (dashed line) (Nakajima *et al.*, 2008). The reverse SV-ST pressure-difference transfer function from cochlea to just in front of the eardrum is shown (right column) for the model with middle-ear cavities open and closed. The transfer-function levels are plotted in the top row and phase in the bottom row.

the left panel of Fig. 8. These magnitude and phase data were similar to measurements with middle-ear cavity open in human temporal bones (O'Connor *et al.*, 2008), and to model predictions (O'Connor and Puria, 2008). The present model predicted the transfer function under both conditions (i.e., middle-ear cavities open or closed), with only minor differences observed between conditions. Measurements in human temporal bones showed a 3 to 4 increase in magnitude below 1 kHz with middle-ear cavity open compared to cavity closed (Voss *et al.*, 2000). The predicted change was in the same direction but much smaller. However, as discussed by Voss *et al.*, the measurements were performed on temporal bones with MACS removed, so that the closed volumes in these samples were much smaller than in a normal middle ear. The larger change in the measurements would appear to be related to this fact. The predicted phase at high frequencies in the present model was similar to results in O'Connor *et al.* (2008).

The predicted ratio of umbo velocity to ear-canal pressure V_u/P_e for forward transmission is also shown in the left panels of Fig. 8. The general shape of this transfer function was similar to values measured from 0.1 to 5 kHz (Nakajima *et al.*, 2005). The predicted transfer function magnitude had a slight minimum at 5.3 kHz, whereas the measured transfer function had a more narrow minimum near 3.7 kHz. Nakajima *et al.* (2005) also measured V_{st}/P_e for forward transmission over the same bandwidth; these data were similar to the predicted results except that the data showed a narrow minimum magnitude just above 4 kHz, which was not present in data of O'Connor and Puria (2008).

Overall, the predicted umbo velocity was slightly larger in magnitude than the stapes velocity, and there was increased phase delay in the stapes motion relative to the

umbo motion, in agreement with measurements (Nakajima *et al.*, 2005). Although not plotted, the forward umbo-stapes velocity transfer function V_{st}/V_u is implicit by comparing the ratio of the forward V_{st}/P_e to V_u/P_e in Fig. 8.

C. Reverse transfer functions

The reverse SV pressure transfer function is the ratio of SV pressure to the ear-canal pressure generated by a sound source within the middle ear. The ear canal was terminated in the model by an Etymotic ER-10B+ probe microphone, and in the ear canals in which data were acquired by an Etymotic ER-7C microphone (Puria, 2003). The insertion distance from the TM in both cases was 2 mm. The prediction was limited to a bandwidth from 0.25 to 8 kHz, because this was the measurement bandwidth for the source reflectance of the probe (Keefe and Abdala, 2007). The predictions were practically identical for middle-ear cavities open or closed.

The second row of Fig. 7 shows the predicted and mean measurements (Puria, 2003) of this reverse SV pressure transfer function. The predicted transfer function was generally similar to the measured transfer function except that the measured transfer function was more sharply tuned in both magnitude and phase near 1.4 kHz.

The predicted reverse-transmission pressure difference between SV and ST, which is shown in the right panels of Fig. 6, was nearly identical for cavity open and closed conditions. The transfer-function level decreased by 30 dB over five octaves from 0.25 to 8 kHz, and its phase decreased from 151° at 0.25 kHz to -160° at 8 kHz with a zero crossing at 3.4 kHz.

The reverse middle-ear impedance $Z_{in,v}^R$ is defined as the ratio of P_{ow} in SV to the volume velocity $-U_{ow}$ swept out by

FIG. 7. (Color online) Magnitude responses in left column and phase responses in right column. In all panels, the measured results are plotted from Puria (2003). Row 1: Forward pressure transfer function from SV relate to the ear canal comparing measurements of Puria (2003) and Nakajima *et al.* (2008), and model predictions. The data of Nakajima *et al.* and model predictions are repeated from Fig. 5. Rows 2–4 show reverse transmission. Row 2: Reverse pressure transfer function between SV and ear canal. Row 3: Reverse middle-ear impedance at SV plotted with comparison to stapes impedance (in acoustical units). Row 4: Reverse middle-ear pressure reflectance at oval window. In all panels, the absence of apparent differences between the curves of model open and model closed conditions resulted from the fact that the predicted transfer functions were similar irrespective of whether the middle-ear cavity was open or closed.

the stapes footplate for a sound source located within the middle ear, i.e.,

$$Z_{in,v}^R = \frac{P_{ow}}{-U_{ow}} \bigg|_R. \quad (39)$$

As described in the Appendix, this transfer function was included within the optimization procedure to calculate the model parameters. The model dataset used for the optimization procedure was that of Puria (2003). The third row of Fig. 7 shows that the predicted reverse middle-ear impedance level was larger on average than the measured level between 0.25 and 5 kHz, with similar levels above 5 kHz. The predicted and measured mean phases were similar except that a predicted resonance peak level near 3 kHz resulted in a typical resonant phase pattern at frequencies just above and below 3 kHz. Over the common frequency range from 0.25 to 8 kHz, the RMS difference between the

predicted and measured reverse middle-ear impedance level was 6.5 dB, and the RMS difference in phase was 22°.

The constant magnitude of the differential cochlear impedance $|\Delta Z_{co}|$ (from Table I) is also shown with which to compare the variation of $Z_{in,v}^R$ across frequency. The acoustical impedance Z_{st} of the stapes and annular ligament with respect to the inner-ear fluid is expressed using Eq. (28) by (see also Fig. 2)

$$Z_{st} = k_3^2 [j\omega m_s + (j\omega C_{mal})^{-1} + R_{mal}]. \quad (40)$$

This stapes impedance, which represents in Table I the measured data of Merchant *et al.* (1996), is shown in the third row of Fig. 7 using the solid thick line. The predicted $Z_{in,v}^R$ was largely controlled by Z_{st} .

The reverse middle-ear pressure reflectance $\mathcal{R}_v^R$ is expressed in terms of the complex $Z_{in,v}^R$ and ΔZ_{co} by Shera and Zweig (1991b)

FIG. 8. (Color online) The predicted transfer function between stapes footplate velocity V_{st} and ear-canal pressure is plotted for forward (left column) and reverse transmission (right column) for the middle-ear cavities open and closed. The predicted transfer function between umbo velocity V_u and ear-canal pressure is plotted for forward transmission (left column) with thicker lines. The inverse of the predicted transfer function between stapes footplate velocity V_{st} and ear-canal pressure is plotted for reverse transmission (right column) so that each transfer function is the ratio of output to input variable. The H_z and H_y transfer functions are described in the Sec. IV [see Eqs. (51), (52)].

$$\mathcal{R}_v^R = (Z_{in,v}^R / \Delta Z_{co}^* - 1) / (Z_{in,v}^R / \Delta Z_{co} + 1), \quad (41)$$

in which ΔZ_{co}^* is the complex conjugate of ΔZ_{co} . This expression assumes that the differential cochlear impedance ΔZ_{co} in a long-wavelength approximation is equal to the wave impedance of the forward cochlear traveling wave, which is consistent with negligible reflection of the cochlear traveling wave from the helicotrema (and that fact that the measured ΔZ_{co} is real). In general, the wave impedance of the reverse cochlear traveling wave is ΔZ_{co}^* (Shera and Zweig, 1991b). Because the differential cochlear impedance is real in the present model, it follows that $\Delta Z_{co}^* = \Delta Z_{co}$ in Eq. (41). The wave impedances may vary locally from base to apical positions within the cochlea, but do not depend on external boundary impedances such as Z_{rw} .

Puria (2003) used a different definition of reverse reflectance in which ΔZ_{co} in Eq. (41) was replaced by the cochlear input impedance Z_{co} in Eq. (12) in the limit that $P_{tc} = 0$, i.e., as the ratio of pressure in SV to the volume velocity swept out by the stapes. This definition of Z_{co} was used in Puria (2003) and Aibara *et al.* (2001). The Puria definition has the result that the reverse pressure reflectance depends on the round window impedance and its complex conjugate.

The differing definitions of $\mathcal{R}_v^R$ in Puria and the present model are numerically similar in the limit that $|Z_{rw}| \ll \Delta Z_{co}$. As a practical approximation, the bandwidth over which $|Z_{rw}| < 0.5 \Delta Z_{co}$ in the data of Nakajima *et al.* (2008) is the frequency range from 0.16 to 2.6 kHz. It is meaningful to compare $\mathcal{R}_v^R$ in the present model with the measurements of Puria (2003) over this restricted frequency range, although effects related to Z_{rw} may not be entirely negligible.

The predicted magnitude and phase of $\mathcal{R}_v^R$ are plotted in the bottom row of Fig. 7. The predicted pressure reflectance

magnitude exceeded 0.7 at frequencies below 0.71 kHz, and was less than 0.4 for frequencies in the range from 1.3 to 6.3 kHz. The predicted reflectance magnitude was similar to the mean measurements of Puria (2003) at frequencies up to 4 kHz. Both reflectance phase functions decreased with increasing frequency up to 4 kHz, although the predicted phase decreased more uniformly than did the mean measured phase, which had a pronounced change in slope near 1.6 kHz. There were strong differences between the model and data above 4 kHz, which cannot be interpreted without evaluating the difference in how reflectance was defined. Nevertheless, the difference in the predicted and measured mean $Z_{in,v}^R$ near 3 kHz would produce differences in $\mathcal{R}_v^R$.

It is evident in all panels of Fig. 7 that each transfer function was nearly the same for the middle-ear cavity closed and open conditions. For example, the largest relative difference in the magnitudes of the reverse middle-ear impedance was 1.1%; the largest relative difference in the magnitudes of the reverse middle-ear reflectance was 3.3%.

The ratio of ear-canal pressure to stapes velocity for reverse transmission is illustrated in the right panels of Fig. 8. This reverse transfer function is inverted with respect to the forward transfer function (in the left panels) so that each is a ratio of an output variable to an input variable. There was a negligible difference in the reverse transfer function for the open- and closed-cavity conditions. The magnitude of the reverse transmission function decreased with increasing frequency. The phase decreased with increasing frequency for reverse transmission, such that the absolute phase difference between low and high frequencies was smaller for reverse than for forward transmission.

D. Shunt flow through third window in SV

Effects of shunt pathways in inner fluid were introduced in Secs. II A and II H (see also Fig. 1). The forward and reverse transfer functions H_{sc}^F and H_{sc}^R , respectively, between stapes velocity and pressure difference across the cochlea are written as

$$\begin{aligned} H_{sc}^F &= \left(\frac{V_{st}}{P_{ow} - P_{rw}} \right) \bigg|_F, \\ H_{sc}^R &= \left(\frac{V_{st}}{P_{ow} - P_{rw}} \right) \bigg|_R. \end{aligned} \quad (42)$$

Following the case considered by Stieger *et al.* (2013), it was assumed that Y_{3v} was non-zero and Y_{3t} was zero. The exact numerical solutions for H_{sc}^F and H_{sc}^R were calculated from the numerical procedures described in the Appendix.

Approximate solutions were also calculated by assuming that $P_{tc} = 0$, i.e., that the pressure in the tympanic cleft was negligible compared to pressures within the inner-ear fluids. This assumption with Eqs. (10)–(14), (29), (39), and (42) leads to

$$\begin{aligned} H_{sc}^F &= \left(\frac{k_3}{\Delta Z_{co}} \right) [1 + Y_{3v}(\Delta Z_{co} + Z_{rw})], \\ H_{sc}^R &= \left(\frac{k_3}{\Delta Z_{co}} \right) \frac{1}{1 + Y_{3v}Z_{in,v}}. \end{aligned} \quad (43)$$

In the latter equation, it is sufficient to estimate $Z_{in,v}^R$ at $P_{tc} = 0$ by its value calculated with the middle-ear cavities open.

The left panels of Fig. 9 show H_{sc}^F for forward transmission for the no-leak condition [see Eq. (34)], the model

conditions with middle-ear cavities open and closed, and the approximate solution in Eq. (43). The results were insensitive to whether the middle-ear cavity was open or closed except for a small difference above 8 kHz, and the approximate solution was very accurate. The open-cavity model predictions were similar to measured magnitude results in human temporal bone (Stieger *et al.*, 2013) with the third-window SV admittance in Eq. (10) set to the value $Y_{3v} = 0.35/\Delta Z_{co}$ as given in Table I. That is, $|Y_{3v}|$ in a normal middle ear was predicted to be 35% as large as the inverse of the differential cochlear impedance.

The right panels of Fig. 9 show H_{sc}^R for reverse transmission for the same four conditions. The magnitudes of H_{sc}^R were nearly the same for all conditions. The phases of H_{sc}^R showed a larger deviation from zero degrees at frequencies below 2 kHz for the closed-cavity condition, while the exact model and approximate predictions for the open-cavity condition were nearly identical. The magnitudes of H_{sc}^R were similar in the model (with the above value of Y_{3v}) and the data (Stieger *et al.*, 2013). The approximate solution revealed that the reverse middle-ear impedance controlled the inverse frequency dependence of H_{sc}^R below 1 kHz.

E. Forward power transfer and minimum-audible pressure

Middle-ear forward transmission constrains the behavioral threshold of hearing. In contrast, a behavioral threshold measurement combined with a middle-ear model can predict the pressure difference acting across the cochlea at the threshold of hearing. The minimum audible pressure (MAP), denoted by P_e^{MA} , is the ear-canal pressure just in front of the TM at the behavioral threshold of hearing (Killion, 1978).⁵

FIG. 9. (Color online) The magnitude (top) and phase (bottom) of H_{sc} are plotted for forward transmission (left column) and reverse transmission (right column). The responses for the case of a SV leak are identified in the legend for the middle-ear cavities open or closed, the no-leak case, and the approximate solutions in Eq. (43).

FIG. 10. Left: The sound level of the minimum-audible cochlear pressure difference $|\Delta P_{co}^{MA}|$ is plotted for the condition that the ear-canal SPL is the MAP (0 dB based on same pressure reference as for SPL). Right: The MEE of cochlea and middle ear is plotted as a level (in dB).

A corresponding cochlear pressure difference ΔP_{co}^{MA} at the MAP is predicted using Eq. (36) by

$$\Delta P_{co}^{MA} = P_{ow}^{MA} - P_{rw}^{MA} = (H_{ev}^F - H_{et}^F)P_e^{MA}, \quad (44)$$

in which P_{ow}^{MA} and P_{rw}^{MA} are the minimum-audible P_{ow} and P_{rw} , respectively. This predicted minimum audible cochlear pressure difference is plotted as a level (in dB) in the left panel of Fig. 10 for the open-and closed-cavity conditions. These show small differences in level on the order of a couple dB. The data plotted in the panel were based on the measured MAP, and H_{ev}^F and H_{et}^F measured by Nakajima *et al.* (2008). Whereas the MAP varied strongly with frequency, the level of the minimum audible cochlear pressure difference was relatively constant at around 25 dB from 0.25 to 3 kHz, with a 5–15 dB reduction in level at higher frequencies up to 11 kHz. The predicted $|\Delta P_{co}^{MA}|$ for closed- and open-cavity conditions were similar up to 8 kHz. The predicted level for the open-cavity condition was similar to the measured level up to about 7 kHz, with values up to 10 dB lower at 10 kHz.

An important problem in middle-ear mechanics is to understand how well the middle ear delivers the sound power collected in the ear canal to the power absorbed by the cochlea. In forward transmission, the acoustical power W_e absorbed by the middle ear is

$$W_e = \frac{1}{2} G_e |P_e|^2, \quad (45)$$

in which the acoustical conductance of the middle ear G_e is the real part of Z_e^{-1} [see Eq. (35)],

$$G_e = \text{Re}(1/Z_e). \quad (46)$$

The acoustical power W_{co} absorbed by the cochlea is related to the pressure difference driving the cochlea [see Eq. (11)] by

$$W_{co} = \frac{1}{2} \Delta G_{co} |\Delta P_{co}|^2, \quad (47)$$

in which the acoustical differential conductance of the cochlea ΔG_{co} is

$$\Delta G_{co} = \text{Re}(1/\Delta Z_{co}), \quad (48)$$

with a real value of ΔZ_{co} listed in Table I. Using Eq. (44), the minimum audible power W_{co}^{MA} absorbed by the cochlea at the threshold of hearing is

$$W_{co}^{MA} = \frac{1}{2} \Delta G_{co} |\Delta P_{co}^{MA}|^2. \quad (49)$$

A middle-ear efficiency (MEE) of the cochlea (Rosowski, 1991) is defined as the fraction of the forward-transmitted power absorbed by the middle ear to the power that is subsequently absorbed by the cochlea [any power re-radiated as otoacoustic emissions (OAEs) is neglected in the present analysis]. Using Eqs. (44), (45), and (49), the MEE is

$$\begin{aligned} MEE &= \frac{W_{co}}{W_e} \\ &= |H_{ev}^F - H_{et}^F|^2 \frac{\Delta G_{co}}{G_e}, \end{aligned} \quad (50)$$

with H_{ev}^F and H_{et}^F defined in Eq. (36) and their level difference $|H_{ev}^F - H_{et}^F|$ plotted in the left column of Fig. 6. The model MEE level, defined by $10 \times \log_{10}(MEE)$, is shown in Fig. 10 (right panel). An experimental estimate of MEE level is also shown in this panel that was constructed using temporal-bone measurements of H_{ev}^F , H_{et}^F , and ΔG_{co} (Nakajima *et al.*, 2008), and G_e calculated from *in vivo* measurements of Z_e (Margolis *et al.*, 1999) using Eq. (46).

The model MEE levels were within a couple dB for the closed-and open-cavity conditions across all frequencies. The data and open-cavity model values of MEE level were within a couple dB for frequencies 0.25–4.2 kHz, but the level of the data was as much as 11 dB lower near 5 kHz. A similar local reduction in level occurred for the data in the forward SV-ST pressure difference level transfer function in Fig. 6 (upper left panel).

The spectral features of the MEE shared by the model and the data were a relative constant level near –10 dB from 0.25 up to 2 kHz, followed by an attenuation rate in the neighborhood of 9 dB per octave between 2 and 8 kHz. Middle-ear power transmission was relatively flat up to 2 kHz and

attenuated at higher frequencies. This is consistent with the minimum audible cochlear pressure difference level in the left panel of Fig. 10, which was also attenuated above 3 kHz.

Previous estimates of MEE in human ears (Rosowski *et al.*, 1986; Rosowski, 1991) from 0.1 to 7 kHz combined experimental results from several studies. Their estimated MEE was 0.1 (−10 dB) at 0.1 kHz increasing slowly with frequency to 0.4 (−4 dB) at 0.9 kHz. This was followed by a rapid decrease at higher frequencies down to 0.04 (−14 dB) at 2 kHz and about 0.004 (−24 dB) at 7 kHz. These results agreed well with the results in Fig. 10 at frequencies above 2 kHz. However, this earlier estimate of MEE was larger at lower frequencies, e.g., as much as 6 dB larger at 0.9 kHz. The definition of MEE in Rosowski (1991) did not include the effect of non-zero pressure in ST just inside the round window. This pressure was included in the definition of MEE in Eq. (50) via the transfer function H_{et}^F ; however, this difference may not explain the observed difference in MEE between 0.25 and 1 kHz.

Results from behavioral and physiological measurements, the latter in terms of stimulus frequency (SF) OAE measurements, suggest that the cochlear mechanics in the human ear is more sharply tuned at higher frequencies (Shera *et al.*, 2002). Two-tone suppression of SFOAEs indirectly estimated the cochlear gain in terms of the tip-to-tail of a SFOAE pressure suppression tuning curve (Keefe *et al.*, 2008). Combining these SFOAE pressure data with ear-canal reflectance measurements, the cochlear gain estimated from the tip-to-tail power level difference of SFOAE suppression increased with increasing frequency between 1 and 8 kHz (Keefe and Schairer, 2011). Such a cochlear mechanism based on nonlinearities in outer-hair-cell function would increase the intra-cochlear pressure levels generated at higher frequencies at sound levels close to threshold in the ear canal. This increase in gain would offset the attenuation above 2 kHz seen in $|\Delta P_{co}^{MA}|$ and MEE.

It is also possible that the cochlear differential conductance ΔG_{co} *in vivo* may vary with stimulus level and frequency, so that the value of ΔG_{co} obtained from temporal-bone measurements represents a limit of passive cochlear mechanics. This would also influence the *in vivo* MEE via Eq. (50).

IV. DISCUSSION

A. Eardrum model: Multiple modes and time delay

The TM motion has a spatially distributed, multi-modal response across frequency (de La Rouchefoucauld *et al.*, 2010; Cheng *et al.*, 2010) in a condition with constant ear-canal SPL just in front of the TM. This property suggested the incorporation of multiple modes of vibration in the free component of a two-component TM model. Some lumped-element circuit models have lacked accuracy in predicting the TM impedance or reflectance at high frequencies because the TM is mass-controlled in such models at those frequencies. This multi-modal TM model solved the mass-control problem at high frequencies by placing one resonance at a very high frequency with small damping.

The TM resonant-mode frequencies calculated in the absence of damping from the parameter values in Table I were 0.973 kHz (i.e., $[2\pi\sqrt{I_1 C_1}]^{-1}$), 2.69 kHz, and 17.6 kHz, with quality (Q) values of 3.85 (i.e., $\sqrt{I_1/C_1}/R_1$), 0.48, and 11.9, respectively. The findings that these multiple modes of oscillation on the TM combined with the presence of TM delay were important in predicting the middle-ear impedance and reflectance in the ear canal, as well as transfer functions through the middle ear, differed from Parent and Allen (2010). They concluded that “complex, multi-modal propagation observed on the TM may not be critical to proper sound transmission along the ear.”

With respect to the bandwidth used in the present model, the relatively small number of TM modes appears smaller than the “multitude” of eardrum resonances described in Fay *et al.* (2006). Spatial integration of forward sound power over the eardrum in the present two-component model comes from the fact that the acoustic pressure acts over the entire surface of the eardrum via its propagating and evanescent modes. The appearance of eardrum modal resonances at high frequencies in the present model is qualitatively consistent with experimental findings of multiple resonant modes of vibration of the tympanic membrane at frequencies above 8 kHz up to as high as 18 or 20 kHz (Rosowski *et al.*, 2011; Cheng *et al.*, 2010). These findings suggest independent motions of the manubrium relative to the remainder of the tympanic membrane.

Holographic measurements of TM motion in response to sound were analyzed at discrete sound frequencies up to 18 kHz for which the signal-to-noise ratio was sufficient to image most of the TM surface (Cheng *et al.*, 2013). These results at higher frequencies showed multiple zero-crossings between the umbo and the rim of the TM, consistent with the presence of modal and traveling-wave components. Their estimated delays at high frequencies ranged from 300 to 1300 μ s, which were much larger than the delay of 30.2 μ s predicted by the present model. Inasmuch as the spatial resolution of these measured TM motions were orders of magnitude finer than the motions associated with the two-component TM used in the present model, the experimental results of Cheng *et al.* cannot be explained by the present model.

Cheng *et al.* (2013) pointed out that the phase delays observed in their TM motion data were too large to explain the phase delays in middle-ear sound transmission. In contrast, the delay τ was used in the present model to fit the phase delay associated with two-point transfer functions between the ear canal and locations within the middle or inner ear.

The phase $-2\pi f\tau$ associated with a pure time delay of 30.2 μ s would be -120° at 11 kHz. The delay τ entered the model only in Eq. (22) for $e^{\hat{T}_u}$. This transfer matrix did not represent a pure time delay between ear-canal pressure at the TM and the force acting on the umbo, as was the case in the model of Puria and Allen (1998), but it was an internal delay that influenced the coupling between the two components of the TM. At 11 kHz, the predicted phase of H_{ev}^F was almost -315° (see Fig. 5), which was less negative than the phase (-380°) of the ratio of stapes velocity to ear-canal pressure (see Fig. 8). Depending on the choice of the open-or closed-

cavity condition, the forward transfer function phase for umbo velocity with respect to ear-canal pressure was about -210° (see Fig. 8).

In terms of the transfer matrices, the relative umbo phase of -210° resulted from the action of ${}^e\hat{\mathbf{T}}_u$; the relative phase to the oval window of -315° resulted from the action of the matrix product ${}^e\hat{\mathbf{T}}_u {}^u\hat{\mathbf{T}}_{ow}$. Thus, the phase of -120° associated with the TM time delay τ at 11 kHz contributed slightly more than half of the phase delay in the umbo velocity to the ear-canal pressure transfer function ${}^e\hat{\mathbf{T}}_u$.

B. Physical interpretation of transfer matrix ${}^e\hat{\mathbf{T}}_u$

The ear-canal to oval-window transfer matrix ${}^e\hat{\mathbf{T}}_u$ defined in Eqs. (1) and (3) describes the model of eardrum and ossicular-chain dynamics between the ear canal and umbo. As described in Shera and Zweig (1992), each matrix element of ${}^e\hat{\mathbf{T}}_u$ corresponds to a particular transfer function which might be measured experimentally or predicted by a model. This section provides a physical interpretation of these matrix elements.

For the matrix elements of ${}^e\hat{\mathbf{T}}_u$ in Eq. (3), the variables $\hat{A}_F$ for force and $\hat{A}_V^{-1}$ for velocity are plotted for the two-component eardrum model in Fig. 11 with respect to the constant total area of the TM and the area of the ossicular-bound component of the TM [as implicitly defined using Eqs. (15) and (19)]. In the left panels, the magnitude of $\hat{A}_F$ was slightly less than S_{TM} at low frequencies, increased to a maximum value close to S_{TM} near 1 kHz, decreased at higher frequencies to a minimum value close to S_o near 5 kHz, and

was relatively constant at higher frequencies. This was a qualitative change from a predominately full-eardrum force transmission below 1 kHz to a predominately ossicular force transmission above 1 kHz. The phase of $\hat{A}_F$ was negative, and tended to decrease with increasing frequency. The predicted forward transfer function F_u/P_e for the ME model closed condition is also plotted in the left panels, inasmuch as $\hat{A}_F = F_u/(P_e - P_{tc})|_{V_u=0}$ [see Eq. (4)]. The magnitude of F_u/P_e is reduced compared to $\hat{A}_F$ up to 5 kHz due to the effects of the motion of the ossicular chain relative to the blocked condition for $\hat{A}_F$. Their phase responses are generally similar.

In the right panels of Fig. 11, the magnitude of $\hat{A}_V^{-1}$ was similar in value to $1/S_{TM}$ at all frequencies. The phase of $\hat{A}_V^{-1}$ was relatively constant up to about 3 kHz, and its phase delay increased with increasing frequency above 4 kHz. The predicted forward transfer function V_u/U_e for the ME model closed condition is also plotted in the right panel, inasmuch as $\hat{A}_V = V_u/U_e|_{F_u=0}$ [see Eq. (4)] is the same transfer function for the boundary condition in which the umbo is free to move. The magnitude of V_u/U_e was slightly more than half of $1/S_{TM}$ for frequencies up to 2 kHz, and it decreased with increasing frequency above 2 kHz. This relative reduction in umbo velocity compared to the free umbo condition reflects the fact that the ossicular chain to the inner ear is intact *in vivo*.

For the off-diagonal matrix element $\hat{Z}_e$ in ${}^e\hat{\mathbf{T}}_u$ in Eq. (3), the transfer impedance $1/\hat{Z}_e$ is plotted for the TM model in Fig. 12 along with the predicted forward transfer function V_u/P_e for the ME model closed condition (this prediction is re-plotted from the left panels of Fig. 8). The $1/\hat{Z}_e$ is the

FIG. 11. (Color online) Left: Magnitude (top) and phase (bottom) of effective area $\hat{A}_F$ and transfer function F_u/P_e with ME cavity closed compared in the top panel to the geometric areas S_{TM} and S_o . Right: Magnitude (top) and phase (bottom) of the inverse effective area $\hat{A}_V^{-1}$ and transfer function V_u/U_e with ME cavity closed compared in the top panel to the inverse geometric area $1/S_{TM}$.

FIG. 12. (Color online) Magnitude (left) and phase (right) of the predicted $1/\hat{Z}_e$ and V_u/P_e with ME cavity closed compared to the measured mean umbo transfer function V_u/P_e of Whittemore *et al.* (2004), for which the data occur at discrete frequencies labeled by circle markers.

relevant *in vivo* transfer function to compare inasmuch as $\hat{Z}_e^{-1} = V_u/(P_e - P_{tc})|_{F_u=0}$ [see Eq. (5)]. Aside from effects related to P_{tc} , $\hat{Z}_e^{-1}$ represents the boundary condition in which the umbo is free, so that the magnitude of $\hat{Z}_e^{-1}$ is larger than the magnitude of V_u/P_e at all frequencies, and the phase of V_u/P_e is delayed with respect to $\hat{Z}_e^{-1}$.

The transfer function V_u/P_e is the umbo transfer function with respect to ear-canal pressure just in front of the TM. This has been experimentally measured *in vivo* using laser Doppler vibrometry for discrete frequencies between 0.3 to 6 kHz. The data reported by Whittemore *et al.* (2004) are also plotted in Fig. 12. The measured mean level was similar, but about 3 dB lower than the predicted level for frequencies up to about 2 kHz. However, the measure mean level was larger than predicted between 3 and 6 kHz, with a maximum difference of 15 dB. The measured mean level remained less than the predicted level of $1/\hat{Z}_e$. The measured mean phase was larger than the predicted phase of V_u/P_e at all frequencies up to 4 kHz, while the frequency range with the largest phase differences was about 2–4 kHz.

The vibrometry measurements were performed with the ear-canal microphone slightly displaced from the center of the TM, which would introduce a difference relative to the predicted transfer function. The prediction was adjusted to estimate V_u at the umbo and the pressure $\tilde{P}_e$ a short distance away (e.g., 4 mm). The magnitude of this predicted $V_u/\tilde{P}_e$ function was slightly increased at higher frequencies in the direction towards the measured data, but the change was small relative to the 15 dB discrepancy. Therefore, the present model was relatively accurate at predicting umbo velocity up to about 2 kHz, but it failed at higher frequencies. Some combination of the assumptions underlying the present TM model and the assumption of one-dimensional transmission in the ossicular chain led to this observed error. The present model was constructed to predict acoustical transmission between the ear canal and the cochlear fluids just inside the oval and round windows, but its parameters were not adjusted using umbo velocity measurements. More research is needed to predict the umbo transfer function. One approach would be to include measurements of this umbo transfer function in the data used to optimally estimate the model parameters.

C. Physical interpretation of transfer matrix ${}^e\hat{\mathbf{T}}_{ow}$

The ear-canal to oval-window transfer matrix ${}^e\hat{\mathbf{T}}_{ow}$ defined in Eqs. (8) and (9) describes the model of eardrum and ossicular-chain dynamics between the ear canal and SV fluid in the inner ear. This section provides a physical interpretation of these matrix elements.

For the matrix elements of ${}^e\hat{\mathbf{T}}_{ow}$, it is convenient for forward transmission to express each of the effective transformer ratios in Eqs. (8) and (9) as a ratio of the output variable in the inner-ear SV fluid to the input variable in the ear canal just in front of the TM. This focuses attention on $\hat{N}_P$ for pressure and $\hat{N}_U^{-1}$ for volume velocity. With the stapes held fixed so that $U_{ow}=0$, then $\hat{N}_P = (P_{ow} - P_{tc})/(P_e - P_{tc})$ is the ratio of pressure in the cochlear vestibule to ear-canal pressure, i.e., it is a blocked forward pressure transfer function (Shera and Zweig, 1992). The first measurements of $\hat{N}_P$ were described in Békésy (1960). With the cochlear load removed so that $P_{ow} - P_{tc}=0$, $\hat{N}_U^{-1} = U_{ow}/U_e$ is the ratio of the volume velocity of the oval window to the volume velocity of the eardrum. As mentioned in the paragraph under Eq. (37), these transformer ratios satisfy $\hat{N}_P = \hat{N}_U = N_1$ for an eardrum modeled as a rigid piston.

The $\hat{N}_P$ and $\hat{N}_U^{-1}$ are plotted in Fig. 13 with respect to the fixed transformer ratio N_1 of the single-piston eardrum [see Eq. (37)] and the fixed transformer ratio N_2 for the ossicular-bound component of the two-component eardrum [see Eq. (38)]. The magnitude of $\hat{N}_P$ was bounded between N_1 and N_2 at all frequencies up to 8 kHz. In comparison with the predicted forward SV pressure transfer function $H_{cv}^F = P_{ow}/P_e$ with ME cavity closed, which is replotted on this figure from Fig. 5, $\hat{N}_P$ was 15 dB larger at 0.25 kHz, and about 8–10 dB larger at frequencies from 1 to 4 kHz with smaller differences at higher frequencies. This illustrated the effect of the motion of the stapes footplate into the inner-ear fluids relative to the blocked stapes condition, as well as any effects related to the fact that P_{tc} was non-zero.

Also in the left panel, the magnitude of $\hat{N}_U^{-1}$ was much less than $1/N_1$ in the level plot at all frequencies, and more so at frequencies above 3 kHz. This curve shows that much smaller volume velocities were swept out by the stapes in its free boundary condition with $P_{ow} - P_{tc}=0$ than by the total surface of the eardrum. The magnitude of the volume

FIG. 13. (Color online) Level (left) and phase (right) of effective transformer ratios $\hat{N}_P$ and $\hat{N}_U^{-1}$, such that each curve shows the ratio of output to input variable in forward transmission. Also shown are predicted responses shown for SV pressure transfer function P_{ow}/P_e (re-plotted from left panel of Fig. 5) and volume velocity transfer function U_{ow}/U_e for the ME cavity closed condition. Ideal transformer ratios N_1 and N_2 are plotted as horizontal lines in the left panel.

velocity ratio U_{ow}/U_e with ME cavity closed was 4–8 dB less than $|\hat{N}_U^{-1}|$ between 1 and 8 kHz. This is a result of the larger stapes velocity in the free boundary condition, as would be expected.

In the right panel, the phases of $\hat{N}_P$ and $\hat{N}_U^{-1}$ were close to zero at frequencies below 0.8 kHz, and decreased with increasing frequency above 1 kHz. The phase of H_{ev}^F with ME cavity closed was similar to the phase of $\hat{N}_P$ at frequencies above about 1 kHz. The phase of U_{ow}/U_e for the middle ear in the closed cavity condition was similar to the phase of $\hat{N}_U^{-1}$ at all frequencies, with the largest differences near 1 and 11 kHz.

Using a model with physiologically plausible constraints, Shera and Zweig (1992) showed that $|\hat{N}_P \hat{N}_U^{-1}| < 1$ at low frequencies. The results in Fig. 13 show that this inequality was satisfied at all frequencies in the present model, and more so at frequencies above 3 kHz.

The matrix element $\hat{Z}$ in Eq. (9) for forward transmission with a free boundary condition at the oval window ($P_{ow} - P_{tc} = 0$) is the transfer impedance of the input pressure difference $P_e - P_{tc}$ relative to the output variable U_{ow} . By using the area S_s of the stapes footplate to convert U_{ow} to stapes velocity V_{st} , a transfer function H_Z is defined and further expressed by

$$H_Z = \frac{V_{st}}{(P_e - P_{tc})} \bigg|_{P_{ow}-P_{tc}=0}^F = \frac{1}{S_s \hat{Z}}. \quad (51)$$

For forward transmission, $|H_Z|$ was larger than the predicted $|V_{st}/P_e|$ at all frequencies, and was at least 6 dB larger at frequencies between 1.1 and 7.1 kHz, with a peak level difference of 8.2 dB (see left panels, Fig. 8). The phase of H_Z was slightly more positive than the phase of V_{st}/P_e below 2 kHz, and very similar at higher frequencies. The fact that the predicted forward-transmission V_{st}/P_e was nearly the same for the ME cavity open and closed conditions in this figure suggested that P_{tc} has negligible importance on this transfer function. The same insensitivity to P_{tc} also applied to reverse transmission.

The matrix element $\hat{Y}$ in Eq. (9) is interpreted using reverse transmission for which the matrix ${}^e\hat{\mathbf{T}}_{ow}$ is inverted. Using the relations in footnote 1 and Eqs. (8) and (9), a transfer function H_Y is defined and further expressed by

$$H_Y = \frac{(P_e - P_{tc})}{V_{st}} \bigg|_{U_e=0}^R = -\frac{\hat{S}_s}{\hat{Y}}. \quad (52)$$

The H_Y acts as a reverse transfer impedance with a blocked boundary condition at the ear canal (i.e., $U_e = 0$) of the output variable $(P_e - P_{tc})$ relative to the input variable V_{st} . For reverse transmission, $|H_Y|$ was similar to but slightly larger than the reverse $|P_e/V_{st}|$ at all frequencies (see right panels, Fig. 8). The phases of H_Y and the reverse P_e/V_{st} were similar at all frequencies, with a slightly larger difference between 2 and 7 kHz.

These comparisons demonstrated the close functional relationships of the individual elements of ${}^e\hat{\mathbf{T}}_{ow}$ to predicted transfer functions for forward and reverse transmission.

D. Ossicular mechanics model

Ossicular motion in the real middle ear includes both translations and rotations in three dimensions. Each “mass” parameter in the present model was not simply a mass or moment of inertia for a single kinematical degree of freedom, but rather represented an equivalent one-dimensional representation across multiple translational and rotational degrees of freedom. A similar comment applies to compliant and resistive elements.

With the above proviso, the model parameter values for the masses of the malleus, incus, and stapes in Table I were 5.38, 4.35, and 4.60 mg, respectively, with the stapes mass fixed at the experimental value of Merchant *et al.* (1996). Inasmuch as the circuit topology of the ossicular chain in the present model was the same as in O’Connor and Puria (2008), it was of interest to compare their model parameters. The estimated malleus and incus masses from the optimization were similar to those in O’Connor and Puria (2008), which were 4.52 and 4.6 mg, respectively (their stapes mass was 3.5 mg). O’Connor and Puria pointed out that these malleus and incus mass parameter values were much smaller than the actual masses. They proposed that the rotational axis of the malleus-incus complex changed orientation at higher frequencies to one with a smaller effective moment of inertia, which would result in smaller effective mass parameters that have their largest effects at high frequencies. Their theory was based on the three-dimensional motion of the

ossicular chain interpreted using an effective one-dimensional model, which may apply as well to the behavior of the present model.

The mechanical compliance of the malleus attachment C_{mm} was $100 \text{ kg}^{-1} \text{ s}^2$ in the present model and $0.00189 \text{ kg}^{-1} \text{ s}^2$ in O'Connor and Puria.⁶ Based on geometry, the area of the ossicular-bound component of the TM was one-tenth of the total TM area used by O'Connor and Puria. The difference in transformer ratios k_1 between single-piston and two-component models would contribute a factor of 100 [i.e., $(S_{TM}/S_o)^2 = 100$], which would imply that C_{mm} might be 100 times more compliant in the present model. For forward power flow through the ossicular-bound component of the TM, the acoustical coupling compliance C_C between the TM components may be expressed as a mechanical compliance by $C_{mC} = C_C/S_o^2$. After the action of the time delay τ , the C_{mC} would act in series with C_{mm} with a combined value of 0.183, which when divided by the k_1 related factor of 100, would result in an effective compliance of 0.00183 kg/s . This value is within 3% of the value of C_{mm} in the single-piston model of O'Connor and Puria.

This suggests for the present model that the main power flow from the ear canal through the eardrum to the ossicular chain is the power flow through the free component of the TM (with 90% of the total area of the TM) that is coupled via a time-delayed motion to move the ossicular-bound component of the TM and the umbo, and thence to transmit power through the ossicular chain. In the absence of the large surface area of the free component of the TM, the sound wave in the ear canal would inefficiently couple directly to the ossicular chain through the ossicular-bound component of the TM alone.

This is reminiscent of power flow in some musical instruments. For example, a piano hammer strikes one or more strings that are attached to a bridge (a quasi-one-dimensional structure), which drives the motion of a soundboard (a two-dimensional structure) to which it is attached, and the soundboard radiates sound to the room. The vibrating string would radiate inefficiently if it were coupled via the bridge with the room, because a one-dimensional system does not efficiently deliver power directly to a three-dimensional system. "Playing the piano in reverse" (as Helmholtz did, which is an example of his acoustic reciprocity theorem in action) by placing a sound source in the room and measuring the resulting vibration of the strings with the damper pedal depressed so the string motion is not attenuated, the sound source efficiently couples to the vibrating string through the intermediary two-dimensional system. In the middle ear, the incident sound field in the ear canal acts over the two-dimensional TM area, which efficiently collects sound power and delivers it to produce a quasi-one-dimensional motion of the umbo.

The mechanical resistance of the malleus attachment R_{mm} was 0.0144 kg/s in the present model and 0.118 kg/s in O'Connor and Puria. The parameter R_{mm} , which also acts at the juncture of the TM and ossicle parts of the model, was more different in the model of O'Connor and Puria and the present model than were the mass parameters. This is likely due to the fact that their model used a single-piston model of

the eardrum whereas the present model used a two-component model. Both models included a time delay parameter on the eardrum, but the delay was incorporated in a different manner.

The shunt pathways in the ossicular chain of the present model included effects of the malleus-incus joint and the incus-stapes joint (see Fig. 2), with each parameterized by a shunt compliance and resistance. Using Table I, the fact that $C_{mmi} = 0.161 \times 10^{-3} \text{ kg}^{-1} \text{ s}^2$ and $C_{mis} = 0.344 \times 10^{-3} \text{ kg}^{-1} \text{ s}^2$ means that the malleus-incus joint was approximately twice as stiff as the incus-stapes joint. The time constant for the malleus-incus joint was $R_{mmi}C_{mmi} = 0.0051 \mu\text{s}$ compared to $R_{mis}C_{mis} = 63.4 \mu\text{s}$ for the incus-stapes joint. The smallness in the time constant for the malleus-incus joint results from the fact that $R_{mmi}/R_{mis} = 1.73 \times 10^{-4}$. In fact, R_{mmi} may be set to zero in the present model without any meaningful changes in any of the transfer functions over the bandwidths analyzed in this study. This result was confirmed by multiple optimizations using a variety of different initial parameter values (see also the Appendix). Nevertheless, the non-zero value of R_{mmi} is retained in Table I, as its small value was an outcome of the model analyses rather than an *a priori* assumption.

Moreover, it was confirmed that setting C_{mmi} also to zero, which would immobilize the malleus-incus joint, resulted in inaccurate model predictions. For example, the predicted forward pressure transfer functions H_{ev}^F and H_{et}^F had large errors at frequencies above 4 kHz with $C_{mmi} = 0$. The importance of a non-zero C_{mmi} is consistent with the measurements of Willi *et al.* (2002), who found that the malleus-incus joint was mobile and influenced the relative rotation of ossicles at frequencies between 1 and 3 kHz. In the model of O'Connor and Puria (2008), C_{mmi} was about seven times larger than C_{mis} (rather than smaller as in the present model), and the resistances R_{mmi} and R_{mis} were approximately equal.

The present study focused on single-point transfer functions of the middle ear at the eardrum and in SV at the oval window, and in two-point transfer functions between the ear canal and inner ear. There was lesser emphasis on analyzing the internal ossicular motions inasmuch as the measured motions (Willi *et al.*, 2002) were found to involve translations and rotations in three dimensions.

In general, the predicted forward-transmission transfer functions had reasonable agreement with measured transfer functions (see Figs. 3, 5, and 6), except for the predicted V_u/P_e above 2 kHz in Fig. 12. The predicted reverse middle-ear impedance had somewhat less agreement (see Fig. 7). This was not simply due to over-weighting forward transmission in the optimization (see Appendix), inasmuch as a slight increase in weighting for reverse transmission degraded the accuracy of fitting the forward transfer functions.

One possibility is that the three-dimensional motions of the ossicular chain may present greater theoretical challenges to lumped-element modeling of reverse transmission compared to forward transmission. This may be related to the fact that an ear-canal sound source in forward transmission couples directly to the TM whereas a cochlear sound source in reverse transmission couples directly to the ossicular chain. More research is needed.

E. MACS model

The optimization resulting in the high-loss viscothermal loss coefficients ξ_V and ξ_T led to predictions of Z_{MACS} and Z_{cav} that were much more highly damped (Keefe, 2015) than the experimentally measured transfer functions in human cadaver ears (Stepp and Voss, 2005). The predicted Z_{MACS} and Z_{cav} using the low-loss coefficients had better agreement with these measurements. Increasing the loss in the MACS reduced the fine structure in the energy reflectance at mid-frequencies (see Fig. 4).

A potential explanation begins with the observation that the predicted peaks in Z_{cav} in which the MACS response played an important role, were strongly influenced by the MACS geometry in Keefe (2015). If the acoustics of the airway branching model showed resonances at different frequencies from those in the actual MACS, and if those resonances would otherwise influence the vibration of the TM, then the final model optimization might have attenuated the resonances by increasing the viscothermal damping in order to fit the measured data. This was the observed pattern, although more research is needed to explore alternative MACS models and more data are needed to evaluate whether Z_{MACS} differs *in vivo* compared to a temporal-bone condition.

As mentioned in Keefe (2015), it would be advantageous to formulate a morphometric model of MACS structure whose structural parameters could be varied within an acoustical model optimization. This would allow the optimization procedure of the acoustical model to shift the resonance frequencies and damping of the MACS, as well as all other model parameters, to find the best fit between predicted and measured transfer functions. The main reason that this approach was not used in the present model is that a change in the airway dimensions or number of generations in the MACS morphometric model did not preserve the ratio of total volume to total surface area. This ratio is known to be fairly constant across ears with a wide range of MACS volumes (Park *et al.*, 2000; Swarts *et al.*, 2011). This lack of invariance in geometrical scaling may mean that the airway structure of the MACS is not adequately represented by a binary symmetrical airway model.

F. Implications for vestibular excitation

A high-level sound presented through the ear canal and middle ear can activate vestibular evoked myogenic potential (VEMP) signals in the otolith organs of the vestibule of the inner ear via movements of inner-ear fluids driven by the motion of the stapes (Young *et al.*, 1977; McCue and Guinan, 1994). An effective stimulus used in cervical (c) VEMP testing of the sensitivity to high-level air-conducted sound is a 0.5-kHz short-duration tone-burst, for which a typical clinical cVEMP threshold is 104 dB peak SPL (McNerney and Burkard, 2011). This SPL corresponds to a peak ear-canal pressure $|P_e|$ of 3.17 Pa. Evidence suggests that such air-conducted sound results in a linear acceleration detected by the saccule, which is located in the inner ear close to the vestibule.

Air-conducted sound that is transmitted to the SV fluid just inside the oval window generates fluid motions into the cochlea and any third window in SV, which refers here to an

acoustic volume velocity in the fluid bounded in part by the saccule. Such a motion would generate a linear force resultant acting on the saccule that would result in a relative linear acceleration of a higher-density otoconia layer relative to lower-density mesh and gel layers into which cilia of the saccular hair cells protrude. This shearing motion of the cilia would modulate the hair cell electromotility that is associated with neural transduction (Jaeger *et al.*, 2002).

Using the inner-ear fluid circuit in Fig. 1, the magnitude of the volume velocity U_{3v} into the third window of SV is

$$|U_{3v}| = |Y_{3v}P_{ow}| = |Y_{3v}P_e H_{ev}^F|. \quad (53)$$

The latter relation uses the forward pressure transfer function in Eq. (36). The level of $|H_{ev}^F|$ at 0.5 kHz from Fig. 5 is about 14 dB, or a magnitude of 5. Using the value of Y_{3v} from Table I, the peak volume velocity into the third window of SV at the cVEMP threshold pressure at 0.5 kHz is predicted to be 0.26 mm³/s. This third window effect is associated with an inner ear with normal physiological function. This information is relevant to constructing a physiological inner-ear model of cVEMP excitation at threshold in response to air-conducted sound.

V. CONCLUDING REMARKS

A model of forward and reverse transmission of sound in the human middle ear with normal function was developed using a two-component TM model and an acoustic model of the air spaces comprising the tympanic cleft. The eardrum model included one component bound along the manubrium and another bound by the tympanic cleft. The latter freely moving component had three resonant modes of vibration. The motion of the eardrum components were coupled by a time-delayed compliant impedance.

The tympanic cleft in the middle-ear closed condition was represented by an acoustical transmission-line for the tympanic cavity, aditus, antrum, and terminated by the MACS. The MACS was modeled using a binary symmetrical airway branching model with total volume and area equal to mean values from x-ray computerized tomography scans. For comparison with middle-ear measurements performed with middle-ear cavity open, the tympanic cleft boundary was also modeled using an acoustic radiation termination.

A model used in previous studies was adapted to represent the dynamics of the ossicular chain, round-window impedance, and cochlear impedance. Effects of shunt inner-ear fluid motion into a third windows in SV were used to estimate the peak volume velocity in the third window at the mean threshold of cervical vestibular evoked myogenic potential responses.

Model parameters were obtained, wherever possible, from measurements reported in the literature, or calculated by an optimization procedure that minimized the error between predicted and measured transfer functions. The forward transfer functions in this optimization set included the middle-ear impedance, energy reflectance, pressure transfer function in SV just inside the oval window relative to the ear canal, and pressure transfer function in ST just inside the round window relative to the ear canal. The reverse middle-ear

impedance was also included in the optimization set to improve predictions of reverse transmission through the middle ear. The upper frequencies used in fitting the unknown parameters to measured data varied from 8 to 13 kHz, depending on the bandwidth of each measured transfer function. Some discrepancies between predicted and measured forward transfer functions were accepted in the optimization results so as to improve the goodness of fit for reverse transfer functions.

The model was used to predict other middle-ear transfer functions and compare them to published data. These predictions included the forward and reverse pressure difference across the cochlea relative to ear-canal pressure, reverse pressure transfer function in SV just inside the oval window relative to the ear canal, reverse pressure reflectance, forward and reverse ratios of stapes velocity and ear-canal pressure, and forward and reverse ratios of stapes velocity to the pressure difference across the cochlea. The forward pressure transfer function between umbo velocity and ear-canal pressure was also modeled, although the predicted transfer function was only accurate up to about 2 kHz.

The model of TM motion included standing waves as well as traveling-wave delay. Intra-cochlear transfer functions were insensitive to whether the middle-ear cavities were open or closed. The overall model performed somewhat better for forward than reverse transmission.

The model predicted the level of the minimum-audible pressure difference across the cochlea, and the MEE for forward sound transmission from the ear canal to the cochlea. This predicted MEE was similar to a new experimental measure of the MEE constructed from published data. Both were similar to a previously published result except for small differences at low frequencies.

The model has clinical significance based on its ability to explain results from a diverse set of middle-ear transfer functions. The form of the model is well-suited to combining with models of ear-canal acoustics and cochlear models.

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APPENDIX: NUMERICAL METHODS AND MODEL OPTIMIZATION

1. Forward and reverse transmission

The complete circuit model in Fig. 1 requires specification of ${}^e\hat{\mathbf{T}}_u$ and ${}^u\hat{\mathbf{T}}_{ow}$, the impedances Z_{rw} , ΔZ_{co} , and Z_{cav} , and the admittances Y_{3v} and Y_{3t} . The unknown dynamical variables are $(P_e, U_e, P_{tc}, P_{ow}, U_{ow}, P_{rw}, U_{rw}, U_{co})$. The variables U_{co} and P_{rw} are first eliminated using Eqs. (10) and (13), respectively, which leaves six unknowns.

To evaluate forward transmission, U_{rw} is eliminated using Eq. (14). An ear-canal volume velocity source U_e is assumed. The remaining unknowns $(P_e, P_{tc}, P_{ow}, U_{ow})$ are calculated using the pair of relations in Eq. (8), and Eqs. (7) and (11). While an analytical solution is straightforward, it would be complicated to interpret and is therefore omitted. It is convenient in practical numerical calculations to express the system of equations in matrix form as follows (in which a superscript T indicates the transpose):

$$\begin{aligned} \mathbf{A}_F \mathbf{x}_F &= \mathbf{b}_F, \\ \mathbf{x}_F^T &= U_e^{-1} (P_e \quad P_{ow} \quad \Delta Z_{co} U_{ow} \quad P_{tc}), \\ \mathbf{b}_F^T &= (0 \quad -1 \quad 1 \quad 0), \\ \mathbf{A}_F &= \begin{pmatrix} 1 & -\hat{N}_P^{-1} & -\Delta Y_{co} \hat{Z} & \hat{N}_P^{-1} - 1 \\ 0 & -\hat{Y} & -\Delta Y_{co} \hat{N}_U & \hat{Y} \\ 0 & Y_{3v} + \Delta Y_{co} Y_{3t} / Y_{rct} & 0 & Y_{cav} + Y_{3t} Y_{rw} / Y_{rct} \\ 0 & \Delta Y_{co} + Y_{3v} - \Delta Y_{co}^2 / Y_{rct} & -\Delta Y_{co} & -\Delta Y_{co} Y_{rw} / Y_{rct} \end{pmatrix}, \end{aligned} \quad (\text{A1})$$

in which new acoustic admittance terms are defined as

$$\begin{aligned} \Delta Y_{co} &= 1 / \Delta Z_{co}, \\ Y_{rw} &= 1 / Z_{rw}, \\ Y_{cav} &= 1 / Z_{cav}, \\ Y_{rct} &= Y_{rw} + \Delta Y_{co} + Y_{3t}. \end{aligned} \quad (\text{A2})$$

The solution vector $\mathbf{x}_F$ contains $\Delta Z_{co} U_{ow}$ rather than U_{ow} with concomitant changes in $\mathbf{A}_F$ and the source vector $\mathbf{b}_F$. This results in a well-conditioned matrix $\mathbf{A}_F$ with all unknowns within the vectors and matrix sharing the same physical units. The solution vector is calculated at each discrete frequency from the source vector and square matrix $\mathbf{A}_F$.

using Gaussian elimination. The solution vector contains the predicted transfer functions from which all other transfer functions of interest are calculated.

To evaluate reverse transmission, P_e is eliminated from the six unknown variables by imposing the boundary condition at the eardrum on the volume velocity $-U_e$ driving into the reverse ear-canal input impedance $Z_{in,e}^R$:

$$P_e = -Z_{in,e}^R U_e. \quad (A3)$$

This input impedance is calculated by terminating the ear canal $L_e = 2$ mm from the eardrum with the insert probe of an Etymotic ER-10B + probe microphone (this length is not used to model forward transmission). The ear canal is modeled by an acoustical transmission line comprised of a cylindrical tube of area S_e and length L_e . This is similar to the geometry used in Puria (2003) to measure reverse transmission, except that Puria used an Etymotic ER 7C probe microphone to terminate the ear canal. To facilitate comparisons between reverse

transmission in the model and the Puria dataset, it is assumed that the source reflectances of the Etymotic ER 7C and ER10B + are identical. Viscothermal losses in this very short ear canal are sufficiently small that they may be neglected. The source pressure reflectance $\mathcal{R}_p$ of the probe measured by Keefe and Abdala (2007) is converted into an input (Thevenin) impedance Z_p by $Z_p = Z_{c,e}(1 + \mathcal{R}_p)/(1 - \mathcal{R}_p)$, with $Z_{c,e}$ from Eq. (2). The resulting impedance using transmission-line theory (Keefe, 2015) with a propagation constant $\Gamma = j\omega/c$ is

$$Z_{in,e}^R = Z_{c,e} \frac{(Z_p/Z_{c,e}) + j \tan(\omega L_e/c)}{1 + j \tan(\omega L_e/c)(Z_p/Z_{c,e})}. \quad (A4)$$

A volume velocity source U_{rw} at the round window is assumed in reverse transmission. The four remaining unknowns (U_e , P_{tc} , P_{ow} , U_{ow}) are calculated using Eqs. (7), (8), and (11). The matrix system of equations is

$$\begin{aligned} \mathbf{A}_R \mathbf{x}_R &= \mathbf{b}_R, \\ \mathbf{x}_R^T &= U_{rw}^{-1} (Z_{c,e} U_e \quad (1/\zeta) P_{ow} \quad \Delta Z_{co} U_{ow} \quad P_{tc}), \\ \mathbf{b}_R^T &= (0 \quad 0 \quad 0 \quad 1), \\ \mathbf{A}_R &= \begin{pmatrix} Z_{c,e}^{-1} [\hat{N}_U Z_{in,e}^R + \hat{Z}] & \zeta & 0 & \hat{N}_U - 1 \\ Z_{c,e}^{-1} [\hat{Y} Z_{in,e}^R + \hat{N}_P^{-1}] & 0 & -\zeta \Delta Y_{co} & \hat{Y} \\ -Z_{c,e}^{-1} & \zeta Y_{cvt} & -\zeta Y_{3t} & Y_{cav} \\ 0 & \zeta Y_{cvt} & -\zeta (\Delta Y_{co} + Y_{3t}) & 0 \end{pmatrix}, \end{aligned} \quad (A5)$$

in which the acoustic admittance Y_{cvt} and dimensionless ζ are defined as

$$\begin{aligned} Y_{cvt} &= Y_{3v} + Y_{3t} + Y_{3t} Y_{3v} / \Delta Y_{co}, \\ \zeta &= \Delta Z_{co} / Z_{c,e}. \end{aligned} \quad (A6)$$

The admittance $Y_{cvt} = 0$ in the absence of third-window effects; ζ is the ratio of the differential cochlea impedance to the characteristic impedance of the ear canal. The solution vector $\mathbf{x}_R$ is calculated using Gaussian elimination and all transfer functions of interest are calculated in a manner analogous to that for forward transmission.

2. Model optimization

Table I lists the 21 model parameters that were determined in an optimization procedure based on a single error function E^2 . This error function was the square of the relative differences in a set of predicted versus measured transfer functions. The three *in vivo* forward input transfer functions included in the optimization set were the energy reflectance (Margolis *et al.*, 1999), and the real and imaginary parts of the equivalent input impedance at the TM (Margolis *et al.*, 1999; Stinson, 1990).

The four forward-transmission transfer functions included in the optimization set were the real and imaginary parts of the pressure transfer functions between oval window

and ear canal, and between round window and ear canal. These temporal-bone data were measured with middle-ear cavity open (Nakajima *et al.*, 2008).

Preliminary modeling used only these experimental data; the resulting fits were satisfactory for all forward transfer functions. However, the predictions of reverse transfer functions using the preliminary model were unsatisfactory. To improve the overall predictions, the final optimization set also included measurements of Z_{in}^R (Puria, 2003), which was defined as the ratio of SV pressure to the volume velocity swept out by the stapes and directed into the middle ear ($P_{ow}[-U_{ow}]$).

The i th model transfer function is denoted as H_i^m , and the i th experimentally measured transfer function as H_i^e , in which i varies from 1 to 9 (see list of transfer functions in Table II). The model H_i^m was evaluated at each 1/12 octave frequency between 0.1 and 13 kHz. The measured transfer-function data were cubic-spline interpolated to the subset of this model frequency range corresponding to the experimental range of frequencies.

The i th transfer function includes a frequency index k that increments from 1 up to the total number of frequencies $N(i)$ available for the measurement of the i th transfer function. The i th model and experimental transfer functions at the k th frequency are denoted as H_{ik}^m and H_{ik}^e , respectively. A dimensionless error function E^2 is defined as

TABLE II. Model weighting coefficients W_i . Each transfer function is for forward transmission except for the reverse middle-ear impedance Z_{me}^R .

i	Transfer function	W_i
1	ER	0.3
2	$\text{Re } Z_e$	0.1
3	$\text{Im } Z_e$	0.1
4	$\text{Re } H_{ev}^F$	0.197
5	$\text{Im } H_{ev}^F$	0.197
6	$\text{Re } H_{et}^F$	0.050
7	$\text{Im } H_{et}^F$	0.050
8	$\text{Re } Z_{me}^R$	0.003
9	$\text{Im } Z_{me}^R$	0.003
Sum		1

$$E^2 = \sum_{i=1}^9 W_i \frac{\sum_{k=1}^{N(i)} (H_{ik}^m - H_{ik}^e)^2}{\sum_{k=1}^{N(i)} (H_{ik}^e)^2}. \quad (A7)$$

The weighting coefficients W_i for the nine transfer functions are listed in Table II and were constrained to sum to 1. The final weightings were equally split between the three ear-canal forward single-point transfer functions and the remaining transfer functions. The ear-canal transfer functions were more sensitive to the multiple modes of the TM, which involved 9 of the 21 model parameters that were fitted by the optimization, and to the structure of Z_{cav} . Energy reflectance was over-weighted relative to the middle-ear resistance and reactance because of greater confidence in its values at high frequencies. The forward SV pressure transfer function H_{ev}^F was over-weighted relative to the forward ST pressure transfer function H_{et}^F because its magnitude was larger. The reverse middle-ear impedance received the smallest weighting inasmuch as the primary emphasis was on fitting the forward transfer functions.

A constrained nonlinear optimization⁷ was used in which the range of parameter values was constrained. These ranges were varied in the process of fitting the model in its final form, for which the optimized error was $|E| = 0.0405$. The preliminary optimization using data from the seven ear-canal and forward pressure transfer functions actually achieved a smaller error with a more accurate fit to energy reflectance at high frequencies, but the errors in predicting reverse transmission were much larger. Increased weighting of reverse transmission reduced the goodness of fit for forward transmission.

The number of resonant modes in the TM was varied between one to six modes in preliminary analyses with accompanying increases in model complexity and reductions in $|E|$. The final model used three resonant modes as a tradeoff between model simplicity and accuracy. Adding more than three resonant modes produced only slight further reductions in $|E|$. This was not a simple numerical analysis inasmuch as all model parameters changed with each increase in the number of modes. Iterative analyses were needed to obtain satisfactory results in each instance.

¹Given a transfer matrix $\mathbf{T} = \begin{pmatrix} A & B \\ C & D \end{pmatrix}$ with complex elements A, B, C, D that are arbitrary subject to $AD - BC = 1$, its inverse transfer matrix is $\mathbf{T}^{-1} = \begin{pmatrix} D & -B \\ -C & A \end{pmatrix}$.

²More precisely, in the absence of an ossicular chain, small pressure differences exist within the tympanic cavity between the oval and round windows that act as a cochlea drive. These pressure differences are neglected in the present model, which are small compared to the pressure acting over the oval window that results from force transmission through the normally intact ossicular chain. Including such separate pressures would modify $P_{ow} - P_{tc}$ to $P_{ow} - P_{tco}$ in Eq. (6) and subsequent equations, and modify $P_{rw} - P_{tc}$ to $P_{rw} - P_{tcr}$ in Eq. (13) and subsequent equations. The slightly different tympanic-cavity pressures P_{tco} acting over the oval window and P_{tcr} acting over the round window would be located in the circuit model of Fig. 1 in Keefe (2015) slightly displaced from the current location of P_{tc} , and a medial tympanic cavity element would be introduced between the pressure locations. This difference in locations of the oval and round windows was omitted in the present model because the pressure difference has been concluded to be “negligibly different” in the normal human ear (Peake *et al.*, 1992).

³The inverse of the product of any transfer matrices $\mathbf{T}_1 \mathbf{T}_2$ is the reversed product of the inverses, i.e., $(\mathbf{T}_1 \mathbf{T}_2)^{-1} = \mathbf{T}_2^{-1} \mathbf{T}_1^{-1}$. For example, this may be used to invert the lower equation in Eq. (8) to solve for the column vector on the right-hand side.

⁴Note that M_f/S_f^2 , C_{mf}^{-1}/S_f^2 , and R_{mf}/S_f^2 in the top line of Eq. (17) have the same physical dimensions for Z_f as do I_n , C_n^{-1} , and R_n , respectively, in Eq. (24). These are all acoustical impedance elements. A similar correspondence of physical dimensions exists between the parameters for Z_o in Eqs. (17) and (25), and the parameters for Z_c in Eqs. (17) and (27).

⁵The MAP data used to generate Fig. 10 were similar to the “best-estimate MAP” described in Killion (1978). The data up to and including 6 kHz were the MAP (monaural) values derived from minimum audible field data. The data at and above 8 kHz were from Northern *et al.* (1971). The data between 6 and 8 kHz were smoothly interpolated between the MAP data at 6 and 8 kHz.

⁶The comparison with the model parameters of O’Connor and Puria (2008) was performed using the “sets A and B (16 ears)” column of their Table I. They used a mechanical stiffness $K_m = 530 \text{ kg/s}^2$; the equivalent value of C_{mm} was $1/K_m$.

⁷Numerical results were calculated using MATLAB release 2014a. All optimizations used the fmincon function with an interior point algorithm from the MATLAB Optimization Toolkit.

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