Proceedings of Meetings on Acoustics

Volume 19, 2013 http://acousticalsociety.org/

ICA 2013 Montreal
Montreal, Canada
2 - 7 June 2013

Psychological and Physiological Acoustics
Session 3aPP: Auditory Physiology and Modeling (Poster Session)

3aPP21. A physiology-based auditory model elucidating the function of the cochlear amplifier and related phenomena. Part I: Model structure and computational method

Herbert Hudde* and Sebastian Becker

***Corresponding author's address: Inst. of Communication Acoustics, Ruhr-University Bochum, Bochum, D-44780, NRW, Germany, herbert.hudde@rub.de**

An auditory model "PhyBAM" is presented which in the long term aims at reproducing the human auditory perception. In recent years the awareness has grown that many perceptive features have their origin in the peripheral ear, above all in the cochlea. In the present stage PhyBAM is actually just a model of the peripheral ear. To simulate the perception of arbitrary sound signals, the signal processing occurring in the cochlea has to be formulated close to the physiological basis. Even so the model must be kept as simple as possible for the given aim. As a compromise PhyBAM is set up as an ordinary circuit model. In this first of two associated papers the model structure and the computational methods are presented. The model covers ear canal, middle ear, and cochlea. The cochlea model is by far the most sophisticated part. To include the unsymmetrical conditions at both cochlear windows and the resulting common and differential modes, a two-canal circuit is used. The main challenge is the implementation of the cochlear amplifier on the basis of measured tuning curves and otoacoustic emissions. Finding an appropriate model structure and proper parameters turns PhyBAM into an instrument of cochlear research.

Published by the Acoustical Society of America through the American Institute of Physics

 [DOI: 10.1121/1.4798788]
Received 9 Jan 2013; published 2 Jun 2013

1. INTRODUCTION

Models of the auditory system can be developed for very different applications. When mainly the auditory perception is to be simulated, it can be reasonable to use a fairly simple model of the peripheral ear and to focus on the signal processing in the auditory pathway. However, many perceptive properties such as dynamic level-dependent processes or the fine structure of the hearing threshold have their origin in the peripheral ear (Epp et al., 2010). Therefore auditory models claiming true reproduction of the perception of arbitrary signals cannot satisfactorily work without a detailed model of the peripheral ear. Such models have to be based on the physiology of the peripheral ear, particularly on that of the cochlea.

A literally physiology-based model would have to be able to reproduce at least all the acoustic, mechanic and electric vibrations occurring in all parts of the peripheral hearing organ. A typical model of that kind would be formulated using finite elements. However, regarding the enormous number, the complex structure, and the diminutiveness of involved elements it is obvious that a numerical model taking into account all these details is unfeasible. Consequently, it is necessary to reduce the effort to a reasonable extent. Only such details should be reproduced that have significant impact on the resulting signal processing taking place in the ear. PhyBAM, our physiology-based auditory model has been developed according to this concept. However, a priori it is in no way obvious which details are really important and which are not. This is a severe problem when designing an appropriate model structure.

As the peripheral ear is essentially nonlinear the model has to work in the time domain. A direct way leading to a true time-domain model (in contrast to models approximating the signals using frame-wise inverse Fourier transformation) is a formulation as circuit model. The main drawback of usual circuit models is the restriction to one-dimensional systems. In such systems the shape of vibrations at each location is predefined and unchangeable. Three-dimensional vibrations as definitely occurring in the middle ear and the cochlea cannot be correctly reproduced by such systems. Only if one believes that all relevant effects of 3D vibrations can be approximated by simple 1D systems, the decision to use an ordinary circuit is reasonable. The validity of this assumption is by no means certain. The relevance of 3D vibrations for the cochlear function has been stressed by Kolston (2000) and Frosch (2010). The only justification for a 1D model is sufficiently good agreement between simulated and measured data. It is fairly easy to reproduce only a single type of data, for instance, cochlear tuning curves. But this alone cannot "prove" the general applicability of a model. Only if many diverse types of data can be reproduced using a fixed set of parameters, the model can be supposed to work close to physiology and to produce realistic results for arbitrary input signals.

The human auditory perception can be measured using psychoacoustic methods. The results obtained this way are determined by the complete hearing organ from the ear canal up to the auditory cortex. All signals pass the peripheral stages. Therefore the function of the peripheral ear has to be known in advance if the central ear is to be examined. However, the functioning of the peripheral ear is still unclear in several details. This typically leads to discussions whether a certain psychoacoustic effect has its origin in the peripheral ear or in the central pathways. For this reason, in the first development phase PhyBAM exclusively covers the peripheral ear, i.e., ear canal, middle ear, and cochlea. From the view point of auditory signal processing the ear canal and the middle are fairly simple, almost linear systems. Therefore PhyBAM is first of all a cochlea model. The ear canal and the middle ear are two-ports which describe filter properties in both directions from the ear canal to the cochlea and back.

To avoid any intermixture with central functions no psychoacoustic data is utilized for the model adjustment. With respect to the cochlear function the only meaningful physical data measurable in living humans can be recorded by microphones placed in the ear canal (auditory electric potentials give little insight into the cochlear mechanics). All kinds of otoacoustic emissions (OAE) are ideally suited to study details of interference and reflection of traveling waves. The most characterizing features of the cochlea, however, are the tuning curves as they immediately refer to the main function of the cochlea being a frequency analyzer. Unfortunately, tuning curves cannot be measured by non-invasive methods. Therefore the only available measurements of tuning curves are obtained from animals. Nevertheless these results have to be utilized as OAE measurements alone do not suffice to derive all relevant parameters of the cochlea. From measurements of psychoacoustical tuning curves one can conclude that physical tuning curves of humans should be at least structurally similar to animal tuning curves. In conclusion, data of tuning curves and different types of OAE is considered as fundament on which the model can be built.

2. MODEL STRUCTURE

The model includes subsystems representing the ear canal, the middle ear, and the cochlea. The cochlear subsystem follows the frequently used approximation as box which contains two fluid-filled canals and the BM in between

(Peterson and Bogart, 1950). All the three subsystems are formulated as acoustic circuits. This means that the variables primarily used are sound pressures p and volume velocities q. The interfaces between subsystems are surfaces A of constant pressure and velocity. They are referred to as "ports" and denoted by the characters E, D, B_U, B_L, A_U, and A_L. The meaning of all ports is given in Fig. 1. A one-port like the helicotrema is often represented by an impedance Z. Usually an impedance is used in the frequency domain. In this paper the term "impedance" is utilized in a generalized manner. It can also mean the equivalent system formulation in the time domain.

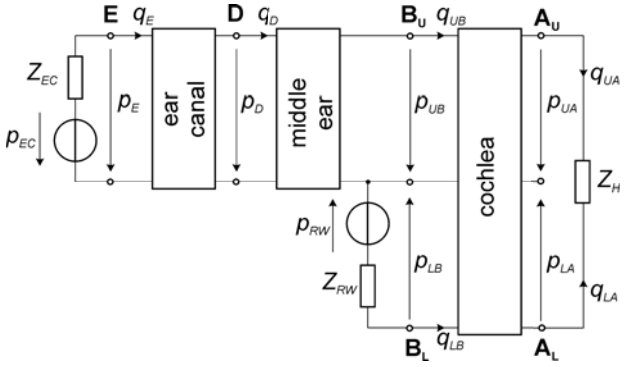

FIGURE 1. Basic model structure covering ear canal, middle ear and cochlea. The ports denote the entrance of the ear canal (**E**), the end of the ear canal at the eardrum (**D**), the base of the cochlea in the upper and lower canal ($\mathbf{B_U}$, $\mathbf{B_L}$), and the apex in the upper and lower canal ($\mathbf{A_U}$, $\mathbf{A_L}$). At the apex both canals are coupled via the impedance Z_H of the helicotrema.

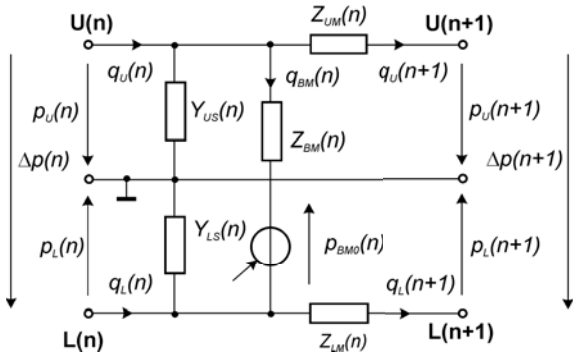

FIGURE 2. Four-port representing the n-th slice of the cochlear system. Indices: **U, L**: upper, lower canal, **BM**: basilar membrane, **M**: mass, **S**: stiffness. The circuit includes a source p_{BM0} (circle symbol) which represents the additional excitation of the BM generated by the cochlear amplifier. The control of the source, indicated by the arrow at the source symbol, is discussed below.

Mostly the model is excited by a Thévenin equivalent source (p_{EC}, Z_{EC}) acting in the ear canal. This way any kind of acoustic excitation, e.g., an external sound source or an OAE measuring probe, can be modeled. The source at the round window (p_{RW}, Z_{RW}) allows examining the effect of excitation at both cochlear windows. Usually the source p_{RW} is made inactive. Then only the impedance Z_{RW} of the round window membrane is present. In addition further sources inside the cochlea can be activated to study backward traveling waves in the cochlea and the reverse transmission from the cochlea to the ear canal.

For the ear canal the simplest approximation as a tube of constant cross-section is used. To allow for calculations in the time domain the tube is modeled using an appropriate number of chained slices. Regarding the middle ear we went back to an own model (Hudde and Engel, 1998). As this model was formulated for usage in the frequency domain including frequency depending circuit elements, some reformulation was necessary. The circuit is fitted to reproduce the input impedances from both ends and the pressure transfer functions in both directions. In contrast to the reference model, all the circuit elements have frequency-independent real values, which is a necessary precondition for calculations in the time domain.

For a realistic simulation of the transmission of otoacoustic emissions to the ear canal a two-canal model of the cochlea is indispensable. Also the cochlea has to be spatially discretized into a number of slices. As the upper and the lower cochlear canals are treated separately each slice corresponds to a four-port. The structure of one slice is shown in Fig. 2. The combination of the acoustic mass impedance $Z_{UM}(n)$ and stiffness admittance $Y_{US}(n)$ corresponds to the usual equivalent circuit of an acoustic transmission line. Both immitances can be supplemented by frictional elements if losses are to be taken into account. The upper and lower canals are coupled by the basilar membrane (BM). If it was completely stiff, the four-port would represent two water-filled transmission lines working independently. Coupling is expressed by the BM impedance $Z_{BM}(n)$ and an additional pressure source $p_{BM0}(n)$. In the frequency domain the BM impedance describes damped mass-spring vibrators according to

$$Z_{BM}(n) = w_{BM}(n) + \mathrm{j}\omega m_{BM}(n) + s_{BM}(n)/(\mathrm{j}\omega) \tag{1}$$

This impedance includes the effect of the organ of Corti resting on the BM. In the normal travelling wave mode the BM and organ of Corti almost vibrate as a whole. Thus the organ of Corti mainly contributes to the mass $m_{BM}(n)$. For simplicity in this paper the compound system of BM and organ of Corti is addressed when the term "basilar membrane" is used. As already mentioned the model is formulated exclusively using acoustic elements. The original mechanic elements are transformed into acoustical ones by the relationship

$$Z_{BM}(n) = Z_{BM,ac}(n) = Z_{BM,mech}(n) / A_{BM}^2(n) \quad (2)$$

$A_{\mathrm{BM}}(n)$ means the part of the BM area falling in the n-th slice. If no pressure source $p_{\mathrm{BM0}}(n)$ is active, the BM is only driven by the pressure difference $\Delta p(n) = p_{\mathrm{U}}(n) - p_{\mathrm{L}}(n)$ between upper and lower canal. This is the passive case.

The most crucial part of the model is the reproduction of the active cochlear system, the cochlear amplifier. The cochlear amplifier actually increases the BM vibrations, not only the excitation of the inner hair cells. Thus somehow spatially distributed forces along the BM must be generated which additionally act on the BM. In the model the additional force sources are represented by the equivalent acoustic pressure sources $p_{\mathrm{BM0}}(n)$ shown in Fig. 2. So far this approach is fairly general as no particular assumptions about the system controlling the source are made. The core of the cochlear amplifier is given by the OHC. According to the simplest notion of the OHC operation, the OHC bodies perform lengthwise vibrations controlled by shearing motions of the cilia. However, the mechanism which transforms these vibrations into forces on the BM is still controversially discussed.

A possible solution of this problem is the concept of "Corti resonators" published by the first author (Hudde, 2011). Using a finite element model of a cochlear section it was found that lengthwise vibrations of the OHC induce characteristic motions of the organ of Corti which are well suited to drive the BM. The Corti mode - the special kind of vibration generated by the OHC - is fundamentally different from the simple motion which appears if the BM is driven by the pressure difference between the upper and lower side (usual travelling wave mode). The Corti mode is significantly governed by the phalanges which divert the lengthwise OHC motion into lateral directions. This leads to strong deformations of the organ of Corti. Two features mostly characterize the Corti mode: the bending of the units formed by the OHC and the supporting Deiter cells and a rotatory motion of the the Hensen cells. This way the mass of the organ of Corti pushes the BM and thereby increases the up-and down motion of the travelling wave mode.

In ordinary circuit models two interacting modes of of vibration cannot be described. It would be possible to use generalized circuit models to cope with three-dimensional vibrations (Hudde and Weistenhöfer, 1997). However, PhyBAM is formulated avoiding such complicated systems. More sophisticated circuits will only be introduced if they turn out to be absolutely necessary.

Like the travelling wave mode also the Corti mode shows a resonance. The resonating system contains the same structural elements as the travelling wave mode, but due to the different types of vibration its resonant frequency differs from that of the passive system. As both resonances are caused by the same elements it is ensured that both systems are similarly tuned along the BM, a precondition necessary to obtain a uniform function of the cochlear amplifier at all places. It turned out that the Corti mode resonators have to work at somewhat lower resonant frequencies compared to that of the BM at the same place. In this case the passive travelling wave is amplified in a certain range of the BM just before the travelling wave reaches the passive characteristic place (Becker and Hudde, 2013).

The circuits representing the OHC and the Corti resonators are depicted in Fig. 3 (next page). For convenience the explicit indication of the slice number (n) is omitted. The OHC circuit is taken from Shamma et al. (1986). Although the original model is set up for inner hair cells, it can be also used for the OHC as the fundamental structures are the same. More recent models like the piezoelectric model proposed by Liu and Neely (2009) include the reaction of the mechanic load to the electric system. For simplicity this is not taken into account in PhyBAM. According to Shamma's model the receptor potential U is varied by a variable conductance $G(\xi_{\mathrm{Ci}})$ which is controlled by the shearing displacement ξ_{Ci} of the Cilia. This yields a voltage u fluctuating about the resting potential U_0.

The voltage $u(n)$ in the slice n produces a proportional change $\xi_{\mathrm{OHC}}(n) = K_{\mathrm{OHC},\xi}\, u(n)$ of the OHC length which evokes the motions of the Corti mode. As already discussed, the coupling between the Corti mode and the travelling wave mode cannot be accurately treated using a circuit model. To approximate the conditions it is assumed that the force produced by an OHC is transmitted from the OHC to the BM via a coupling impedance, which covers the phalanges and other elements of the organ of Corti. This means that the OHC displacement source $\xi_{\mathrm{OHC}}(n)$ acts on the coupling impedance and the BM impedance connected in series. According to the rules of mechanic circuits this means adding of admittances. Therefore the smaller impedance determines the resulting force. Due to the phalanges the coupling impedance is fairly stiff. Therefore the force generated is mainly determined by the smaller BM impedance which in the relevant range of the Corti resonator activity is mainly governed by its stiffness $s_{\mathrm{BM,mech}}(n)$. Thus we can estimate the generated force as

$$F_{OHC}(n) = s_{BM,mech}(n)\xi_{OHC}(n) = s_{BM,mech}(n)K_{OHC,\xi}u(n) = K_{OHC}(n)u(n), \quad K_{OHC}(n) = s_{BM}(n)A_{BM}^2(n)K_{OHC,\xi} \quad (3)$$

This force is assumed to excite the Corti resonator in the Corti mode just described. Whereas $K_{\mathrm{OHC},\xi}$ is a constant characterizing the piezoelectric effect of the OHC, $K_{\mathrm{OHC}}(n)$ considerably depends on the place as its stiffness de-

creases from the base to the apex. The stiffness $s_{BM}(n)$ appearing in Eq. (3) is the acoustic equivalent of the mechanic stiffness $s_{BM,mech}(n)$.

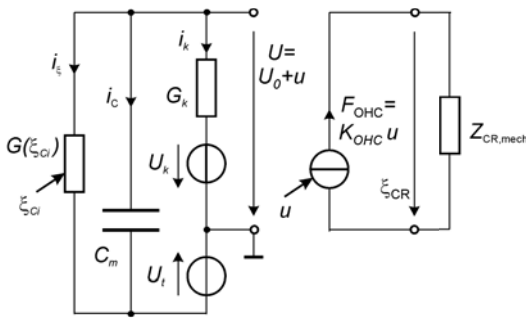

FIGURE 3. Model of outer hair cells (OHC) and Corti resonators. The receptor potential U is generated by variations of the conductance $G(\xi_{Ci})$. The alternating component u of the receptor potential induces a force acting on the Corti resonators. The impedance $Z_{CR,mech}$ of the parallel resonator includes mass $m_{CR,mech}$, stiffness $s_{CR,mech}$, and friction $w_{CR,mech}$.

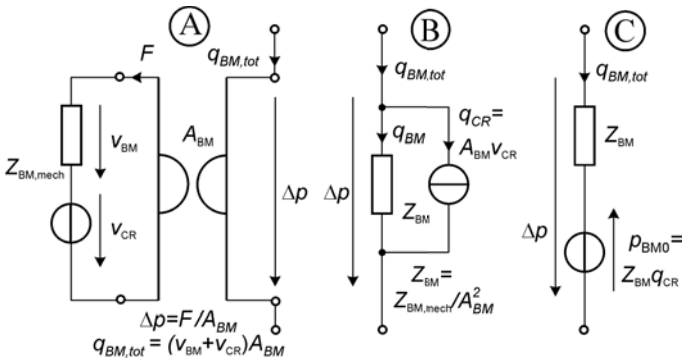

FIGURE 4. Superposition of the motions of the basilar membrane and the Corti resonator. The transformation between mechanic and acoustic systems is formally described by a gyrator with a gyration constant being the surface area A_{BM} relating both systems (panel A). In the acoustic system the source introduced by the Corti resonators is a volume velocity source (panel B) which can also be expressed by a pressure source (panel C).

A further part of the cochlear amplifier is the system relating the cilia shearing displacement $\xi_{Ci}(n)$ to the vibration of the BM. Shearing is induced by relative motions of the tectorial membrane and the cuticular plates on the tops of the OHC. Thus the transfer function from the BM displacement to the cilia displacement is influenced by several elastic and inertial elements in the cochlea. However, if the transmission takes place below any resonant frequency of the involved system the cilia shearing displacement simply follows the BM displacement. The simplest assumption, which is currently used in PhyBAM, is a fixed proportional relationship between the BM and cilia displacement at the same place: $\xi_{Ci}(n)=K(n)\ \xi_{BM}(n)$.

Finally, the calculated vibration of the Corti resonator has to be superimposed to the vibration of the BM. This closes the feed-back loop of the active cochlear system. As the superposition occurs in the mechanic system of the BM the original mechanic conditions underlying the acoustic impedance $Z_{BM}(n)$ have to be considered. The element formally describing the transformation between mechanic and acoustic systems is a gyrator (Fig. 4). It relates forces F and velocities v to acoustic pressures p and volume velocities q according to $p = F/A$, $q = vA$. Thus the gyrator constant is the area A involved, here the area $A_{BM}(n)$ of the BM within the cochlear slice considered.

In panel A of Fig. 4 the superposition of the Corti resonator velocity v_{CR} is represented by a corresponding velocity source adding to the BM velocity. The mid circuit (panel B) is the same as the left one, but completely transformed to the acoustic side. Here the Corti resonator velocity is represented as equivalent acoustic volume velocity source q_{CR} which means a Norton equivalent source. If no Corti resonator velocity v_{CR} is superimposed the acoustic impedance BM impedance reduces to the passive impedance $Z_{BM}(n) = Z_{BM,mech}(n)/A^2_{BM}(n)$ as already used above. In the final step the circuit has to be transformed to the form of the BM branch appearing in Fig. 2, i.e., to a series connection of the impedance Z_{BM} and a pressure source representing the input generated by the cochlear amplifier. This is achieved using well-known source transformations. The result depicted in panel C of Fig. 4 is identical to the corresponding BM branch in Fig. 2 if the volume velocity $q_{BM}(n)$ in Fig. 2 means the total volume velocity $q_{BM,tot}(n)$ as in Fig. 4.

3. PASSIVE COCHLEA ANALYSIS

To derive the basic equations relating the port variables of all cochlear slices, two chained slices have to be considered. A minimum number of equations is obtained when a loop volume-velocity analysis is performed in analogy to the loop current analysis in electrical circuits. This analysis usually carried out in the frequency domain can be used in the time domain as well. In the following the temporal derivative of a volume velocity $q(n)$ is denoted by $\dot{q}(n)$, and the temporal integral by $\widehat{q}(n)$. The volume velocities at three adjacent ports n-1, n, n+1 (see Fig. 2) are coupled by three equations:

$$-s_{US}(n-1)\hat{q}_U(n-1)+s_{US}(n-1)\hat{q}_{BM}(n-1)+m_{UM}(n-1)\dot{q}_U(n)+w_{UM}(n-1)q_U(n)+ \\ +\left[s_{US}(n-1)+s_{US}(n)\right]\hat{q}_U(n)-s_{US}(n)\hat{q}_{BM}(n)-s_{US}(n)\hat{q}_U(n+1)=0 \tag{4}$$

$$-s_{LS}(n-1)\hat{q}_L(n-1)-s_{LS}(n-1)\hat{q}_{BM}(n-1)+m_{LM}(n-1)\dot{q}_L(n)+w_{LM}(n-1)q_L(n)+ \\ +\left[s_{LS}(n-1)+s_{LS}(n)\right]\hat{q}_L(n)+s_{LS}(n)\hat{q}_{BM}(n)-s_{LS}(n)\hat{q}_L(n+1)=0 \tag{5}$$

$$-s_{US}(n)\hat{q}_U(n)+s_{LS}(n)\hat{q}_L(n)+m_{BM}(n)\dot{q}_{BM}(n)+w_{BM}(n)q_{BM}(n)+ \\ +\left[s_{BM}(n)+s_{US}(n)+s_{LS}(n)\right]\hat{q}_{BM}(n)+s_{US}(n)\hat{q}_U(n+1)-s_{LS}(n)\hat{q}_L(n+1)=p_{BM0}(n) \tag{6}$$

The acoustic circuit elements of the BM, stiffness $s_{BM}(n)$, resistance $w_{BM}(n)$, and mass $m_{BM}(n)$, have already been introduced in Eq. (1). The fluid masses $m_{UM}(n)$ and $m_{LM}(n)$ and resistances $w_{UM}(n)$ and $w_{LM}(n)$ belong to the impedances $Z_{UM}(n)$ and $Z_{LM}(n)$ of Fig. 2. The fluid stiffnesses $s_{US}(n)$ and $s_{LS}(n)$ form the admittances $Y_{US}(n)$ and $Y_{LS}(n)$. Here for simplicity no losses are taken into account.

The equations at all ports together constitute a system of differential equations which can be formulated using three vectors $\dot{\mathbf{q}}(k), \mathbf{q}(k), \hat{\mathbf{q}}(k)$ composed of loop volume velocities, their temporal derivatives, and their temporal integrals at all ports at the discrete time k. The volume velocity vector is $\mathbf{q}(k)$=[..., $q_U(n,k)$, $q_L(n,k)$, $q_{BM}(n,k)$,...]^T. Here the time dependence is explicitly indicated (k). The vectors of the temporal derivative $\dot{\mathbf{q}}(k)$ and integral $\hat{\mathbf{q}}(k)$ are composed correspondingly. According to Eqs. (4-6) the system of differential equations has the form

$$\mathbf{M}\cdot\dot{\mathbf{q}}(k)+\mathbf{W}\cdot\mathbf{q}(k)+\mathbf{S}\cdot\hat{\mathbf{q}}(k)=\mathbf{p}_0(k) \tag{7}$$

The matrices **M, W**, **S** are band matrices. In the passive case they only contain constant elements. The first equations are modified as they include the excitation at the input port. Also the last equations are irregular. Here the helicotrema impedance has to be taken into account. In this way the band matrices become ordinary square matrices. The right-hand side $\mathbf{p_0}(k)$ is a vector of the same length as the loop volume velocity vectors. For each of the N ports three variables $q_U(n,k)$, $q_L(n,k)$, $q_{BM}(n,k)$ occur. The actual length is 3N+1 including the additional volume velocity $q_U(N+1)$ through the helicotrema. When the cochlea is excited by a source at the entrance of the upper canal, only the first element of the vector $\mathbf{p_0}(k)$ is nonzero at the first point of time.

If the cochlea is excited somewhere in the ear canal, the system of equations has to be extended by the equations for the ear canal and middle ear. Only five equations are necessary to include the middle ear. The ear canal is modeled by M two ports representing slices of the ear canal. Up to M = 20 slices are used for the ear canal depending on its length. By far the most equations belong to the cochlea. Usually N = 280 slices are used along the BM having a length of 35 mm.

To calculate the response at all locations for a given excitation, the differential equations have to be integrated. A very effective algorithm to do this is the Newmark method which is often applied for systems formulated using finite elements. Then the solution of the differential equations is reduced to the solution of a system of linear equations at each time step. The matrix formulation reads as follows

$$\mathbf{A}\cdot\dot{\mathbf{q}}(k)=\mathbf{R}(k) \tag{8}$$

Herein the system matrix A is calculated from the original matrices as

$$\mathbf{A}=\mathbf{M}+\delta\,\Delta t\,\mathbf{W}+\alpha\left(\Delta t\right)^2\mathbf{S} \tag{9}$$

Δt denotes the sampling interval. The constants α, δ can be optimized for best numerical results. We use the standard choice $\alpha = 1/6$, $\delta = 1/2$. Also the matrix **A** has band structure. Therefore the linear system of equations can be solved very effectively. The right-hand side vector, which is identical to $\mathbf{p_0}(k)$ in the first moment, is changed according to

$$\mathbf{R}(k)=\mathbf{p}_0(k)-\mathbf{W}\cdot\mathbf{q}_p(k)-\mathbf{S}\cdot\hat{\mathbf{q}}_p(k) \tag{10}$$

Herein both volume velocity vectors mean predicted values which are derived from the previous values

$$\mathbf{q}_p(k)=\mathbf{q}(k-1)+(1-\delta)\Delta t\cdot\dot{\mathbf{q}}(k-1),\quad \hat{\mathbf{q}}_p(k)=\hat{\mathbf{q}}(k-1)+\Delta t\,\mathbf{q}(k-1)+(1-2\alpha)\left[\left(\Delta t\right)^2/2\right]\dot{\mathbf{q}}(k-1) \tag{11}$$

After solving the system of linear equations the predicted values are corrected according to

$$\mathbf{q}(k)=\mathbf{q}_p(k)+\delta\Delta t\,\dot{\mathbf{q}}(k),\quad \hat{\mathbf{q}}(k)=\hat{\mathbf{q}}_p(k)+\alpha\left(\Delta t\right)^2\dot{\mathbf{q}}(k) \tag{12}$$

This completes the calculation of the vectors $\dot{\mathbf{q}}(k), \mathbf{q}(k), \hat{\mathbf{q}}(k)$. If harmonic excitation is considered, the solution can be achieved much faster using complex amplitudes. Then Eq. (8) reduces to

$$\left[\mathrm{j}\omega\mathbf{M}+\mathbf{W}+(1/\mathrm{j}\omega)\mathbf{S}\right]\mathbf{q}(\omega)=\mathbf{p}_0(\omega) \tag{13}$$

4. ACTIVE COCHLEA ANALYSIS

The cochlear amplifier includes the OHC and the Corti resonators according to Fig. 3 and the feedback to the basic model via the controlled source as depicted in Fig. 4. The cochlear amplifier is expressed by two additional equations per cochlear slice supplementing Eqs. (4-6). To obtain these equations, the basic equations of the elements involved have to be rewritten in a form that suits to the equations of the passive system. According to Shamma et al. (1986) the alternating component of the receptor potential $u(t)$ is governed by the cilia displacement $\xi_{\mathrm{Ci}}(t)$ as a result of the corresponding alteration of a conductance $G\{\xi_{\mathrm{Ci}}(t)\}$. This can be written as

$$C_m \dot{u}(t) + \left(G_k + G\left\{\xi_{Ci}(t)\right\}\right) u(t) = G_k \left(U_k - U_0\right) + G\left\{\xi_{Ci}(t)\right\}\left(U_t - U_0\right) \tag{14}$$

The nonlinear equation includes a capacitance C_{m}, a constant conductance G_{k}, and several voltages (see the original paper). These parameters and even more the parameters occurring in the function $G\{\xi_{\mathrm{Ci}}(t)\}$ can be used to form the OHC characteristic. Eq. (14) has to be transformed into a linear equation for each time step. To achieve a linear equation small changes of the conductance $G\{\xi_{\mathrm{Ci}}(t)\}$ within the sampling interval Δt have to be considered. The unknown conductance at the "current" time k can be estimated from known previous values. The conductance of slice n is estimated from the previous value $G(n,k\text{-}1)$, the slope $S(n,k\text{-}1)$ of the conductance characteristic at the previous time k-1 and the estimated change of the cilia displacements during the sampling interval

$$\hat{G}(n,k) = G(n,k-1) + S(n,k-1)\left[\hat{\xi}_{Ci}(n,k) - \xi_{Ci}(n,k-1)\right] \tag{15}$$

Using the mean of the temporal slopes of the cilia displacements the estimated change of the cilia displacement can be expressed as

$$\hat{\xi}_{Ci}(n,k) - \xi_{Ci}(n,k-1) \approx 0.5\left[\dot{\xi}_{Ci}(n,k-1) + \dot{\xi}_{Ci}(n,k)\right]\Delta t \tag{16}$$

This way the estimate of the current conductance can be calculated from the volume velocities of the BM

$$\begin{aligned} \hat{G}(n,k) &= G(n,k-1) + 0.5\Delta t\ S(n,k-1)\left[v_{Ci}(n,k-1) + v_{Ci}(n,k)\right] = \\ &= G(n,k-1) + 0.5\Delta t\ K(n)S(n,k-1)\left[v_{BM}(n,k-1) + v_{BM}(n,k)\right] = \\ &= G(n,k-1) + 0.5\Delta t\ K(n)S(n,k-1)\left[q_{BM}(n,k-1) + q_{BM}(n,k)\right] / A_{BM}(n) \end{aligned} \tag{17}$$

Herein a place-depending constant $K(n)$ relating the cilia and the BM displacements is used. If the estimated conductance is utilized to rewrite Eq. (14) one obtains a linear equation of the form

$$A(n,k)q_{BM}(n,k) + B(n)\dot{q}_{el}(n,k) + C(n,k)q_{el}(n,k) = R(n,k) \tag{18}$$

To adopt the new equation to the form of Eqs. (4-6) all variables appearing in the solution vector are expressed as equivalent volume velocities. The volume velocity $q_{\mathrm{el}}(n,k)$ is defined proportional to the receptor potential $u(n,k)$. The right-hand side contains several constants and previous values of the conductance, of its slope, and of BM volume velocities. Note that the matrix elements $A(n,k)$ and $C(n,k)$, and the right-hand term $R(n,k)$ change with each time step. They contain previous values which are known before the matrix inversion at time step k.

The second additional equation expresses that the alternating component of the receptor potential controls the pressure source $p_{\mathrm{BM0}}(n)$. Written in the frequency domain the relationship reads

$$p_{BM0}(n) = Z_{BM}(n)A_{BM}(n)v_{CR}(n) = K_{OHC}A_{BM}(n)\left[Z_{BM}(n) / Z_{CR}(n)\right]u(n) \tag{19}$$

which means

$$\begin{aligned} &m_{CR}(n)\dot{p}_{BM0}(n,k) + w_{CR}(n)p_{BM0}(n,k) + s_{BM}(n)\hat{p}_{BM0}(n,k) - \\ &-K_{OHC}(n)A_{BM}(n)\left[m_{BM}(n)\dot{u}(n,k) + w_{BM}(n)u(n,k) + s_{BM}(n)\hat{u}(n,k)\right] = 0 \end{aligned} \tag{20}$$

in the time domain. If the pressure source $p_{\mathrm{BM0}}(n,k)$ is expressed by an equivalent volume velocity $q_0(n,k)$, also this equation suits to the system of linear equations. It takes the form

$$m_{BM}(n)\dot{q}_{el}(n,k) + w_{BM}(n)q_{el}(n,k) + s_{BM}(n)\hat{q}_{el}(n,k) + D(n)\dot{q}_0(n,k) + w_{BM}(n)q_0(n,k) + E(n)\hat{q}_0(n,k) = 0 \tag{21}$$

wherein $D(n)$ and $E(n)$ have constant values. Note that the equivalent volume velocity sources do not appear on the right-hand side which would mean independent sources. Instead, they are part of the solution vector. The extended solution vector contains the volume velocities $\ldots, q_U(n,k), q_L(n,k), q_{BM}(n,k), q_{el}(n,k), q_0(n,k), \ldots$ and their temporal derivatives and integrals for all slices.

For very small cilia displacements the conductance can be linearized according to $G\{\xi_{\mathrm{Ci}}(t)\} = G_0[1+\kappa\xi_{\mathrm{Ci}}(t)]$. Thus at very low levels the active cochlear system works linearly. In this case the slope of the OHC characteristic appearing in Eq. (18) is a time-invariant constant

$$S(n) = S(n,k-1) = S(n,k) = \kappa G_0 \tag{22}$$

and Eq. (18) takes the form

$$A'(n)\hat{q}_{BM}(n,k) + B(n)\dot{q}_{el}(n,k) + C(n)q_{el}(n,k) = 0 \tag{23}$$

In contrast to Eq. (18) the right-hand side vanishes in the low-level case and the coefficients $A'(n)$ and $C(n)$ become time-invariant. Note that the coefficient $A'(n)$ belongs to the temporal integral $\hat{q}_{BM}(n,k)$, not to the BM volume velocity $q_{\mathrm{BM}}(n,k)$ as in the nonlinear case.

For the linear active case the resulting impedance of the BM can be calculated as

$$Z_{BM,act}(n) = \frac{\Delta p(n)}{q_{BM,tot}(n)} = Z_{BM}(n)\left\{1 - \frac{K(n)K_{OHC,\xi}s_{BM}(n)}{\mathrm{j}\omega Z_{CR}(n)}\frac{\kappa G_0\left[U_t - U_0\right]}{G_{tot} + \mathrm{j}\omega C_m}\right\} \tag{24}$$

Thus the passive impedance $Z_{\mathrm{BM}}(n)$ is altered by a complex factor. On the stiffness-controlled increasing slope of the tuning curve the phase of $Z_{\mathrm{BM}}(n)$ is close to -90°. Hence a phase smaller than -90° results if the factor has a negative phase. This means a negative resistance or negative damping and therefore active gain. In other models the active BM impedance is the difference of the passive impedance and another impedance term which can also explain negative resistances. However, the form of Eq. (24) allows more flexible positioning of the region where the resistance becomes negative. Varying the active region and forming the spatial resistance curve allows "designing" of tuning curves in a wide range.

5. SUMMARY AND CONCLUSIONS

An auditory model which can simulate responses to arbitrary acoustical input has been presented. At present, the model is restricted to the peripheral ear. The most prominent feature of the model is its close connection to the physiological basis, which is expressed in the name PhyBAM (physiology-based auditory model). This does not mean that the model aims at maximum fidelity. The ear as a biological system is such complex that a comprehensive simulation of all the vibrations occurring in the peripheral ear is impossible anyway. Therefore considerable simplifications are necessary if system responses are to be calculated in feasible computer running times. Nevertheless all the variables occurring in the model have a clear physical meaning. The model is formulated as circuit model as this facilitates refinements and extensions if necessary for certain reasons.

The heart of the model is the system describing the cochlea. Here a comparably high effort has been made taking into account two fluid-filled canals in contrast to mostly used symmetrized one-canal models. Only in this way the asymmetry of the cochlea at the oval and the round window can be taken into account. For quantitative investigations of OAE a two-canal model is mandatory anyway.

The implementation of active processes is the most ambitious part of the model, and that for several reasons:

a) There is no general agreement about the exact mechanism behind the cochlear amplifier. Most researchers assume that the OHC act as motors, but many details are unclear.

b) Active processes excited by BM motions in combination with feedback to the BM yield instability if the effect of the OHC vibrations is not controlled in a proper way.

c) The implementation of active processes must reproduce the shape of tuning curves at low levels which differs from that of simple undamped resonators. Of course, also the level dependence of the tuning curves must follow measured data.

d) Tuning curves and all types of OAE have to be simulated using the same model and parameters.

The requirement of reproducing many diverse types of measurement data with a single model adjustment is simultaneously a challenge and a chance. If a model can actually meet all the requirements it is most likely to work close to reality. The best strategy to achieve such a model is starting with simple structures and extending these structures only if necessary.

Actually the model of the cochlear amplifier presented in this paper is fairly simple. The most important assumptions and features are shortly summarized in the following (for more details see the companion paper: Becker, Hudde 2013).

1) PhyBAM follows the notion of Corti resonators. These resonators are tuned to lower frequencies compared to the basilar-membrane resonant frequencies at the same locations. This means that the active excitation takes place in a region before the travelling wave reaches the characteristic place. Only this condition turned out to be consistent with the shape of active tuning curves. Stability problems are considerably reduced by this choice.

2) The only nonlinear part of the OHC model is the characteristic of a conductance controlled by the cilia displacement. The model includes neither a nonlinear capacitor nor a nonlinear spring. Actually even the constant capacitance implemented in the model is not used as it yields an unrealistic decrease of sensitivity at higher frequencies.

This is justified following the arguments found in Lu et al. (2006). Nevertheless, the OHC model will be probably extended in future to become able to reproduce all types of OAE.
3) Unlike most models the feedback to the BM is modeled as superposition of the Corti resonator motions to the BM motions, not by using forces sources driving the BM. Of course, also the superposition leads to forces on the BM, but the forces are proportional to the BM impedance in this case. As a result the actively altered BM impedance can be better adopted to reproduce the shape of tuning curves.
4) Shearing of the OHC cilia is simply assumed to be proportional to BM displacement. A further circuit introducing a more elaborate transfer function seems unnecessary so far.

In conclusion, PhyBAM can accomplish more than pure reproduction of measured results. As all the model variables and parameters have a specified physical meaning, the model helps understanding the operation of cochlear elements. For instance, the question in which region the active processes must drive the BM could be uniquely answered. This is a good example showing that the model can actually help deciding scientific questions. Other problems, e.g., finding the kind of waves which transmit OAE to the cochlear base, or examining the impact of parameter roughness on cochlear features can be directly assessed without need for any specific modeling. Thus PhyBAM can be used as a tool of cochlea research, not only for auditory signal processing.

ACKNOWLEDGEMENT

This work was supported by the Deutsche Forschungsgemeinschaft (grant HU 352/10).

REFERENCES

Becker, S. and Hudde, H. (**2013**),"A physiology-based auditory model elucidating the function of the cochlear amplifier and related phenomena. Part I: Model structure and computational method", ICA 2013, Montreal, next paper

Epp, B., Verhey, J. L., and Mauermann, M. (**2010**). "Modeling cochlear dynamics: interrelation between cochlea mechanics and psychoacoustics", J. Acoust. Soc. Am. **128**, 1870-1883

Frosch, R. (**2010**). "Introduction to cochlear waves", vdf Hochschulverlag Zürich, 2010

Hudde, H. (**2011**). "The Corti resonator - an actively driven system underlying the cochlear amplifier", in: Proceedings Forum Acusticum, Aalborg 2011, ISSN 2221-3767, 1085-1089

Hudde, H., Engel, A. (**1998**). "Measuring and modeling basic properties of the human middle ear and ear canal. Parts I-III", ACUSTICA/acta acustica **84**, 720-738, 894-913, 1091-1108

Hudde, H., Weistenhöfer, Ch. (**1997**). "A three-dimensional circuit model of the middle ear", ACUSTICA/acta acustica **83**, 535-549

Kolston, P. J. (**2000**). "The importance of phase data and model dimensionality to cochlear mechanics", Hear. Res. **145**, 25-36

Liu, Y.-W. and Neely, S. T. (**2009**). "Outer hair cell electromechanical properties in a nonlinear piezoelectric model", J. Acoust. Soc. Am. **126**, 751-761

Lu, T. K., Zhak, S., Dallos, P., and Sarpeshkar, R. (**2006**). "Fast cochlear amplification with slow outer hair cells", Hear. Res. **214**, 45-67

Peterson, L. C. and Bogert, B. P. (**1950**). "A dynamical theory of the cochlea", J. Acoust. Soc. Am. 22, 369-381

Shamma, S. A., Chadwick, R. S., Wilbur, W. J., Morrish, K. A., and Rinzel, J. (**1986**). "A biophysical model of cochlear processing: intensity dependence of pure tone responses.", J. Acoust. Soc. Am. **80**, 133-145