Cochlear Traveling Waves parametrically amplified by Outer Hair Cells

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Introduction
To prove the effect of parametric amplification (pa) of acoustic signals for increasing the hearing sensitivity by the cochlea we studied a 1D cochlear mechanical model in the form of a partial differential equation based on a former passive approach [1].

![Box model of the human cochlea. The upper front area (oval window) is excited by a sinusoidal velocity with the frequency 2 kHz and amplitude 1 nm/s.](image)

Partial differential equation (parametric traveling wave amplifier)
Equation (1) describes the pressure of the one-dimensional parametric system. The width of the basilar membrane (bm) changes linearly from 0.1 mm at the base of the cochlea to 0.5 mm at the helicotrema.

\[
\rho \frac{\partial^2 u}{\partial t^2} + k_d \frac{\partial u}{\partial t} + [E_y + \Delta E_y(x,t)] h^3 S \left[ \frac{\partial^2 u}{\partial x^2} \right] = 0
\]

(1)

| \(\rho_l\) | fluid area density | 1000 kg/m² |
| b(x) | width of the bm | 0.1 - 0.5 mm |
| u(x,t) | displacement of the bm | m |
| \(k_d\) | damping constant | 4000 kg/(m²s) |
| \(E_y\) | E modulus (transverse) | 100 GPa |
| \(\Delta E_y(x,t)\) | E modulus change | Pa |
| h | thickness of the bm | 10 μm |
| S | section area of the canals | 1 mm² |
| L | length bm | 32 mm |

All necessary material parameters are given in the table. Equation (1) is solved along the length of the bm from 0 mm to \(L = 32\) mm. The nonlinear stiffness changes of outer hair cells lead to a time dependence of the axial modulus of elasticity \(\Delta E_y(x,t)\) for each outer hair cell along the bm. Because of the material nonlinearity additional frequency components result in the form of nonlinear distortions. The input signal consists of time dependent displacements (harmonic velocities) at the stapes footplate which is the front area (oval window) at Scala vestibuli (S.v.) at \(x = 0\) mm.

The solutions of equation (1) are found by a finite difference scheme.

Finite difference scheme for the damped wave equation
We solved equation (1) by applying an explicit finite difference scheme (2) according to those presented in Najafi and coworkers [2].

\[
u_{i+1} = c_1 (2u_i - u_{i-1}) + c_2 u_{i-1} + \frac{ve l^2}{c_3 \Delta x^2} \left[ \frac{u_i}{(b/b_i)_{i+1}} - \frac{2u_i}{(b/b_i)_i} + \frac{u_{i-1}}{(b/b_i)_{i-1}} \right]
\]

(2)

The \((b/b_i)^4\) terms are time independent but space variable normed bm width factors. The normed damping constant of dimension \(s^{-1}\) is \(k'_d = k_d \cdot \frac{m^2}{\Delta x^2}\). Further abbreviations are

\[
c_1 = \frac{1}{\Delta t^2} + \frac{k'_d}{\Delta x^2}, \quad c_2 = \frac{k'_d}{\Delta x^2}, \quad c_3 = \frac{1}{\Delta t^2} + \frac{k'_d}{2 \Delta t}
\]

and \(i, n\) denoting space and time steps, respectively.

Nonlinear stiffness of outer hair cells
We assume that nonlinear stiffness changes of outer hair cells (OHC) cause time dependent variations of the Young’s modulus \(\Delta E_y(x,t)\) and the generation of nonlinear distortions and pa in the cochlea. For a derivation we follow the assumption that the nonlinear bm function is due to the nonlinear growth function of the OHC membrane potential [3]. The outer hair cell membrane potential \(V_{mp}\) is fitted by a second-order Boltzmann function

\[
V_{mp} = V_h + \frac{V_{pp}}{1.0 + e^{-z_1(x_{st} - x_i)/kT}} \cdot \frac{1.0 + e^{-z_2(x_{st} - x_2)/kT}}{1.0 + e^{-z_3(x_{st} - x_2)/kT}}
\]

(3)

\(V_{pp}\) is the peak-to-peak value and \(V_h\) is the membrane potential for maximum hyperpolarization. The constants \(z_1\) and \(z_2\) were determined as 60 fN and 120 fN and \(x_1 = 56.8\) nm and \(x_2 = 27.3\) nm by the Levenberg-Marquardt algorithm, respectively and with kT, the product of the Boltzmann constant k and the temperature T. \(x_{st}\) is the
radial deflection of the stereocilia. In a next step the somatic axial stiffness of an OHC as a function of the membrane potential is derived. This is impossible in vivo and therefore results of measurements of isolated OHCs are used [4] [5]. Applying again the Levenberg-Marquardt algorithm to fit experimental data of OHC stiffness measurements a stiffness function

\[ k(x_{st}) = 0.001 + 0.001 \cdot (a e^{bV_{mp}} + c e^{dV_{mp}}) \quad [N/m] \quad (4) \]

\[ a = 0.001415, b = -0.0419, c = 2.665, d = -0.003801 \]

is formulated. The nonlinear equations (3, 4) describe the axial somatic stiffness change in dependence of OHC stereocilia bundle displacements \( k(x, t) = f(x_{st}(t)) \). The stiffness \( k(x_{st}) \) multiplied by a factor \( v = 8.2 \cdot 10^{-10} \) is inserted into equations (1) and (2) as an elasticity modulus change \( \Delta E_y(x, t) \) and therefore as an equivalent velocity change, finally. The factor \( v \) was maximized by numerical experiments until an instability of displacements occurred. The equivalent acoustic velocity change according to the nonlinear stiffness of OHC is 1.7 \( \mu m/s \) and therefore a small fractional amount \( 0.053 \cdot 10^{-6} = \frac{3.162 \mu m/s}{31.62 m/s} \) of the undisturbed (basal) velocity 31.62 \( m/s \) calculated by equation (1) with constant elasticity \( E_y \) at \( b(0) = 0.1 \) \( mm \).

**Results**

The input signal is the time dependent displacement \( u(0, t) = \dot{u} \cdot \sin(\omega t) \) at \( x = 0 \) \( mm \) with \( u = 1 \) \( mm \) representing the amplitude of displacement at the oval window at the base of the cochlea. In the passive case with the constant Young’s modulus \( E_y \) the maximum bm displacement reaches a value of 3.14 \( nm \) at \( n = 40 \) corresponding to 6.4 \( mm \) distance from the base (Fig. 2).

**Figure 2:** Displacements along the bm with stimulation frequency 2000 \( Hz \) at the base (passive).

In case of pa (Fig. 3) the amplitude of bm displacement increases to 18.8 \( nm \) and the place of maximum displacement shifts to the middle of the bm length at 16 \( mm \) or \( n = 100 \). This increase corresponds to a bm displacement amplification of 15.53 \( dB \) evaluated by the fraction of the maximum displacement at the middle of the bm (n = 100) with pa to the maximum at the more basal place 6.4 \( mm \) (n = 40) in the passive case. Figure 4 shows the spectrum of bm displacement at \( n = 40 \) for the passive case. Because there is no OHC activity and nonlinearity a discrete spectrum at the input frequency 2 \( kHz \) occurs.

Discussion and Outlook

The examples proves the effect of pa of bm displacements in a 1D mechanical-mathematical model of the cochlea. The amplification of 15.53 \( dB \) and the place shift of maximum displacement along the bm with the same input frequency corresponds to experimental data from the squirrel monkey measured by Rhode in the mid 1970s (not cited here and discussed in a subsequent work). The pa is achieved by changing the axial stiffness of OHC represented by the Young’s modulus \( \Delta E_y \) by a small amount. In contrast to former approaches of pa applied to the cochlea [6] where the OHC contraction is in syn-
chrony with the input signal frequency and also constant in space we change the stiffness time and space dependent according to arbitrary bm displacements. Though the presented approach is nonlinear because of the nonlinear stiffness change of OHC (Equations 3,4) with the resulting additional frequency components (Fig. 5) the approach is at this time independent of the input level. Therefore the presented results are valid for low level input signals, i.e. $1 \text{ nm}$ input bm displacement at the base and maximum bm displacement $15.8 \text{ nm}$ (Fig. 3) inside the cochlea with pa. For higher input levels geometrical nonlinearities of the cells inside the organ of Corti become relevant [7] and saturate the displacements overall leading to the known compressive nonlinearity of bm displacements and the hearing mechanism. Next the nonlinear behavior of a deflected string (restoring force increases nonlinear with elongation) described by a conventional nonlinear wave equation (ignoring bm bending stress) representing the bm will be studied.

References


