Power Amplification and Selectivity in the Cochlear Amplifier

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This paper presents a new model that describes the physical phenomena occurring in an individual Outer Hair Cell (OHC) in the human hearing organ (Cochlea). The new model employs the concept of parametric amplification and piezoelectricity. As a consequence, the proposed model may explain in a natural way many as yet unresolved problems about the mechanisms of: 1) power amplification, 2) non-linearity, 3) fine tuning, or 4) high sensitivity that take place in the human hearing organ. Mathematical analysis of the model is performed. The equivalent electrical circuits of an individual OHC are established. The high selectivity of the OHC parametric amplifier is analyzed by solving the resulting Mathieu and Ince differential equations. An analytical formula for the power gain in the OHC's parametric amplifier has been developed. The proposed model has direct physical interpretation and all its elements have their physical counterparts in the actual structure of the cochlea. The numerical values of the individual elements of the electrical equivalent circuits are consistent with the experimental physiological data. It is anticipated that the proposed new model may contribute in future improvements of human cochlear implants as well as in development of new digital audio standards.

Keywords: piezoelectricity, parametric amplification, mechanism of hearing, electroacoustic transducers.

1. Introduction

Understanding of the human hearing process is of fundamental importance in speech and audio acoustics as well as in medicine and biology. In fact, all modern MPEG digital audio codecs exploit heavily psychophysical properties of the human hearing organ, such as tone masking, nonlinearity, etc. On the other hand, cochlear implants are often only one alternative for peoples with severely impaired hearing capabilities.

A very important role in the human auditory mechanism play electric and electromechanical phenomena occurring in the cochlea. Electromechanical phenomena taking place in the human hearing organ (the cochlea) are still a fascinating and unsolved mystery (Liao *et al.*, 2007; Maoileidigh, Julicher, 2010; Eliot, Shera, 2012). In particular, the mechanism of active power amplification and a mechanism that sharpens the output amplitude frequency characteristics, which provides selectivity, are not known.

For a long time it was believed that cochlea is a passive structure. Gold was the first who concluded the necessity of existence of an active process of power amplification in the cochlea (Gold, 1948). The presence of power gain can explain remarkable properties of cochlea, such as its frequency selectivity, high sensitivity and nonlinear behavior.

The most important processes determining the selectivity and sensitivity of the human hearing organ occur in the inner ear, namely in the organ of Corti. A key role is played by the cochlear amplifier. It consists of about 20,000 outer hair cells (OHC), located between the basilar membrane (BM) and the tectorial membrane (TM). The outer hair cells (OHCs) are the electro-mechanosensory cells in the cochlea. They are considered to be critically important and responsible for the amplifying and sharp frequency sensitivity of the human ear (Dimitriadis, 1999).

In the outer hair cells (OHCs) mechanical signals are transformed into electrical signals, and conversely, electrical signals are converted into mechanical ones (simple and inverse piezoelectric effect).

Objective of the paper

The main scientific objective of the paper is development of a new mathematical and electro-mechanical model of the physical phenomena occurring in a single OHC (Outer Hair Cell). The mechanism of physical phenomena that take place in a single OHC is

still not fully understood and described, even though it was, and is the subject of an intense research in many renowned scientific institutions worldwide. Among others, it is also not known as yet, the role of individual components occurring in a single OHC, such as e.g., the nonlinear capacitance.

The existing models describing the operation of a single OHC are incomplete and do not exactly correspond to physical phenomena occurring in a single OHC (Liu, Neely, 2009; Cohen, Furst, 2004; Mountain, Hubbard, 1994; de Boer, 1995). In fact, there are a few models describing the phenomenon of power amplification . However, these models are phenomenological in nature and to large extend speculative (Shera, 2007).

In this paper the author presents a new physical model for outer hair cells (OHCs) in the cochlea, which are represented by hollow piezoelectric cylinders with nonlinear mechanical and electrical properties.

A key element of the proposed model is the parametric amplifier composed of a nonlinear capacitance and other physical elements that are components of a single OHC.

The author proposes a new theory of power amplification in the outer hair cells (OHCs) embedded in the cochlea using (known in electronics and physics) concept of parametric amplification (Louisell, 1960). In fact, the nonlinear capacitance that occurs between the inner and outer surfaces of the OHC constitutes a nonlinear reactive element of the proposed parametric amplifier. This nonlinear capacitance is a crucial element of the proposed OHC's parametric amplifier model.

In the present work the author provides the theory of power gain and selectivity (sharpness of frequency characteristics) that occur in a single OHC treated as a parametric amplifier. A quantitative analysis of the processes of power amplification and selectivity, which occur in the parametric amplifier based on a single OHC, was carried out. The proposed new model of operation of an individual OHC, compared to so far existing models, is entirely original.

Properties of the model

The proposed model has direct physical interpretation and is not only a mathematical formalism. All elements of the OHC's model have their counterparts in the real structure of the cochlea. Physical explanation of the role that play the individual components of a single OHC, including the role that plays nonlinear capacitance, is given.

The developed parametric amplification model may describe in a natural way the following effects and phenomena occurring in the human cochlea:

1) how mechanical signals are transformed into electrical signals and *vice versa* (direct and inverse piezoelectric effect),

2) how power amplification phenomenon occurs in an input electromechanical amplifier, by the operation of the input electromechanical transistor,

3) in which manner, sharpening of the output characteristics and power amplification due to parametric amplifier operation takes place,

4) how operates the input electroacoustic transducer (electromechanical transistor or electromechanical control element). Operation of the electromechanical transistor will be the subject of the next publication.

State of the art

Cochlear modeling has a long tradition, beginning with Helmholtz in 1863, who was the first to elaborate an anatomically motivated cochlear model (the so-called resonance tonotopic model) (Helmholtz, 1954). The essentials of this model were confirmed by von Bekesy's physiological measurements performed some half a century later (1928). He observed traveling acoustic waves along the cochlear basilar membrane (von Bekesy, 1960). Von Bekesy's discovery gave rise to formulation of a passive hydrodynamic model.

Gold (1948) hypothesized that cochlear tuning and selectivity is the result of a feedback system consisting of a mechanical-to-electrical transduction process coupled to a piezoelectric-like electric-to-mechanical one. A number of models of cochlear mechanics have been proposed, which incorporate some form of the feedback enhancing sensitivity and frequency selectivity. In these models the details of the electromechanical properties of the OHC are not included, but rather the OHC role is simulated via a force acting on the basilar membrane. Gold further assumed that an active process in the cochlea is similar to that taking place in regenerative or super-regenerative receivers that can provide power amplification.

Recently, in 2000 Eguiluz et al. introduced a Hopf bifurcation concept to describe observed experimental phenomena (Eguiluz *et al.*, 2000; Camalet *et al.*, 2000). In this model an active amplifier is represented by a set of mechanosensors, which are maintained at the threshold of an oscillatory (Hopf) instability.

However, this concept is very complicated mathematically and unphysical. In practice, this type of amplifiers (Hopf) can be unstable, generates large amount of noise and is characterized by low fidelity of signal reproduction.

The existing so far models (Ramamoorthy *et al.*, 2007; Deo, Grosh, 2005; Rattay *et al.*, 1998; Magnasco, 2003) of the hearing processes are often complex and incomplete, without direct representation in the human auditory organ.

Assumptions

In the proposed model of an individual OHC it is assumed that:

1) the energy for power amplification is taken from the (DC) voltage source (the endolymphatic potentials),

2) the input and output circuits of the OHC's amplifier are electro-mechanical circuits,

3) the input and output signals are mechanical (acoustic) signals,

4) signal processing, power amplification and tuning take place on the electrical side. Input and output mechanical (acoustic) signals are transformed into electrical side and *vice versa* through the piezoelectric effect,

5) each individual OHC along with surrounding structures of the TM and the BM can be regarded as an active electromechanical OHC's resonant circuit that has one characteristic frequency (CF), at which it can perform resonance vibrations,

6) an individual OHC acts as a sensor (transforms an input acoustic signal into an electrical signal), actuator (transforms an output electrical signal into a mechanical displacement), piezoelectric electroacoustic transducer, power amplifier and the parametric amplifier,

7) each individual OHC together with adjacent regions of the TM and the BM can be treated as an electromechanical OHC's parametric receiver.

OHC's parametric amplifier

Electromechanical parametric amplifier established on the basis of a single OHC performs the following functions:

1) amplifies the power of the input acoustical (electrical) signal,

2) increases the amplitude of the input acoustical (electrical) signal,

3) enhances the selectivity of the OHC's receiver (larger Q-factor),

4) improves the sensitivity of the OHC's receiver.

In this article, a physical model of a single OHC and electrical equivalent circuits (series and parallel) of a single OHC, operating as a parametric amplifier, are presented.

The selectivity of the OHC's parametric amplifier is analyzed by solving differential equations of the Mathieu and Ince type.

Analytical formula for power gain that occurs in the OHC's parametric amplifier has also been derived.

Elements of the developed model are uniquely linked to the physical elements that are present in a single OHC and in the whole cochlea, and to the physical phenomena occurring in a single OHC and in the inner ear (electromotility, the flow of ionic currents, piezoelectricity, nonlinear capacitance, stereocilia movements, movements of the basilar and tectorial membrane, nonlinear effects, metabolic processes in the stria vascularis, etc.).

The proposed model is a physical model, not a phenomenological model. Phenomenological models are constructed so as to match the input and output characteristics. By contrast, in the proposed model, the numerical values of the individual elements of the electrical equivalent circuit are consistent with the physiological data.

The development of mathematical and electronic base of physical model of a single OHC will enable designing of a new generation of hearing aids and cochlear implants, more functional and efficient than those used today. The results obtained in this paper can be used to design various types of electro-acoustic devices, musical instruments and audio coding systems, new in relation to currently existing codecs of the MP-3 type.

The outline of this paper is as follows. Section 2 presents a new electromechanical model for an individual outer hair cell. Section 3 shows electrical equivalent circuits of an OHC's electromechanical resonator operating as a parametric amplifier. Analysis of the selectivity of an OHC's parametric amplifier is included in Sec. 4. Section 5 describes parametric mechanism of power amplification in the cochlea. Conclusions and directions for future research are given in Sec. 6.

2. Proposed electromechanical (physical) model of an individual OHC

An individual OHC is a complex electromechanical system. To describe physical phenomena occurring in the cochlea the following concepts are used:

1) piezoelectricity,

2) the ionic currents,

3) the transistor effect,

4) nonlinear capacitance,

5) parametric amplifier.

Electrical and mechanical phenomena that occur in a single OHC are mutually coupled via the piezoelectric effect (WEITZEL *et al.*, 2003). An individual OHC can be represented by a hollow piezoelectric cylinder with a nonlinear capacitance between inner and outer surface of the OHC, located between the BM and TM in the cochlea, see Fig. 1. OHCs have a diameter of 9 microns and a length that ranges from 20 microns to 90 microns depending of their location in the cochlea.

The OHC's capacitance consists of the linear and nonlinear component (IWASA, 1994). The nonlinear component is due to movement of localized charges and
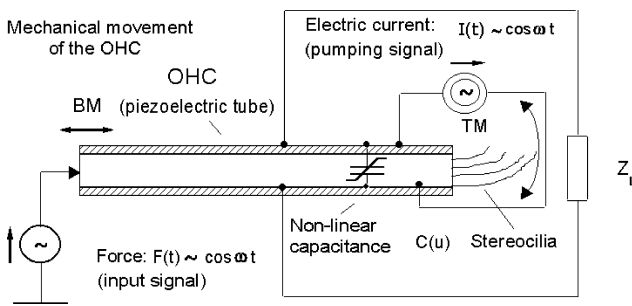
Fig. 1. Hypothetical simplified electro-mechanical diagram of a single OHC operating as a parametric amplifier. $F(t)$ – represents the input acoustic signal, Z_L represents the electrical load impedance, $C(u)$ – is a nonlinear capacitance.

is a prominent feature of the OHC (SPECTOR, 2005). The magnitude of the nonlinear component is comparable to that of the linear component. Non-linear (voltage-dependent) capacitance measured across the inner and outer cylindrical surfaces of the OHC is one of the major features of the electrical behavior of the OHC. From the circuit theory point of view this capacitance is a nonlinear reactive element. The capacitance varies like a bell-shaped function with respect to changes in transmembrane voltage.

Here, the sequence of the physical phenomena that occurs in an individual OHC is presented:

1. The incoming acoustic signal sets in motion the BM and TM.

2. The movement of BM acts on a considered OHC and causes its motion in relation to the TM. Consequently deflection of OHC' stereocilia occurs, what triggers the operation of electro-mechanical input transistor.

3. Subsequently, charging of nonlinear capacitance occurs. Electrical signal which pumps a nonlinear capacitance is represented by an AC current source ($I(t) \sim \cos \omega t$). This source is produced by an input electromechanical amplifier, which is based on the electromechanical transistor. This transistor transforms changes in the mechanical deflection of stereocilia (see right side of Fig. 1) to the channel conductance variations and consequently to changes in the ion channel current (K^+ ions) (OSPECK *et al.*, 2003). Here there is a power gain on a principle similar to the operation of the electronic (unipolar) field effect transistor with a modulated channel conductance. A thorough analysis of an electromechanical transistor will be the subject of future work.

4. The input driving signal is an acoustic (mechanical) signal (represented by the force $F(t) \sim \cos \omega t$ or velocity $v(t)$) acting on the piezoelectric tube from the basilar membrane (BM) side, (see left side of Fig. 1). Through the direct piezoelectric effect this input (acoustic) mechanical signal is transferred to the electrical side as a voltage source $E(t)$ and subsequently is amplified in the parametric amplifier based on a nonlinear capacitance $C(u)$. Power to the nonlinear capacitance is supplied by AC electric pump signal represented by a variable current source $I(t)$.

5. Electric signal amplified in a parametric amplifier, as an output electrical signal is dissipated (performs useful work) at the electrical load impedance Z_L. The output useful electrical signal is then transferred to the mechanical side by the inverse piezoelectric effect.

6. The resulting useful output signal is therefore the mechanical signal (force velocity or displacement). The power of this output mechanical signal can surpass many times the power of an input acoustic signal. Subsequently, this output mechanical signal acts on the Basilar Membrane (BM) and Tectorial Membrane (TM), and consequently also on the Inner Hair Cells (IHC). IHCs are sensors which transform mechanical signals into electrical signals (electric pulse trains).

Since the parametric amplifier is a highly selective system, so this amplifier can get a very narrow output characteristics (sharp tuning).

Summing up, the proposed OHC's model implies the following sequence of the physical phenomena occurring in an individual OHC:

1) incoming acoustical signal $\Rightarrow$,

2) basilar membrane movement $\Rightarrow$,

3) mechanical stimulation (deflection) of stereocilia $\Rightarrow$,

4a) small "ac" voltage signal generation in the OHC due to the direct piezoelectric effect (at the BM side) $\Rightarrow$,

4b) ion channels activation and inactivation (at the TM side) $\Rightarrow$,

5) operation of the input electromechanical transistor,

5a) "ac" current source generation $\Rightarrow$,

6) pumping of the nonlinear capacitance $\Rightarrow$,

7) parametric amplification of the power of the small "ac" input voltage signal $\Rightarrow$,

8) inverse piezoelectric effect $\Rightarrow$,

9) large axial mechanical displacement of the OHC $\Rightarrow$,

10) augmentation of the basilar and tectorial membrane mechanical displacement (output useful mechanical signal) $\Rightarrow$,

11) IHCs (inner hair cells) movement $\Rightarrow$,

12) generation of sequences of electrical impulses in neurons.

3. Electrical equivalent circuits of an individual OHC

3.1. Non-linear equivalent circuit of an electromechanical OHC's resonator

Analyzing an electromechanical system from Fig. 1, one can specify the following nonlinear electrical equivalent circuit (series) of a single OHC, see Fig. 2.
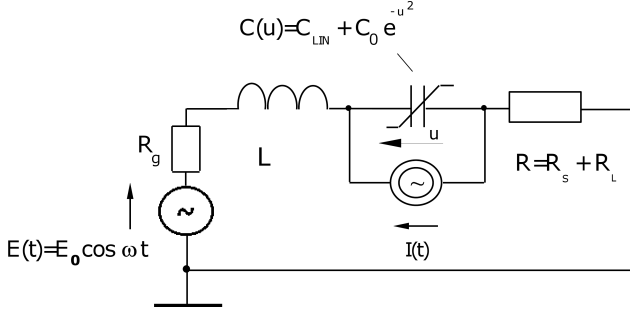

Fig. 2. Hypothetical simplified Thevenin electrical equivalent circuit of the OHC's parametric amplifier treated as a nonlinear oscillator. Circuit represents the operation of a single OHC.

In Fig. 2, $E(t)$ represents an input electrical signal, $C(u)$ is the sum of linear capacitance and nonlinear capacitance with a Gaussian bell shape voltage dependence, $I(t)$ represents the pumping (AC) signal, L represents the loading mass of a single OHC along with the surrounding TM and BM areas, R_g is the resistance of the input electrical (source), R_s represents losses of a nonlinear oscillator circuit, and R_L is the load resistance.

Using the electrical equivalent circuit of Fig. 2, one can analyze the variations of the electrical variables such as voltage, current and charge flowing in the circuit, and as a consequence the course of the physical phenomena occurring in the individual OHC's resonators.

Elements of the resonant circuit (inductance L, linear and nonlinear capacitance, load resistance R_L, loss resistance R_s, along with an input signal represented by the voltage source $E(t)$, and resistance R_g, and pumping signal $I(t)$), constitute the electrical equivalent circuit of an electromechanical parametric amplifier formed from an individual OHC. In this parametric amplifier, the energy flows from a strong pump signal $I(t)$ to weak useful signal wave represented by $E(t)$.

By analyzing the circuit from Fig. 2, one can investigate the linear and nonlinear behavior of the OHC's parametric amplifier.

In this work a quantitative analysis of physical phenomena occurring in an individual OHC is performed, using the linearized model of the parametric amplifier based on a single OHC. Analysis of nonlinear effects occurring in a single OHC will be the subject of future work.

3.2. Linearized equivalent circuits of an OHC's resonator

3.2.1. Series (Thevenin) equivalent circuit

For moderate level of input driving signal, assuming that the pumping signal (represented by the current source $I(t)$) is much larger than the input signal (represented by the voltage source $E(t)$), the system from Fig. 2 can be linearized.

Consequently, one arrives at the equivalent circuit such as in Fig. 3. In this circuit, $C'_0 = C_{\text{Lin}} + C_0$ is the static component of an overall capacitance of the OHC's resonator. $C(t)$ is a time varying transmembrane capacitance resulting from the pumping of the nonlinear capacitance by the electrical current $I(t)$, see Fig. 2. Inductance L represents the inertial effects in the OHC's resonator. Resistance R_s represents losses in the OHC's resonator. $E(t)$ is the driving voltage generated by an input force $F(t)$ and transformed into the electrical side through the direct piezoelectric effect. R_L is the load resistance, and R_g is the resistance of an input voltage source.
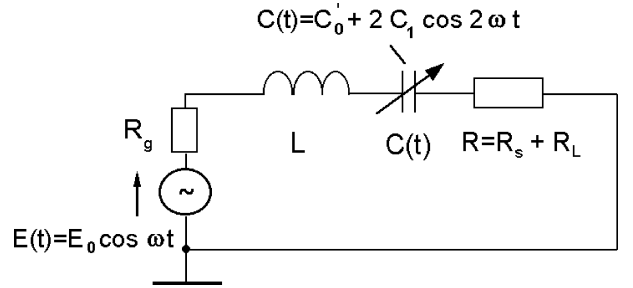

Fig. 3. Linearized (lumped-element) Thevenin electrical equivalent circuit of an individual OHC operating as an electromechanical resonator.

Differential equation that describes the flow of charge in the circuit of Figure 3 is a linear differential equation with variable coefficients:

$$\frac{d^2q}{dt^2} + \frac{\omega_0}{Q_{\text{pass}}} \frac{dq}{dt} + \omega_0^2\left(1 - \frac{2C_1}{C'_0}\cos 2\omega t\right)q = \frac{1}{L}E(t), \qquad (1)$$

where q is the electric charge flowing in the circuit, ω_0 is the angular resonant frequency ($\omega_0^2 = 1/LC'_0$), and Q_{pass} is the quality factor of the passive resonant circuit ($Q_{\text{pass}} = \omega_0 L/(R + R_g)$).

Equation (1) is an inhomogeneous differential equation of the Mathieu type. This equation describes the operation of the parametric OHC's amplifier for moderate levels of driving input signals.

By solving Eq. (1) one can determine the electric charge, current and voltage distribution in the circuit and describe the electrical and electromechanical properties of the OHC's resonator (e.g., obtain the output

frequency amplitude characteristics, power amplification etc.).

3.2.2. Parallel (Norton) equivalent circuit

A parallel (Norton) equivalent circuit of an individual OHC (see Fig. 4), similar to the series equivalent circuit from Fig. 3, can also be specified.
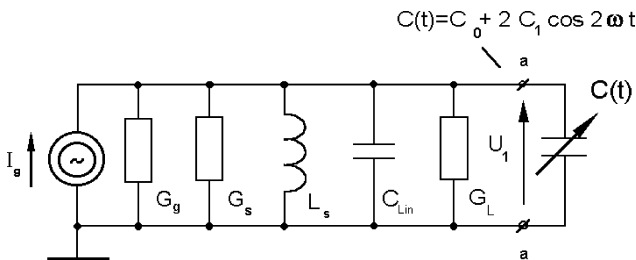

Fig. 4. Norton linear equivalent circuit of a degenerate OHC's parametric amplifier.

I_g is the source current, G_g is the source conductance, G_L is the load conductance, G_s is the loss conductance, L_s is the inductance of the OHC's resonator, $C(t)$ is a time varying capacitance.

As shown in Fig. 4, the input electric signal represented by the current source I_g of admittance G_g is amplified in the parametric amplifier (formed with a time-variable capacitance). After amplification, this signal is dissipated as the useful signal at the output load conductance G_L. The useful output power is then transformed (through the inverse piezoelectric effect) to the mechanical side, where it performs useful work on the TM and BM, which in turn will stimulate further IHCs.

Applying Kirchhoff's laws to the circuit from Fig. 4, the following differential equation that describes voltage (u_1) changes in the circuit is obtained:

$$1/\omega_0^2 \left(1 + \frac{2C_1}{C_0'} \cos 2\omega t\right) \frac{\mathrm{d}^2 u_1}{\mathrm{d}t^2}$$
$$+ L_s \left(G_w - 4C_1\omega \sin 2\omega t\right) \frac{\mathrm{d}u_1}{\mathrm{d}t} + u_1 = L_s \frac{\mathrm{d}I_g}{\mathrm{d}t}, \quad (2)$$

where $G_w = G_g + G_L + G_s$, $C_0' = C_{\mathrm{Lin}} + C_0$, $\omega_0^2 = 1/L_s C_0'$.

Equation (2) is a nonhomogeneous differential equation of the Ince type. Solving this differential equation Eq. (2), one can also determine the time course of the voltage u_1 on the load conductance, output frequency characteristics, and power gain.

4. Selectivity (sharpening of frequency characteristics)

Single OHC with adjacent areas of the BM and the TM acts as a selective parametric power amplifier of an input acoustic signal. In addition to power, the amplitude of the input signal (deflection, velocity or voltage) is also amplified. Consequently, amplification of the input signal amplitude is also accompanied by an increase in the quality factor of the OHC's resonance vibrating circuit. This makes it also narrower resonance curve of the oscillating OHC's resonant circuit.

The result of the input signal power gain is:

1) increasing the level of the input signal (displacement, velocity, amplitude or current),
2) enhancing the sensitivity of the OHC's receiver,
3) improving the selectivity of the OHC's receiver (higher quality factor).

Damped Mathieu differential equation Eq. (1) describes the behavior of the resonant OHC's parametric amplifier. By solving this equation one can determine the selectivity of the resonant circuit from Fig. 3. For this purpose, Eq. (1) was solved numerically (for various values of frequency about the resonant frequency f_0) using Mathcad software package. In this way, the resonant curve of Fig. 5 was obtained. Also one gets a similar curve by solving the differential equation of the Ince type Eq. (2).
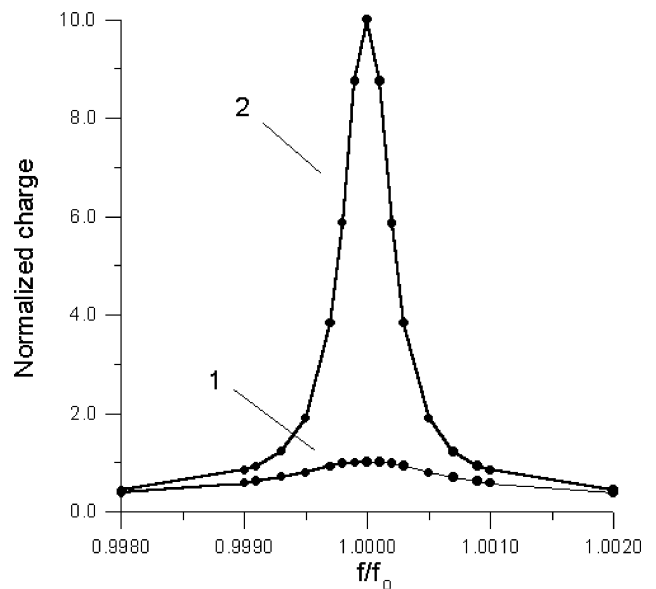

Fig. 5. Sharpening of the resonant curve of the OHC's electromechanical resonator due to the parametric amplification. Curve 1 – passive vibrations, curve 2 – active vibrations. f_0 is a resonant frequency.

The following parameters of the damped vibrating parametric system from Fig. 3 were assumed in the numerical calculations:

$$f_0 = \omega_0/2\pi = 1000 \text{ Hz}, \qquad Q_{\mathrm{pass}} = 12,$$

$$C_1/C_0' = 0.075.$$

The above data were chosen according to the physiological data given in (WEITZEL *et al.*, 2003; OSPECK

et al., 2003; Liu *et al.*, 2006; Reinchenbach *et al.*, 2010).

Consequently, the resonant curves representing the vibrating OHC's structure were derived in two cases a) passive vibrations of the OHC's structure without parametric effect (curve 1), and b) active vibrations of the OHC's resonator with the parametric amplification (curve 2), see Fig. 5.

It can be seen in Fig. 5, that the resonant curve of the circuit with the variable capacitance and parametric amplification (curve 2) has a higher selectivity (bandwidth is about 10 times narrower), and higher quality factor ($Q_{act} = 10 \cdot Q_{pass}$) compared to the resonance curve without the parametric amplification (curve 1).

The amplitude of the amplified signal (active vibration) at the resonant frequency f_0 is 10 times larger than the amplitude of the signal that is not subject to parametric amplification (passive vibration).

Numerical calculations show that the level of the amplitude near the resonant frequency and the quality factor augment with the increase in capacitance modulation ratio C_1/C_0'.

5. Power gain in the OHC's parametric amplifier

The physical mechanism of power amplification in the cochlea is not yet known. As a result, there is no a satisfactory quantitative theory of the power gain occurring in the cochlea. The existing attempts to explain this phenomenon are rather qualitative, descriptive and nonphysical.

In the model presented in this paper the phenomenon of power amplification in an individual OHC resonator is explained using the concept of the parametric amplification. In order to calculate the power gain of the OHC's parametric amplifier, a parallel Norton equivalent circuit from Fig. 4 is used.

The input power amplification in the electromechanical OHC's amplifier occurs in two stages 1 and 2, described below.

The incoming input acoustic signal acts on an individual OHC from the BM side and TM side simultaneously. As a results, the following sequence of events will take place in the OHC:

1. BM movement sets in motion a considered OHC. The movement of an OHC in relation to the TM causes deflection of its stereocilia. The movement of the stereocilia initializes the influx of K^+ ions into the OHC and consequently triggers the operation of an electromechanical input transistor. This transistor in turn amplifies the power of the input signal, and as a consequence loads the nonlinear OHC's capacitance [$C(u)$ from Figs. 1, 2, and also $C(t)$ from Figs. 3, 4]. The amplifier formed from the electromechanical transistor is of aperiodic (nonselective) type. The electrical signal, amplified in the electromechanical transistor amplifier, powers the nonlinear OHC's capacitance. In this way, the modulation of the nonlinear capacitance is produced. For moderate levels of input signals, the nonlinear capacitance can be approximated by the time-variable capacitance $C(t) = C_0 + 2C_1 \cdot \cos(2\omega_s t)$, see Figs. 3 and 4. Frequency of the capacitance modulation $2\omega_s$ is equal to exactly twice the frequency of the input signal, ω_s.

2. Input acoustic signal (acting from the BM side) is transformed to the electrical signal through a direct piezoelectric effect. The mass, compliance and mechanical losses of the adjacent areas of the TM and BM are also transformed on the electrical side through a direct piezoelectric effect. These electrical elements, including existing linear and nonlinear (time varying) capacitance, form the electrical equivalent circuit of the parametric amplifier constructed from a single OHC, see Figs. 2, 3 and 4. Due to the parametric amplifier operation, the power gain of the electrical (AC) input signal occurs. Subsequently, by an inverse piezoelectric effect this amplified input electrical signal is transformed into the mechanical side, where it performs a useful work on the BM and TM.

At the same time, due to the parametric amplifier operation, the output frequency characteristics of the OHC are also sharpened, what results in a higher frequency selectivity.

5.1. Analytical formula for power amplification

The effective resonant power gain k_p of the parametric amplifier, represented in Fig. 4, is defined as the ratio of the output power $\left(|U_s|^2 \cdot G_L\right)$ in the load G_L, to the available input power $\left(|I_g|^2/4G_g\right)$ from the source, and can be expressed as follows:

$$k_p = \frac{|U_s|^2 \, G_L}{|I_g|^2/4 \, G_g} = \frac{4 \, G_g \, G_L}{(G_g + G_L + G_s + G_{zs})^2}, \quad (3)$$

where $G_{zs} = -\omega_s \, C_1$ is the negative conductance introduced to the circuit by the parametric effect, see Eq. (17). This negative conductance is due to the delivery of the additional energy to the circuit by ionic currents K^+, triggered by stereocilia movement.

The derivation of the analytical expression for the conductance G_{zs} is given in the Appendix.

Formula (3) can be rewritten in the form:

$$k_p = \frac{4 \, G_g \, G_L}{G_w^2 \, (1 - \gamma)^2}, \quad (4)$$

where $G_w = G_g + G_L + G_s$ and $\gamma = -\dfrac{G_{zs}}{G_w} = \dfrac{\omega_s \, C_1}{G_g + G_s + G_L}$ is the un-damping coefficient.

The maximum power amplification is achieved when the load conductance G_L is matched to the source conductance, i.e.,

$$G_{L\text{opt}} = G_g + G_s. \tag{5}$$

Substituting Eq. (5) into Eq. (4) one has:

$$k_{p\,\text{max}} = \frac{G_g}{G_g + G_s} \frac{1}{(1 - \gamma)^2}. \tag{6}$$

If $G_s \ll G_g$ then Eq. (6) reduces to

$$k_{p\,\text{max}} = \frac{1}{(1 - \gamma)^2}, \tag{7}$$

where $\gamma = \dfrac{\omega_s \, C_1}{2 \, G_g}$ is the resulting un-damping coefficient.

Equation (7) shows that the power gain $k_{p\,\text{max}}$ depends, among others, on the capacitance coefficient C_1, which characterizes the level of the pumping signal. Formula (7) was used in the sequel in calculations of the power gain occurring in the OHC's parametric amplifier.

The power gain was calculated for the following set of electrical parameters for the vibrating OHC's parametric resonator (from Fig. 4):

$$P = 10^{-14} \text{ W}, \qquad C_0' = 30 \text{ pF}, \qquad Q_{\text{pass}} = 12,$$

where P is the available power of an input electrical signal, C_0' is the static component of an overall capacitance of the OHC's resonator, and Q_{pass} is the quality factor of the passive resonant circuit (without the parametric amplification).

The estimated value of the input power ($P = 10^{-14}$ W) corresponds to a moderate level of acoustic driving signal i.e., 50 dB. The results of calculations of the power gain and other electrical parameters characterizing the operation of the OHC's parametric amplifier from Fig. 4 are presented in Table 1.

Table 1. Coefficient of power amplification $k_{p\,\text{max}}$, source conductance G_g, negative un-damping conductance G_{zs} introduced to the resonant circuit, input source current I_g, capacitance modulation ratio C_1/C_0', and quality factor Q_{act} of the active resonant circuit with the parametric amplification.

Resonant frequency f_0 [Hz]	$k_{p\,\text{max}}$	$2\,G_g$ [nS]	G_{zs} [nS]	I_g [pA]	$\dfrac{C_1}{C_0'}$	Q_{act}
1000	100	15.70	−14.12	17.72	0.075	120
	18	15.70	−11.93	17.72	0.063	50.9
3000	100	47.10	−42.39	30.69	0.075	120
	18	47.10	−35.80	30.69	0.063	50.9

Values of the parameters used in the numerical calculations are in accordance with the experimental data obtained for mammalian cochleas (WEITZEL *et al.*, 2003; OSPECK *et al.*, 2003; LIU *et al.*, 2006; REINCHEN-BACH, HUDSPETH, 2010).

As it is seen from the Table 1, the OHC's parametric amplifier can effectively provide power gain of the useful acoustic input signal. Table 1 shows also that the negative conductance G_{zs}, introduced to the resonant circuit by the parametric amplification, un-damps the circuit, and enhances the effective quality factor, Q_{act}.

For low levels of input signals the governing equation for the OHC element is a nonlinear differential equation. The solution of this equation provides an augmented value of the quality factor and therefore higher value of amplification of the signal amplitude. Numerical solutions of this nonlinear differential equation will be performed in future works.

6. Conclusions

The theory developed in this study, explains quantitatively in a natural way the physical phenomena occurring in an individual OHC. It was shown that the phenomena of power gain and sharpening of the output amplitude frequency characteristics are particularly important. The developed theory also may explain the phenomenon of otoacoustic emission.

It was demonstrated that an individual OHC can operate as an electromechanical parametric amplifier, that can amplify the power of an input acoustic signal and improve selectivity.

Series and parallel electrical equivalent circuits of a single OHC that operates as a parametric amplifier have been established.

Physical and mathematical models describing the course of electrical signals in the developed series and parallel electric equivalent circuits have been formulated.

The derived inhomogeneous Mathieu and Ince differential equations that describe the operation of a single OHC as a parametric amplifier, have been solved numerically. Output amplitude frequency characteristics of a single OHC working as a parametric amplifier are evaluated.

Sharpening of frequency response amplitude (enhancement in quality factor and selectivity), as a result of operation of the parametric amplifier based on a variable in time capacitance, was stated.

Analytical formula for the input signal power gain occurring in the OHC's parametric amplifier was also derived. Depending on the assumed values of the parameters of equivalent circuits and driving level, the opportunity to amplify the input signal power in a wide range (from several to several hundred times) has been stated.

The developed electromechanical model of a single OHC is a physical model, not a phenomenological model. Each element of the model has its physical

counterpart in the actual structure of the cochlea. The proposed in this work a new parametric-piezoelectric model of a single OHC, along with its mathematical and electronic description, is an original contribution to the state-of-the-art in modeling of the human hearing organ.

The presence of the parametric amplification provides a sharp resonant curve of the oscillating circuit (representing a vibrating OHC), and large output signal to noise ratio.

The material presented in this paper is the first stage of the research. In the next step the author aims to develop a complete electromechanical model of the cochlea and description of the physical phenomena occurring in the whole cochlea's structure. Future analysis will be conducted on nonlinear effects occurring in the considered OHC's parametric amplifier.

The developed model conforms qualitatively to the existing experimental data. New refined theory of the hearing processes based on the piezoelectricity and parametric amplification can open new horizons for research, e.g., deeper understanding of the physical phenomena underlying auditory processes, new phenomena in musical and speech acoustics. This will allow the design of new musical instruments and audio codecs, that will be new in relation to the existing MP3 codecs.

Appendix

The nonlinear OHC's capacitance has a bell shape voltage dependence (Iwasa, 1994), therefore it can be approximated by the following Gaussian function:

$$C(u) = C_0 \cdot \exp(-u^2), \qquad (8)$$

where u is a normalized voltage.

Expanding the above formula into the Taylor series gives rise to:

$$C(u) = C_0 \left(1 - u^2 + \frac{1}{2} u^4 - \dots \right). \qquad (9)$$

The incoming pumping signal, that is applied across the nonlinear capacitance, can be expressed as:

$$v = v_1 \cos(\omega t). \qquad (10)$$

The voltage given by formula (10) is next substituted into formula (9). As a consequence, the resulting time variable (time-dependent) capacitance is produced:

$$C = C(t) = C_0 + 2C_1 \cos(2\omega_s t)$$
$$+ 2C_2 \cos(4\omega_s t) + \dots + \qquad (11)$$

For the useful input electrical signal u_s of frequency ω_s, the electric charge δQ resulting from the parametric effect equals (Golde, 1976):

$$\delta Q = C(t)U_s. \qquad (12)$$

For a time-harmonic input signal:

$$U_s = U_{sm} \cos(\omega_s t + \varphi_s), \qquad (13)$$

where φ_s is a phase shift between the pump and useful input signal, the current flowing through the time varying capacitance is given by:

$$i(t) = \frac{d(C(t)U_s)}{dt}. \qquad (14)$$

Inserting Eqs. (11)–(13) into Eq. (14) and neglecting in Eq. (14) all components of frequency other than ω_s one obtains:

$$i(\omega_s t) = -C_0 U_{sm} \omega_s \sin(\omega_s t + \varphi_s)$$
$$- C_1 U_{sm} \omega_s \sin(\omega_s t - \varphi_s). \qquad (15)$$

The second term in Eq. (15) is due to the parametric effect and can be represented by the effective admittance Y_{zs} introduced across the $a - a$ terminals in Fig. 4.

According to Eq. (13) and Eq. (15) the admittance Y_{zs} equals:

$$Y_{zs} = j\omega_s C_1 \exp(-2j\varphi_s) = -\omega_s C_1 \sin(2\varphi_s)$$
$$+ j\omega_s C_1 \cos(2\varphi_s) = G_{zs} + jB_{zs}. \qquad (16)$$

For $\varphi_s = -\pi/4$ one has:

$$Y_{zs} = G_{zs} = -\omega_s C_1 < 0. \qquad (17)$$

Therefore, the presence of a time varying capacitance C_1 gives rise to a negative conductance G_{zs} in the circuit from Fig. 4. This negative conductance can be responsible for the power gain in the OHC's parametric amplifier.

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