A three-dimensional nonlinear active cochlear model analyzed by the WKB-numeric method

Kian-Meng Lim a,*, Charles R. Steele b

a Department of Mechanical Engineering, National University of Singapore, 10 Kent Ridge Crescent, Singapore 119260
b Division of Mechanics and Computation, Department of Mechanical Engineering, Stanford University, Stanford, CA 94305-4035, USA

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Abstract

A physiologically based nonlinear active cochlear model is presented. The model includes the three-dimensional viscous fluid effects, an orthotropic cochlear partition with dimensional and material property variation along its length, and a nonlinear active feed-forward mechanism of the organ of Corti. A hybrid asymptotic and numerical method combined with Fourier series expansions is used to provide a fast and efficient iterative procedure for modeling and simulation of the nonlinear responses in the active cochlea. The simulation results for the chinchilla cochlea compare very well with experimental measurements, capturing several nonlinear features observed in basilar membrane responses. These include compression of response with stimulus level, two-tone suppressions, and generation of harmonic distortion and distortion products. © 2002 Elsevier Science B.V. All rights reserved.

Key words: Nonlinear cochlear model; Response suppression; Distortion

1. Introduction

Numerous models have been proposed and used to simulate the activity in the cochlea. Many are extensions of passive cochlear models with the inclusion of the micro-mechanics of the organ of Corti, in particular the active behavior of the outer hair cells.

The inclusion of negative damping in one-dimensional, lumped parameter models had been used by de Boer (1983) and Diependaal et al. (1987). Kanis and de Boer (1996, 1997) extended this model to include nonlinearity in the activity and obtained both frequency and time domain solutions using a quasi-linear method. They also demonstrated the phenomena of two-tone suppression and distortion product generation which are commonly observed in experimental measurements.

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2. Formulation

First, a macroscopic model based on the WKB method subjected to harmonic excitation is briefly described. Next, the nonlinear feed-forward active mechanism of the outer hair cells for the micro-mechanics in the organ of Corti is formulated. Combining both formulations for the macro- and micro-mechanics gives a coupled system of equations governing the responses for the various frequency components. An iterative procedure needs to be used to solve this set of nonlinear equations.

2.1. Macroscopic model

A schematic drawing of the macroscopic model showing the top, side, and end views is given in Fig. 1. This model consists of a straight tapered chamber with rigid walls filled with viscous fluid. The chamber is divided longitudinally by a cochlear partition into two equal rectangular ducts representing the scala vestibuli and scala tympani. The two fluid ducts are joined at the apical end via a hole representing the helicotrema. The cochlear partition represents a collapsed scala media with its structural properties dominated by the pectinate zone of the basilar membrane. This partition is modeled as an elastic orthotropic plate which is simply supported by rigid shelves on both sides along its length. The variations in width, thickness, and fiber density along the length of the basilar membrane are included, resulting in a partition with varying stiffness along its length.

The flexible cochlear partition is set into motion when the stapes pushes against the fluid in the scala vestibuli. The anti-symmetric pressure wave in the chamber is considered, since only this gives a significant displacement to the partition (Peterson and Bogert, 1950; Steele and Lim, 1999). Due to symmetry present in the model, only one fluid duct needs to be considered in the simulation. The fluid displacement field in the ducts is represented by a sum of the divergence of a scalar field $\phi$ and the curl of a vector field $\vec{\psi}$

$$\vec{u} = \nabla \phi + \nabla \times \vec{\psi}$$

where $\phi$ and $\vec{\psi}$ take the following forms:

$$\phi(x, y, z, t) = e^{-i\omega t} \Phi(x) \sum_{n=0}^{H} R_m(x) \cos \left( \frac{m\pi y}{L_2} \right) \cosh \left( \beta_m(x)(L_3-z) \right)$$

Other researchers (Zweig, 1991; Allen and Fahey, 1993) used a 'second filter' to describe the micro-mechanics of the organ of Corti in addition to a passive transmission line model. Hubbard et al. (1996) implemented the second filter using a traveling wave amplifier in their active cochlear model.

Higher dimensional active models have also been constructed. Diependaal and Viergever (1989) extended the negative damping model to two dimensions using a combination of integral equation and finite difference method. Two-dimensional finite difference models constructed by Neely (1985, 1993) used a feedback law to model the active mechanism. Full three-dimensional finite element models including varying details and complexities of the organ of Corti were also built by Kolston and Ashmore (1996), Böhnke and Arnold (1998) and Dodson (2001).

Finally, there is a class of models that include the activity in the organ of Corti as a feed-forward mechanism, taking into account the longitudinal tilt of the outer hair cells. Kolston et al. (1989) developed a linear lumped parameter model with the feed-forward mechanism, and Fukazawa and Tanaka (1996) further included the nonlinear behavior in the one-dimensional model. Two-dimensional (Geisler and Sang, 1995) and three-dimensional models (Steele et al., 1993; Steele and Lim, 1999) with the active feed-forward mechanism were also constructed. But these higher dimensional models are normally restricted to a linear analysis due to the formidable computations needed for the iterative solution procedure of a nonlinear problem.

The present work extends the linear three-dimensional feed-forward model to include the nonlinear behavior of the outer hair cells. This model is based on the phase-integral method, commonly known as the WKB (Wentzel–Kramers–Brillouin) method, which provides significantly faster computations than the finite difference or finite element methods, especially for high frequency responses. The viscous effects of the fluid in the scala and the variation of dimensions and material properties along the length are included. The frequency domain formulation in the linear model is retained, but all the harmonic components need to be considered together since they are coupled in the nonlinear problem. The time domain solution can readily be obtained by synthesis of these harmonic components. The frequency domain results also prove to be convenient for comparison with previous linear models and experimental measurements of frequency responses. The simulation results obtained from this active nonlinear model successfully demonstrate various features of the response in a live cochlea, as observed in in vivo experiments.
Here, a harmonic excitation with frequency $\omega$ is applied at the stapes. The displacement field satisfies the rigid wall boundary conditions at $y = 0$, $y = L_2$, and $z = L_3$ where the normal fluid displacements are zero. The coefficients $\Psi_m^1$ and $\Psi_m^2$ are related to the amplitude $\Phi$ and $R_m$ through no-slip boundary conditions on the cochlear partition where the tangential displacements are also zero. The coefficients $R_m$ are determined by matching the normal displacement of the fluid with that of the partition at their interface. Incidentally, the pressure in the fluid is given by

$$p_t = -\rho_f \ddot{\Phi}$$

where $\rho_f$ is the density of the fluid. Using the following definition of the wave number $n(x)$

$$n^2(x) = \frac{\Phi_{xx}}{\Phi}$$

the continuity equation for the fluid

$$\Delta \Phi = 0$$

reduces to the algebraic form

$$\beta_m(x) = \sqrt{n^2 + \left(\frac{m\pi}{L_2}\right)^2}$$

The WKB approximation is applied here with the assumption of large $n$. Similarly, the vorticity equation given by

$$\rho_f \ddot{\psi} = \mu \Delta \psi$$

can be expressed as

$$\gamma_m(x) = \sqrt{\beta_m^2 - i\omega \rho_f \mu}$$

where $\mu$ is the dynamic viscosity of the fluid. The equation governing the bending motion of the cochlear partition, modeled as an orthotropic tapered plate with width $b(x)$ and thickness $h(x)$, is

$$\rho_p h \ddot{w} + \frac{\partial^2}{\partial x^2} \left( D_{11} \frac{\partial^2 w}{\partial x^2} \right) + 2 \frac{\partial^2}{\partial x \partial y} \left( D_{12} \frac{\partial^2 w}{\partial x \partial y} \right) + \frac{\partial^2}{\partial y^2} \left( D_{22} \frac{\partial^2 w}{\partial y^2} \right) = p_p$$

Fig. 1. Schematic drawing of the macroscopic model: (a) side view of chamber, (b) end view of chamber, and (c) top view of cochlear partition. A typical basilar membrane vibration response due to harmonic excitation is shown.
bending stiffness components. Taking into account the sandwiched nature of the pectinate zone with the fibers occupying the lower and upper thirds of the entire thickness, the bending stiffness is determined from Young’s modulus \( E_{ij} \) in the respective directions, Poisson ratio \( \nu \), fiber volume density \( f \), and thickness \( h \), as given by

\[
D_{ij} = \frac{fE_{ij}h^3}{1-\nu^2} \frac{13}{162}
\]  

(11)

The displacement profile of the partition is assumed to take the following form

\[
w(x, \eta, t) = e^{-iat} W(x) \sin \frac{\pi \eta}{b}
\]  

(12)

The fluid and partition displacements are matched at their interface (with \( W(x) = \Phi(x) \)) and the coefficients \( R_m \) are determined from this assumed shape function of the displacement.

Integrating the pressure across the width and summing up the Fourier harmonics gives the force per unit length in the time domain for the partition and fluid. For the partition,

\[
F_{BM}(x, t) = \sum e^{-iat} \left( \int p_p(x, y, \omega_j) \, dy \right)
\]  

(13)

\[
= \sum e^{-iat} \mathcal{F}_{BM}(x, \omega_j)
\]  

(14)

where

\[
\mathcal{F}_{BM}(x, \omega_j) = (K_p(n; x, \omega_j) - \omega_j^2 M_p(x)) \, W(x, \omega_j)
\]  

(15)

with the plate’s stiffness given by

\[
K_p = \frac{2h}{\pi} \left\{ -\rho_p \omega^2 h + D_{11} n^4 + 2D_{12} n^2 \left( \frac{\pi}{b} \right)^2 + D_{22} \left( \frac{\pi}{b} \right)^4 \right\}
\]  

(16)

and mass given by

\[
M_p = \frac{2h}{\pi} \rho_p h
\]  

(17)

For the fluid,

\[
F_I(x, t) = \sum e^{-iat} \left( \int p_I(x, y, \omega_j) \, dy \right)
\]  

(18)

\[
= \sum e^{-iat} \mathcal{F}_I(x, \omega_j)
\]  

(19)

where

\[
\mathcal{F}_I(x, \omega_j) = \rho_f \omega_j^2 h_f(n; x, \omega_j) \, W(x, \omega_j)
\]  

(20)

\[
= \omega_j^2 M_I(n; x, \omega_j) \, W(x, \omega_j)
\]  

(21)

with \( M_I \) and \( h_f \) being the effective mass and thickness of the fluid layer over the width of the plate. These quantities are functions of the wave number \( n(x, \omega_j) \), as shown in Lim (2000).

The above provides a physically consistent and systematic reduction of the three-dimensional model to a one-dimensional formulation in spatial coordinates. The stiffness and mass quantities are reminiscent of those used in lumped parameter models, but these are derived from a physically based three-dimensional model here.
2.2. Nonlinear micro-mechanics

In this model, the force exerted by the outer hair cells on the cochlear partition is assumed to be proportional to the total force acting on the partition. This can be seen from the following simplistic arguments. The force acting on the basilar membrane is transmitted to the stereocilia by the stiff arches of Corti, as depicted in the transverse view in Fig. 2a. For moment equilibrium of the arches of Corti about its joint at the spiral ligament,

\[ F_{\text{cilia}}(x, t) = C_1(x) F_{\text{BM}}(x, t) \]

(22)

where \( F_{\text{cilia}} \) is the force acting on the stereocilia, \( F_{\text{BM}} \) is the resultant force acting on the basilar membrane, and \( C_1 \) is a constant which accounts for the ratio of the moment arms of each force about the pivot. The resultant force acting on the basilar membrane consists of those from the fluid in both ducts and the outer hair cells

\[ F_{\text{BM}}(x, t) = 2F(t, x) + F_c(x, t) \]

(23)

The above relations expressing the balance of forces is illustrated in Fig. 2c.

Due to the longitudinal tilt of the outer hair cells, the force acting on the stereocilia at \( x \) causes the outer hair cell to push at a point \( x+\Delta \) downstream on the basilar membrane, as shown in the longitudinal view in Fig. 2b,

\[ F_c(x+\Delta, t) = C_2(x, t) F_{\text{cilia}}(x, t) \]

(24)

where \( C_2 \) is a transfer function coefficient relating the two forces and \( \Delta \) depends on the outer hair cell length \( l_c \) and its angle to the \( x \)-axis \( \theta \),

\[ \Delta = l_c \cos \theta \]

(25)

Combining Eqs. 22, 23 and 24 yields

\[ F_c(x+\Delta, t) = \frac{C_1(x) C_2(x, t)}{2} (2F(t, x) + F_c(x, t)) \]

(26)

\[ = \alpha(x, t) (2F(t, x) + F_c(x, t)) \]

(27)

where \( \alpha = (C_1 C_2)/2 \) is referred to as the feed-forward gain factor. Fig. 3 shows the typical variation of the cell force \( F_c \) with the force on the basilar membrane \( F_{\text{BM}} \). Experiments have shown that the outer hair cell force saturates as the force on the basilar membrane increases (Pickles, 1988). From the relation in Eq. 27,

the gain factor \( \alpha \) is given by the chord joining a point on the curve to the origin. Fig. 4 shows the profile of the gain factor \( \alpha \) with the basilar membrane displacement \( w \). The gain factor remains fairly constant for small basilar membrane displacement and tapers off to zero as the basilar membrane displacement increases, due to the saturation in the outer hair cell force.

The force \( F_c \) and the gain factor \( \alpha \) can be expressed in terms of their Fourier coefficients, \( F_c(x, \omega_j) \) and \( A(x, \omega_j) \), in the frequency domain

\[ F_c(x, t) = \sum_j e^{-i\omega_j t} F_c(x, \omega_j) \]

(28)

\[ \alpha(x, t) = \sum_j e^{-i\omega_j t} A(x, \omega_j) \]

(29)

Eq. 27 becomes

\[ \sum_j e^{-i\omega_j t} F_c(x+\Delta, \omega_j) = \left( \sum_k e^{-i\omega_k t} A(x, \omega_k) \right) \]

(30)

\[ \left( \sum_l e^{-i\omega_l t} (2F_l(x, \omega_l) + F_c(x, \omega_l)) \right) \]

and the product on the right hand side can be replaced by a convolution of the two Fourier series giving

\[ \sum_{j=-N}^{N} e^{-i\omega_j t} F_c(x+\Delta, \omega_j) = \]

\[ \sum_{j=-N}^{N} e^{-i\omega_j t} \sum_{k=j-B}^{j+B} A(x, \omega_{j-k})(2F_l(x, \omega_k) + F_c(x, \omega_k)) \]

(31)

where \( N \) is the number of harmonics considered for the
vibration of the basilar membrane, and B+1 gives the number of terms used in the expansion for \( \alpha \). To determine \( \mathcal{F}_c(x+\Delta; \omega) \), the functional form of \( \mathcal{F}_c \) is assumed to be similar to \( \mathcal{F}_f \), which is a phase-integral form

\[
\mathcal{F}_c(x; \omega) = \mathcal{F}_c(x; \omega)e^{i\int n(\zeta; \omega)d\zeta}
\]

where \( \mathcal{F}_c \) is the slowing varying amplitude, after the rapidly varying part due to the ‘phase’ is being factored out. For small \( \Delta \), the following approximations are made

\[
\mathcal{F}_c(x+\Delta; \omega) \approx \mathcal{F}_c(x; \omega)
\]

\[
\int_{x}^{x+\Delta} n(\zeta; \omega)d\zeta \approx \int_{x}^{x} n(\zeta; \omega)d\zeta + n(x; \omega)\Delta
\]

The approximation in Eq. 34 is first order accurate, similar to the explicit Euler scheme commonly used in numerical integration. The error induced depends on the variation of \( n \) over the interval \( \Delta \), and this is small in the long-wave region near the stapes and tends to increase towards the apical short-wave region of the cochlea. The outer hair cell forces at \( x+\Delta \) and \( x \) are then related by

\[
\mathcal{F}_c(x+\Delta; \omega) = \mathcal{F}_c(x+\Delta; \omega)e^{i\int_{x}^{x+\Delta} n(\zeta; \omega)d\zeta}
\]

\[
\approx \mathcal{F}_c(x; \omega)e^{i\int_{x}^{x} n(\zeta; \omega)d\zeta + n(x; \omega)\Delta}
\]

\[
= \mathcal{F}_c(x; \omega)e^{in(x; \omega)\Delta}
\]

\[
= \Gamma(x; \omega)\mathcal{F}_c(x; \omega)
\]

where \( \Gamma \) is given by

\[
\Gamma(x; \omega) = e^{in(x; \omega)\Delta}
\]

Equating the Fourier coefficient in Eq. 31 gives

\[
\Gamma(x, \omega)\mathcal{F}_c(x, \omega) - \sum_{j=1}^{B} A(x, \omega_{j-1})\mathcal{F}_c(x, \omega_{j}) = 2\sum_{k=1}^{B} A(x, \omega_{k-1})\mathcal{F}_f(x, \omega_{k})
\]

The above equation can be put in a compact matrix form

\[
\Gamma(x)\mathcal{F}_c(x) - A(x)\mathcal{F}_c(x) = 2A(x)\mathcal{F}_f(x)
\]

and its rearrangement gives the following expression for the outer hair cell forces in terms of the fluid forces

\[
\mathcal{F}_c(x) = 2(\Gamma(x) - A(x))^{-1} A(x)\mathcal{F}_f(x)
\]

Here, the vectors \( \mathcal{F}_c(x) \) and \( \mathcal{F}_f(x) \) contain the Fourier coefficients \( \mathcal{F}_c(x, \omega) \) and \( \mathcal{F}_f(x, \omega) \) respectively,

\[
\begin{bmatrix}
\mathcal{F}_c(x, \omega_{N}) \\
\vdots \\
\mathcal{F}_c(x, \omega_{1}) \\
\mathcal{F}_c(x, \omega_{0})
\end{bmatrix}
\]

and

\[
\begin{bmatrix}
\mathcal{F}_f(x, \omega_{N}) \\
\vdots \\
\mathcal{F}_f(x, \omega_{1}) \\
\mathcal{F}_f(x, \omega_{0})
\end{bmatrix}
\]
\( \Gamma \) is a diagonal matrix with the elements given by \( \Gamma(\omega) \)

\[
\Gamma(x, \omega) = \begin{bmatrix}
\Gamma(x, \omega-N) & 0 & \cdots \\
0 & \cdots & \cdots \\
\cdots & \cdots & \cdots \\
\cdots & \cdots & \cdots \\
\cdots & \cdots & \cdots \\
\cdots & \cdots & \cdots \\
\end{bmatrix}
\]

(44)

and \( A(x) \) is a banded matrix with bandwidth \((2B+1)\) and components \( A(x, \omega_{j-k}) \)

\[
A(x) = \begin{bmatrix}
A(x, \omega_0) & \cdots & A(x, \omega_B) & 0 & \cdots \\
A(x, \omega_B) & \cdots & A(x, \omega_0) & \cdots & \cdots \\
\cdots & \cdots & \cdots & \cdots & \cdots \\
\cdots & \cdots & \cdots & \cdots & \cdots \\
\cdots & \cdots & \cdots & \cdots & \cdots \\
\cdots & \cdots & \cdots & \cdots & \cdots \\
\end{bmatrix}
\]

(45)

The off-diagonal terms in the matrix \( A \) provide the coupling between various harmonic coefficients of the forces and the extent of this coupling is determined by the parameter \( B \).

### 2.3. Solution of nonlinear system

Eq. 23 expressing the balance of forces on the partition can also be expressed in its Fourier components and put in the vector form

\[
F_{BM}(x) = 2 F_{f}(x) + F_{c}(x)
\]

(46)

where \( F_{BM} \) is vector of Fourier coefficients of \( F_{BM}(x, t) \) similar to \( F_{c} \) and \( F_{f} \) in Eq. 43. Eq. 15 written in the similar matrix-vector form gives

\[
F_{BM}(x) = (K_{p}(x) - \Omega^{2}M_{p}(x)) W(x)
\]

(47)

where \( \Omega \), \( K_{p}(x) \), and \( M_{p}(x) \) are diagonal matrices with entries \( \omega_{0}, K_{p}(x, \omega_{0}) \), and \( M_{p}(x, \omega_{0}) \) respectively. The column vector \( W(x) \) contains the displacement amplitudes at various frequencies \( \omega_{0} \). Also, the vector of Fourier coefficients of the fluid force is given by

\[
F_{f}(x) = \Omega^{2} M_{f}(x) W(x)
\]

(48)

where the mass matrix \( M_{f}(x) \) is also diagonal with entries \( M_{f}(n, x, \omega_{0}) \).

The system of equations in Eq. 46 is generally nonlinear because the gain \( \alpha \) depends on the displacement. However, for small displacements, \( \alpha \) is constant as shown in Fig. 4, and this gives a linear system whose solution can be obtained readily (Steele and Lim, 1999). Subsequently, the solution to the nonlinear case can be obtained through successive corrections on the linear solution. The solution procedure is described as follows.

First, for the linear case with small displacements, the off-diagonal terms of the matrix \( A \) are zero and the diagonal terms are given by the constant \( \alpha_{0} \). The matrix \( A \) can be written as

\[
A = \alpha_{0} I
\]

(49)

where \( I \) is the identity matrix. The outer hair cell force for this linear system, denoted as \( F_{c}^{L} \) for clarity, is then given by

\[
F_{c}^{L} = 2 \alpha_{0} (I - \alpha_{0} L)^{-1} F_{f}
\]

(50)

The force balance equation (46) becomes

\[
[K_{p} - \Omega^{2} M_{p} - 2(I + \alpha_{0} (I - \alpha_{0} L)^{-1}) \Omega^{2} M_{f}] W = 0
\]

(51)

The dependence on \( x \) is implied but omitted in the
above equations for clarity. Since all the coefficient matrices in this case have a diagonal structure, the equations in the system are uncoupled. Each individual equation gives an eiconal equation from which the wave numbers can be obtained for that particular frequency. Each equation has multiple complex solutions for the wave numbers. The complex wave numbers with a significant real part correspond to propagating waves, and the sign of the real part determines the direction of wave propagation. In the present formulation, positive and negative real parts correspond to forward and backward propagating waves, respectively. Normally, two propagating waves traveling in opposite directions can be found for each frequency and these provide the fundamental solutions for the Helmholtz equation (53) given below.

The amplitudes can be obtained from the transport equations which are obtained by considering the integral of the continuity equation over a thin slice of the duct cross-section \( \partial V = L_2 L_3 \delta x \)

\[
\int \delta V \Delta \phi = 0 \tag{52}
\]

which gives

\[
F_{xx} + n^2 F = 0 \tag{53}
\]

where

\[
F = \frac{WR_0 \sinh nL_3}{n} \tag{54}
\]

The amplitude \( W \) is obtained by solving for \( F(x) \) from the Helmholtz equation (53) using a combination of the asymptotic method in the short wave region \( (n \text{ large}) \) and the numerical Runge-Kutta method in the long wave region \( (n \text{ small}) \). The boundary conditions of matching the volume displacement at the stapes and zero pressure at the helicotrema are taken into account for solving the Helmholtz equation.

For the nonlinear case, \( A \) is not a diagonal matrix and the equations in the system (46) are coupled with each other. In order to derive the nonlinear solution from the linear solution, the linear system of equations (51) needs to be isolated from the nonlinear system. This is achieved by decomposing the cell force \( F_c \) into a sum of a linear part \( F_c^L \) as given by Eq. 50 and a nonlinear part \( F_c^{NL} \)

\[
F_c = F_c^L + F_c^{NL} \tag{55}
\]

### Table 1

<table>
<thead>
<tr>
<th>Gross properties in chinchilla cochlear model</th>
<th>Basilar membrane</th>
<th>Scala fluid</th>
<th>Stapes area</th>
<th>Outer hair cell</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \rho_b = 1.0 \times 10^3 \text{ kg/m}^3 )</td>
<td>( E_{11} = 1.0 \times 10^{-2} \text{ GPa} )</td>
<td>( \rho_s = 1.0 \times 10^3 \text{ kg/m}^3 )</td>
<td>( A_s = 0.7 \text{ mm}^2 )</td>
<td>( \alpha_i = 0.35 )</td>
</tr>
<tr>
<td>( E_{22} = 1.0 \text{ GPa} )</td>
<td>( E_{33} = 0.0 \text{ GPa} )</td>
<td>( \mu = 0.7 \times 10^{-3} \text{ Pa s} )</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
where
\[
F_{NLc} = 2 \left( \frac{(I - \alpha L)^{-1} A - \alpha_0 (I - \alpha_0 L)^{-1}}{K_0} \right) F_I
\] (56)

The nonlinear system of equations for force balance then becomes
\[
[K_p - \Omega^2 M_p - 2(I + \alpha_0 (I - \alpha_0 L)^{-1}) \Omega^2 M_I] \dot{W} = F_{NLc}
\] (57)

The left hand side of the above equation is the same as the homogeneous system in the linear case (Eq. 51). The extra term $F_{NLc}$ on the right can be treated as a forcing function to the linear system. The solution of the linear system provides the homogeneous part of the nonlinear solution. The particular solution due to the driving term on the right hand side of the nonlinear system can be found from the homogeneous solution using the method of variation of parameters. Since the driving term $F_{NLc}$ contains $A$ which depends on the displacement $W$, the particular solution obtained also depends on the final displacement. This leads to an iterative procedure in which the final displacement and the driving term are repeatedly calculated until the system of equations (57) is satisfied within a given tolerance.

Table 2
Property variations in chinchilla cochlear model

<table>
<thead>
<tr>
<th>$x$ (mm)</th>
<th>$b$ (mm)</th>
<th>$h$ (mm)</th>
<th>$f$</th>
<th>$L_2$, $L_3$ (mm)</th>
<th>$l_c$ (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0</td>
<td>0.130</td>
<td>0.0150</td>
<td>0.030</td>
<td>0.750</td>
<td>25.0</td>
</tr>
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<td>2.2</td>
<td>0.165</td>
<td></td>
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<td></td>
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<tr>
<td>4.3</td>
<td>0.187</td>
<td></td>
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</tr>
<tr>
<td>5.3</td>
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<td>0.708</td>
</tr>
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</tr>
<tr>
<td>8.8</td>
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<td></td>
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</tr>
<tr>
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<td></td>
<td>0.531</td>
</tr>
<tr>
<td>12.6</td>
<td>0.226</td>
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</tr>
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</tr>
<tr>
<td>15.3</td>
<td>0.240</td>
<td>0.0030</td>
<td>0.007</td>
<td>0.470</td>
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<tr>
<td>18.0</td>
<td>0.287</td>
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Fig. 6. Active basilar membrane response at various input levels. The basilar membrane response of the nonlinear active model is given for various stimulus levels. Most parts of the membrane behave linearly, except for the region around the characteristic place (5 mm) where the response curves are ‘compressed’, i.e., close to each other.
Fig. 7. Nonlinear compression of response with input level. The basilar membrane response at 5 mm is plotted against the input sound pressure level. The response gets compressed nonlinearly as the input level increases, due to suppression of the activity in the cochlea. Experimental data (expt) from Ruggero et al. (1997) are included for comparison.

Fig. 8. Nonlinear frequency response of basilar membrane. The frequency response at 5 mm from the base on the basilar membrane with characteristic frequency of 10 kHz is shown. The input level is varied from 20 dB SPL to 80 dB SPL. The amplitude of the normalized response is reduced with increasing input level, as the activity in the cochlea is suppressed. Experimental data (expt) from Ruggero et al. (1997) are included for comparison.
3. Results

The nonlinear active model is used to simulate the response of a chinchilla cochlea. The input parameters used in the model are based on anatomical data (Smith, 1968; Dallos, 1970; Cabezudo, 1978; Bohne and Carr, 1979; Lim, 1980). Table 1 gives the gross properties, such as density of fluid, and modulus basilar membrane, and angle of tilt of outer hair cells. Table 2 gives the properties whose variations along the length of the cochlea have been taken into account, such as basilar membrane width and thickness, and outer hair cell length.

The cochlear model is discretized into 1600 sections along its length of 18 mm, and \( N = 40 \) terms are used in the Fourier expansion across the width of the model. Results for the nonlinear coupling of frequencies are obtained using a coupling bandwidth of \( B = 3 \) in order to maintain a manageable level of computational operations without significant compromise to the accuracy of results. The average time taken for a single frequency calculation within an iterative step is about 12 s on a 600 MHz Pentium-III desktop computer. A distortion product generation problem involving about 30 frequencies and requiring about 100 iterations to achieve a convergence tolerance of 5% would take about 10 h for solution. This method provides a fast and efficient solution compared to a full-scale finite element model taking into account the complexities and strong nonlinearity present in the model. Therefore results are obtained without the need of computational resources such as high performance super-computers and workstations. We note that the computation time indicated by Parthasarathi et al. (2000) is measured in hours of computing time for the linear solution for a single frequency.

The model produces a frequency-place map with characteristic frequency range of 20 kHz to 20 Hz from the basal to the apical end of the cochlea, in line with animal measurements made by Eldredge et al. (1981), as shown in Fig. 5. Also shown is the location of the local resonance of plate strip and infinite fluid, discussed in Steele and Zais (1983) for several mammals, and given by

\[
\omega^2 = \frac{D_{22}}{2\rho t} \left( \frac{\pi}{h} \right)^5
\]

The local ‘resonance’ involves the plate stiffness and the fluid inertia, and marks a point near the actual peak amplitude in Fig. 5. Thus from this simple formula, the variation in physical properties of the pectinate zone of
the basilar membrane can explain the frequency mapping. Naidu and Mountain (1998) measured the distribution of point load stiffness along the gerbil cochlea. Compared to their results, the stiffness of the present model (with pectinate zone only) is the same near the base but much more compliant at the apex. However, the calculation of the complete organ of Corti of the water buffalo by Steele (1999) gives a distribution remarkably close to that measured by Naidu and Mountain (1998). So to the best of our knowledge, the pectinate zone dimensions and properties used for the present study correspond to the actual chinchilla cochlea.

Several response features commonly observed in in vivo experimental measurements are captured by this model, including compression of the response with stimulus level, harmonic distortion, two-tone suppression, and distortion generation. For quantitative comparison with experimental measurements on sound pressure levels, a simple model of the middle ear with 20 dB gain in pressure at the stapes, accounting for the ratio of areas of the eardrum and stapes and the lever effects of the ossicles, is used.

3.1. Response compression with stimulus level

Fig. 6 shows the basilar membrane responses when the stapes is excited at 10 kHz at various input levels. The figure gives a plot of the velocity amplitude against the distance along the cochlea duct measured from the stapes. The response of the basilar membrane increases with increase in the input level. This occurs linearly over most of the region basal to the characteristic place which is located at about 5 mm for the frequency of 10 kHz. For the region around the characteristic place, the response of the membrane is nonlinear. The response gets suppressed with increasing input level, as the response curves get ‘compressed’ close to each other. The peak of the response is also shifted in the basal direction, towards the stapes, with increase in the input level.

The response at the characteristic place is plotted against the input level in Fig. 7. The response increases linearly for low input level (up to 20 dB SPL), but turns nonlinear as activity in the model gets suppressed with higher stimulus level. At high input level, the response is suppressed by about 30 dB. This nonlinear compression in the response with input stimulus level is also observed in the experimental measurements by Ruggero et al. (1997), as shown by the points in the plot. The computation and experimental data agree quite well with each other.

The frequency response over a range of excitation frequencies for the same location is shown in Fig. 8. Each curve gives the amplitude and phase of the response on the basilar membrane normalized by the stapes input displacement, for various input levels.
For a low input level, a large amplification is present due to the active process in the cochlea. With increasing input level, the response is suppressed. The experimental measurements of Ruggero et al. (1997) are also included in the amplitude plot, and they compare quite well with the model computation results. The phase of the response obtained from the model shows a much larger roll-off with frequency than the experimental measurements. In the model, the phase is normalized to the volume flow at $x=0$, as the stapes is assumed to be a piston at the end of the fluid chamber. The actual position of the stapes in the cochlea extends over a small portion of the basal end of the scala which may result in this discrepancy in the phase. Nevertheless, the phase calculated from the model shows little dependence on the stimulus level, similar to the experimental data. This is also in agreement with the invariance of fine time structure in the basilar membrane with variation of stimulus intensity (Shera, 2001). A study on the transient response for the linear case of the feed-forward model also shows the invariance of the phase of time oscillations with variation of the feed-forward gain (Lim and Steele, 1999).

3.2. Harmonic distortion

Fig. 9 shows the generation of higher harmonics due to the nonlinearity in the model. The model is excited with a single fundamental frequency of 5 kHz, at various input levels (50, 60, 70, and 80 dB SPL). The plots show the amplitudes of the basilar membrane response normalized by the stapes input plotted against the distance along the cochlea. For low input level (up to 50 dB SPL), there is almost no harmonic distortion generation. At 50 dB SPL input level, the basilar membrane only has a response at the fundamental frequency. As the input level is raised, the basilar membrane begins to respond with the higher harmonics of the excitation frequency (second harmonic 10 kHz, third harmonic 15 kHz, and fourth harmonic 20 kHz). The higher harmonic responses also increase in relative amplitude, as the nonlinearity in the cochlea increases with the input level. At the high input level of 80 dB SPL, the higher harmonic responses become almost comparable to the response at the fundamental frequency. The presence of harmonic distortions in the basilar membrane response at high stimulus levels had been measured by Cooper and Rhode (1992) in the cat cochlea.

3.3. Two-tone suppression

When more than one tone is presented to the ear, inter-modulation occurs between the various tones. The following demonstrate the interplay between two tones that are presented simultaneously to the cochlea.
Fig. 10 shows the case of two-tone suppression by the high frequency. A probe tone of frequency 8 kHz is presented to the cochlea and monitored at its characteristic place. This probe tone is presented alone, or with a higher frequency suppressor tone of 10 kHz at various levels. The response of the basilar membrane at the location with characteristic frequency of the probe tone (8 kHz) is plotted against the input level of the probe tone. The solid line gives the response with the probe tone alone, and the dashed and dotted line, the response with the suppressor tone at 40 and 60 dB SPL. In all cases, the curves are similar to that of nonlinear compression shown in Fig. 7. The response is linear for low input levels of the probe tone and slowly gets nonlinear and suppressed with increase in input level. However, the response gets reduced in the presence of the suppressor tone as depicted by the downward shift of the curves. Over its linear response region (less than 60 dB SPL), the response to the 8 kHz probe tone gets reduced by about 10 dB in the presence of a 10 kHz suppressor tone at 60 dB SPL. The experimental measurements by Ruggero et al. (1992) are also included in the figure (plotted as points) for comparison with the model computation. It can be seen that both set of data are in very good agreement with each other.

Suppression can also occur with the suppressor at a lower frequency than the probe. Fig. 11 shows the results for this case. Here, the probe frequency is 7 kHz, and the suppressor frequency is 1 kHz. The response of the basilar membrane at the location with characteristic frequency of the probe tone (7 kHz) is plotted against the probe input level. The response due to the probe tone alone is given by the solid line, and that in the presence of the probe and suppressor tones is given by the dashed line. Again, the response is reduced (by about 10 dB) by the suppressor which is applied at a very high level of 80 dB SPL. Also, the computation results agree quite well with the experimental measurements by Ruggero et al. (1992), plotted as points in the figure.

3.4. Distortion products

When two tones of frequencies $f_1$ and $f_2$ are presented simultaneously to the cochlea, distortion products of frequencies $mf_1 + nf_2$ (where $m$ and $n$ are integers) are generated due to the nonlinearity in the cochlea. The strongest distortion product that is measured by researchers is the $2f_1 - f_2$ distortion. The active model is hereby used to compute the distortion product generation. Two tones with frequency $f_1$ and $f_2$ of equal...
intensity are presented to the cochlea, and the basilar membrane response at the location with characteristic frequency $2f_1 - f_2$ is monitored. Fig. 12 gives the case where $f_1$ and $f_2$ are close together with $f_2/f_1 = 1.05$, and Fig. 13 gives the case where $f_1$ and $f_2$ are far apart with $f_2/f_1 = 1.15$. In each case, the plot of the basilar membrane velocity spectrum is given. The input levels of the two tones are prescribed at four different values ranging from 30 to 80 dB SPL as shown in the four plots in each figure. It can be seen that for a high input level, a broad frequency spectrum of the response is obtained, due to the nonlinear distortion generation. As the input level is reduced, the spectrum narrows since the distortions get trimmed down and disappear. The experiment measurements of Robles et al. (1990, 1997) are also given in the plots as points. The experimental and computational data are not in excellent agreement with each other, but they show a similar trend. The discrepancy in distortion generation results is probably due to the simplified middle ear model that assumed a constant gain of pressure over the range of frequencies. A complete system consisting of realistic models of the cochlea, the middle ear and the ear canal would certainly provide better simulation results for comparison with experimental data.

4. Conclusions

The current nonlinear active cochlear model is an extension of the linear model based on the WKB method, with the inclusion of the three-dimensional viscous fluid effects, an orthotropic tapered cochlear partition, and the active nonlinear feed-forward micro-mechanics in the organ of Corti. The hybrid asymptotic and numerical method combined with the use of Fourier series expansions provides a fast and efficient iterative procedure for modeling and simulating the strong nonlinear activity in the cochlea. Using a single set of physiologically based parameters, the model is able to reproduce several characteristic nonlinear behaviors of the active cochlea commonly observed in experimental measurements on the chinchilla.

It is remarkable that a simple feed-forward model gives simulation results with reasonably good agreement with experimental data. No specific material ‘second filtering’ is needed, although the gain factor of the feed-forward mechanism may be interpreted as an abstract but simplified representation of the ‘filter’. Nevertheless, the interaction between the feed-forward mechanism and the propagating wave mechanics is the main contribution to the characteristic active behavior ob-
tained in the simulations. For further improvement, a physically based piezo-electric model of the outer hair cells should be used to provide a more realistic material description of the gain factor (Baker, 2000). In general, this gain factor may be represented by a complex transfer function with explicit dependence on the frequency of excitation, longitudinal position along the cochlea, and displacement of the basilar membrane. Finally, the present cochlear model can be coupled with realistic middle and outer ear models, providing a complete system model of the ear. More complicated hearing-related phenomena, such as otoacoustic emissions, can be simulated using this complete model.

References


