Cochlear Traveling Waves parametrically amplified by Outer Hair Cells

Frank Böhnke, Christian Scheunemann, Maximilian Sigloch
HNO-Klinik der TUM, 81675 München, Germany, Email: frank.boehnke@tum.de

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].

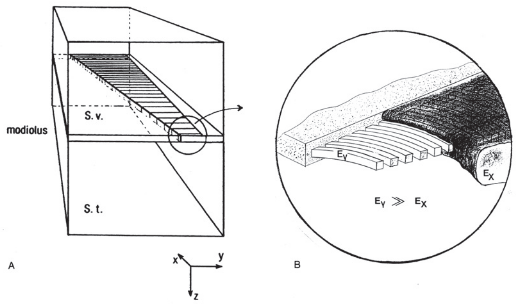

Figure 1: Box model of the human cochlea. The upper front area (oval window) is excited by a sinusoidal velocity with the frequency $2\,kHz$ and amplitude $1\,nm/s$.

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 $0.1mm$ at the base of the cochlea to $0.5\,mm$ at the helicotrema.

$$\rho_{fl}\frac{\partial^2 u}{\partial t^2} + k_d\frac{\partial u}{\partial t} + [E_y + \Delta E_y(x,t)]h^3 S\frac{\partial^2}{\partial x^2}[\frac{u}{b^4(x)}] = 0 \tag{1}$$

ρ_{fl}	fluid area density	$1000\ kg/m^2$
b(x)	width of the bm	$0.1 - 0.5\,mm$
u(x,t)	displacement of the bm	m
k_d	damping constant	$4000\,kg/(m^2 s)$
E_y	E modulus (transverse)	$100\,GPa$
$\Delta E_y(x,t)$	E modulus change	Pa
h	thickness of the bm	$10\,\mu m$
S	section area of the canals	$1\,mm^2$
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].

$$u_i^{n+1} = c_1\,(2u_i^n - u_i^{n-1}) + c_2\,u_i^{n-1} +$$

$$\frac{vel^2}{c_3\Delta x^2}\left(\frac{u_{i+1}^n}{(b/b_0)_{i+1}^4} - \frac{2u_i^n}{(b/b_0)_i^4} + \frac{u_{i-1}^n}{(b/b_0)_{i-1}^4}\right) \tag{2}$$

The $(b/b_0)^4$ terms are time independent but space variable normed bm width factors. The normed damping constant of dimension s^{-1} is $k'_d = k_d \cdot \frac{m^2}{kg}$. Further abbreviations are

$$c_1 = \frac{\frac{1}{\Delta t^2}}{\frac{1}{\Delta t^2} + \frac{k'_d}{2\,\Delta t}} \qquad c_2 = \frac{\frac{k'_d}{2\,\Delta t}}{\frac{1}{\Delta t^2} + \frac{k'_d}{2\,\Delta t}} \qquad c_3 = \frac{1}{\Delta t^2} + \frac{k'_d}{2\,\Delta t}$$

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

$$V_{mp} = V_h + \frac{V_{pp}}{1.0 + e^{-z_1(x_{st}-x_1)/kT}\cdot[1.0 + e^{-z_2(x_{st}-x_2)/kT}]} \tag{3}$$

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

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

$a = 0.001415, b = -0.0419, c = 2.665, d = -0.003801$ 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 modul 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 occured. The equivalent acoustic velocity change according to the nonlinear stiffness of OHC is $1.7\mu m/s$ and therefore a small fractional amount $0.053 \cdot 10^{-6} = \frac{1.7\mu m/s}{31.62\, m/s}$ 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 $u(0,t) = \hat{u} \cdot sin(\omega t)$ at $x = 0\, mm$ with $\hat{u} = 1\, nm$ 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).

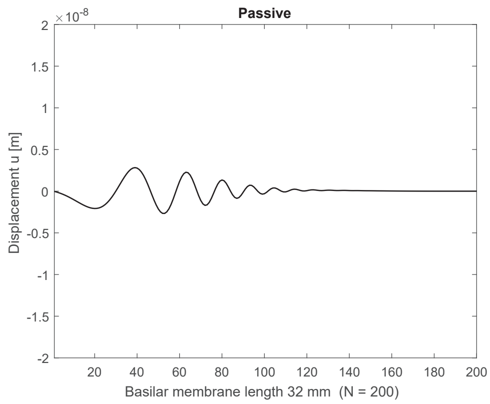

Figure 2: Displacements along the bm with stimulation frequency $2000\, Hz$ at the base (passive).

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

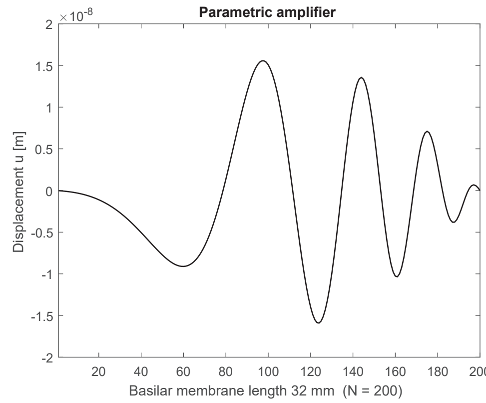

Figure 3: Displacements with stimulation frequency $2000\, Hz$ (parametric amplified).

case. Because there is no OHC activity and nonlinearity a discrete spectrum at the input frequency $2\, kHz$ occurs.

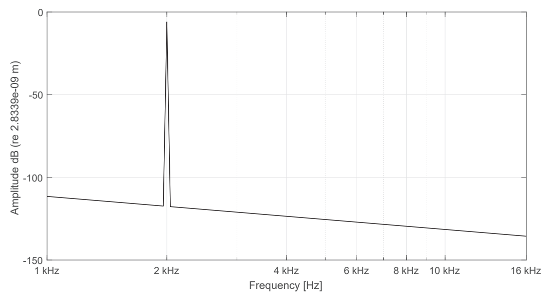

Figure 4: Spectrum of bm displacement at $6.4\, mm$ (n = 40) and stimulation frequency $2000\, Hz$ (passive).

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-

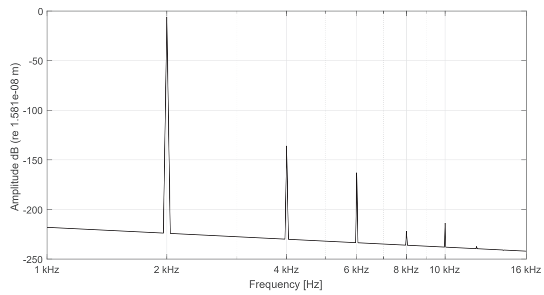

Figure 5: Spectrum of bm displacement at $16\, mm$ (n = 100) and stimulation frequency $2000\, Hz$ (parametric amplified).

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. $1\,nm$ input bm displacement at the base and maximum bm displacement $15.8\,nm$ (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

[1] Böhnke F., Janssen T., Steinhoff H.-J., Zimmermann, P.: Structural Cochlear Model including the Coupling of Basilar Membrane Fibers in the Longitudinal Direction. Il Valsalva 54, (suppl 1): (1989), 10-16

[2] Najafi H.S., Izadi F.: Comparison of two finite-difference methods for solving the damped wave equation. International Journal of Mathematical Engineering and Science (IJMES), vol. 3 Issue 3 ISSN: (2014) 2277-6982

[3] Preyer S., Gummer A.W.: Nonlinearity of mechanoelectrical transduction of outer hair cells as the source of nonlinear basilar-membrane motion and loudness recruitment. Audiology Neuro-Otology;1: (1996) 3–11

[4] He D.Z., Dallos P.: Somatic stiffness of cochlear outer hair cells is voltage-dependent. Proc. Natl. Acad. Sci. USA, vol. 96, July, Neurobiology, (1999) 8223–82289.

[5] Deo N., Grosh K.: Two-State Model for Outer Hair Cell Stiffness, Biophysical Journal Volume 86 June (2004) 3519–3528

[6] Ko W., Stockie J.M.: An immersed boundary model of the cochlea with parametric forcing, SIAM J. Appl. Math., Vol. 75, no. 3, (2015) 1065-1089

[7] Böhnke F., Arnold W.: Mechanics of the Organ of Corti Caused by Deiters Cells, IEEE Transactions on Biomedical Engineering, Vol. 45, No. 10, October (1998) 1227-1233