Power Amplification and Frequency Selectivity in the Inner Ear: A New Physical Model

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http://dx.doi.org/10.5772/66542

Abstract

This Chapter presents a new physical model for signal processing phenomena (power amplification and frequency selectivity) occurring in the inner ear (Cochlea). It is generally accepted that Outer Hair Cells (OHCs) play a pivotal role in the Cochlear signal processing. In the proposed new model we postulate that all signal processing phenomena in the Cochlea are due to electrical currents flowing in the Cochlea structure. Three crucial characteristics of the OHCs are: 1) a forward mechanoelectrical transduction, 2) a strong piezoelectric effect (direct and inverse), and 3) a transmembrane nonlinear capacitance. The new model postulates existence of a biological electromechanical transistor (EMT) in each of the OHCs (based on a forward mechanoelectrical transduction phenomenon), which enhances the power of an incoming acoustic signal. Consequently, the nonlinear capacitance of the appropriate OHCs is charged (pumped) by an AC current source generated at the output of the proposed EMT transistor. Power amplification and frequency selectivity are realized on the nonlinear capacitance, which constitutes an essential part of a parametric amplifier circuit. The amplified and sharpened in frequency electric signal is then converted to a mechanical signal by the OHCs (inverse piezoelectric effect) and transferred to the Inner Hair Cells that transform this mechanical signal into an output electrical signal supplied to the afferent nerves.

Keywords: mechanism of hearing, cochlear amplifier, equivalent circuits, nonlinear capacitance, electromechanical transistor, parametric-piezoelectric amplifier, piezoelectric effect, power amplification, selectivity

1. Introduction

Acoustic signals, which can be detected by human auditory organ, are acoustic (pressure) waves propagating in a material medium, such as gas, liquid, or solid. Acoustic waves cannot propagate in vacuum, contrary to light waves. Acoustic waves are in fact pressure disturbances that propagate in air and are characterized by longitudinal (compressional) particle movements. Initially, acoustic waves enter the ear pinna and ear canal (outer ear). Then, acoustic waves travel through a sequence of elements in the auditory pathway, such as middle ear and inner ear, where they are converted into electrical impulses transmitted directly into the central nervous system. The most important element in the auditory pathway is the inner ear with the cochlea. In turn, the main constituent of the cochlea is the organ of Corti located between the basilar membrane (BM) and tectorial membrane (TM). The organ of Corti contains a large number of sensory cells such as the outer hair cells (OHCs) and inner hair cells (IHCs). It is generally assumed that the process of power amplification of input acoustic signals occurs in the cochlea and is accompanied by sharpening of its frequency selectivity. High sensitivity of the cochlea enables hearing of low-level acoustic signals. On the other hand, high selectivity allows for frequency discrimination between two tones with nearly the same frequency.

The inner ear is one of the most complex sensory elements of the human body. It receives acoustic stimuli of various amplitudes and frequencies, carrying information from the external world. It is a highly nonlinear element presenting remarkable properties, such as:

1. Ultra-low power consumption ($14\ \mu W = 14 \times 10^{-6}\ W$) [1].

2. Possibility to amplify power of very weak input acoustic signals. The human ear can receive and distinguish acoustic signals with power slightly above the power of thermal noise in air ($1.9 \times 10^{-18}\ W$). Power density (intensity) of these acoustic signals equals $10^{-12}\ W/m^2$ at a frequency of 1000 Hz [2].

3. Very high dynamic range (120 dB). The power level of a very loud sound ($1\ W/m^2$), such as roaring of jumbo-jet engines, can exceeds trillion times the threshold of human hearing ($10^{-12}\ W/m^2$). Thus, the dynamic range of reception amounts to ($1\ W/10^{-12}\ W = 10^{12}$), 12 orders of magnitude, i.e., 120 dB [3].

4. Very high frequency selectivity. Humans (who have perfect pitch) are able to distinguish between musical sounds differing only by 0.2%, e.g., 1000 cycles per second (Hz) and 1002 Hz. It is noteworthy that the frequency difference between the tones generated by any two adjacent keys (semitone), in the contemporary piano tuned to an equal (well) tempered scale, equals ~6%, or exactly $\left(\sqrt[12]{2} - 1\right) \times 100\%$ [4]. The frequency range of the human ear spans approximately 10 octaves, i.e., from ~20 to ~20,000 Hz.

None of the technical devices built up to date by humans can even approach the above characteristics. This would be impossible if an input acoustic signal were processed in a passive manner. Achievement of such an amazing performance requires that some active processes take place in the cochlea, i.e., an extra energy has to be added to the input acoustic signal, in order to amplify the power of the received acoustic signal and enhance the frequency selectivity (narrow bandwidth) of the cochlea characteristics.

For nearly 2000 years humans tried to elucidate the nature of the physical processes occurring in the human hearing organ (cochlea). So far, there is no complete theory and understanding of the physical phenomena occurring in the cochlea.

Modeling of physical processes occurring in the cochlea is indeed a very complex task. There are still many exciting and unresolved research problems related to the complicated electrical

http://dx.doi.org/10.5772/66542

and mechanical phenomena responsible for the mechanism of hearing. For example, a fascinating area of research is reception and perception of acoustic signals generated by musical instruments. Do aesthetic impressions, offered by music, depend on proper operation of the human auditory organ (cochlea)? Does music have healing properties for autistic children with a perfect pitch?

Accurate knowledge of the mechanism of hearing may allow construction of an artificial cochlea and determination of a possible correlation between the cochlea characteristics and musical skills. Is the construction of the human hearing organ (cochlea) significantly different for musical geniuses (Bach, Mozart, Chopin, etc.) and those individuals only moderately gifted in music?

The mechanism of hearing is not yet fully understood, even though it was, and is the subject of intense research activities in many renowned scientific centers around the world (in USA, Japan, France, Germany, Switzerland, etc.). In particular, the following features of the cochlea are not yet explained:

1. power amplification,

2. high sensitivity in reception of faint (low-level) acoustic signals,

3. high frequency selectivity of acoustic signals (narrow bandwidth analyzer),

4. nonlinear phenomena, and

5. emphasis of weak acoustic signals and compression of large acoustic signals.

A complete and accurate model of the physical processes occurring in the cochlear amplifier (CA) should explain the course of these aforementioned processes.

Full understanding of the physical mechanism of hearing may be of paramount importance for:

a. automation of the speech recognition processes,

b. investigation of emotional behavior of human by using speech analysis,

c. explanation of how the speech perception depends on the cochlea,

d. explanation of how the perception of musical sounds occurs (why some individuals are musical geniuses, e.g., Chopin, and the others are tone-deaf),

e. construction of effective tools for man-computer communication,

f. invention of new and more effective methods for digital coding of sound signals, and

g. construction of new hearing aids.

1.1. What is the sensitivity?

The sensitivity of a given device or system is defined as the lowest amplitude of the signal, which can be detected by the system. In case of the human auditory organ (cochlea) sensitivity is defined as the lowest level of the input acoustic signal, for which the cochlear amplifier, treated as a receiver, produces an output electrical signal of an appropriate level, i.e., the signal with a satisfactory signal to noise ratio. In other words, sensitivity of the human hearing organ (cochlea) corresponds to a threshold acoustic signal, for which one can still hear with an acceptable quality and perception.

1.2. Active processes in the cochlea

Postmortem measurements of BM motion in the cochlea (passive cochlea) show that increase of the amplitude of sound gives rise to a linear increase in the amplitude of BM mechanical vibrations. However, passive cochlea is not able to explain the amazing amplitude sensitivity and frequency selectivity of the human hearing organ. It was found that with a passive cochlea only very loud sound could be heard (low sensitivity) with a poor frequency selectivity.

1.2.1. What are the active processes?

In order to explain the fabulous properties of the human hearing organ (sensitivity and selectivity), the concept of the active element and the cochlear amplifier were introduced as early as in 1948 by Gold [5] and later extended by many researchers (e.g., Davis in [6]). The introduction of the active element served to explain the phenomenon of power amplification and sharpening the frequency characteristics that occur in the cochlea, see Refs. [5, 6]. In general, power amplification process requires that some extra energy is delivered from an external source to the system. The system with power amplification capability is called active in contrast to a passive system, which can only dissipate (lose) the energy.

Properties of active elements (where active processes can occur) allow in a natural way to explain such features of human hearing organ as high sensitivity and selectivity (narrow bandwidth). An example of active elements found in classical electronics can be transistors, bipolar, as well as unipolar (field effect transistors). These elements operating in the amplifier circuit can amplify the power of the electrical input signals.

At present the existence of the cochlear amplifier is widely accepted in the literature, see Ref. [7]. However, the exact mechanism of the power amplification in the cochlea is still the subject of extensive research. It is also generally accepted that OHCs play a key role in the cochlear power amplification process [8]. Power amplification and sharpening of the frequency response occurs in the OHCs, see Ref. [6], that are located in the Cochlea. In fact, loss of the OHCs causes that the cochlear amplifier is not operating, and as a consequence hearing capabilities are lost.

1.2.2. IHC operates as sensors

Another type of sensing element is inner hair cells (IHCs) that are also located in the cochlea, between the BM and TM. The inner hair cells (IHCs) detect the mechanical signal, which was previously amplified by the OHCs. The IHC plays the role of sensor [9]. The IHC converts the input mechanical signal into an electrical signal and transmits the latter to the central nervous system via the afferent innervation. In this case the afferent innervation of the IHCs may be called an output circuit of the entire cochlear amplifier.

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1.2.3. OHC can operate as sensor and actuator

The OHC is not only the mechano-mechanical transducer. The OHC is both the mechano-electrical transducer and the electromechanical transducer. This can be attributed to two phenomena, i.e., the "forward mechano-electrical transduction" and the inverse piezoelectric effect (electromotility), which play an essential role in the operation of the OHC and the cochlear amplifier as a whole [10]. An input acoustic signal entering the OHC is transferred to the electric side through the direct piezoelectric effect. There, on the electric side the signal is amplified.

1.2.4. What is the piezoelectric effect (direct and inverse)?

The direct piezoelectric effect is the ability of certain materials to generate an electric charge (voltage) in response to applied mechanical stress [11]. The inverse piezoelectric effect in turn is responsible for generating of mechanical deformations (stresses) induced by voltage applied to the material. Piezoelectric properties were found in certain solid media and biological materials, such as bones, ligaments, OHCs, and selected proteins. The piezoelectric effect, which is present in OHCs, is also termed in the literature as the electromotility or somatic motility. The piezoelectric effect is reversible, i.e., if the direct piezoelectric effect occurs in a material then the inverse piezoelectric effect will be present as well.

1.2.5. Electric side and mechanical side

A rectangular plate cut-off from the piezoelectric material, with two parallel electrodes attached to the plate, forms the simplest piezoelectric transducer used in practice. The transducer is in fact a three-port device with one electrical and two mechanical ports. Application of an electrical signal to the electric port (two parallel electrodes) of the transducer will force the two parallel surfaces of the plate (two mechanical ports) to vibrate with the frequency equal to that of the electrical excitation. Conversely, application of a mechanical signal (force) to the mechanical port(s) will generate voltage in the electrical port with the frequency equal to that of the mechanical driving force. In this way, mechanical and electrical quantities are mutually interrelated and can be transformed one to each other via the piezoelectric effect.

1.2.6. Importance of the electrical phenomena in the OHC

The role of electrical phenomena occurring in the OHC is not merely auxiliary, but in the contrary, is essential. According to the author's analysis, the process of power amplification of the input acoustic signal (applied to one mechanical port of the OHC), as well as the process of sharpening the frequency characteristics (increased frequency selectivity), is carried out on the electrical side of the OHC. Consequently, sharpened electrical signal with amplified power is transferred back to both ports of the mechanical side of the OHC, through the inverse piezoelectric effect. Therefore, the OHC performs mechanical work on its both mechanical ports, i.e., on the BM and on TM. The mechanical energy supplied by the OHC to the TM is transferred to the corresponding IHC by the movement of its stereocilia. The IHC processes its input (in relation to the IHC) mechanical signal into an output electrical signal by opening ion channels (mechano-electric transduction effect). These ionic currents affect the afferent nerve endings, where they are transformed into a series of electrical impulses that are transmitted into the central nervous system. It is assumed that there is no phenomenon of the power amplification in the IHC, which works as a passive sensor. Effectively, the IHC is a mechano-electrical transducer that converts the mechanical signal received from the OHC, into a useful electrical signal, which is an "electrical image" of the received acoustic waves that we can hear.

In this chapter, the author emphasizes the crucial role of the electrical phenomena in the processes of power amplification of input acoustic signals and sharpening of the frequency characteristics of the cochlea. In the second part of this chapter (Sections 9–13), the results of the original author's research, i.e., new model and concept of the cochlear amplifier are presented.

2. Role of the outer hair cells in the cochlear amplification

It is generally accepted that most important processes governing the selectivity and sensitivity of the human ear occur in the organ of Corti located in the cochlea. The cochlea contains about 20,000 outer hair cells (OHCs) spanned between the basilar membrane (BM) and the tectorial membrane (TM). The outer hair cells (OHCs) are nonlinear electro-mechanosensory cells and are critically important for the high sensitivity and frequency selectivity of the human ear. The electromechanical properties of the outer hair cells (OHCs) are believed to be the critical component of the cochlear Amplifier (CA) concept, but its internal "circuitry" still remains unknown. Mode of operation of this amplifier still arouses controversy and it is still unclear.

The OHC is a layered piezoelectric cylinder, with a diameter of about 9 μm and length that varies from 15 to 90 μm, depending on their location in the cochlea. The OHC wall thickness is equal to 100 nm. The membrane capacitance of the OHC comprises a linear component and nonlinear component. The most striking feature of the OHC is its giant piezoelectric effect, which is four order of magnitude higher than that in the best known piezoelectric materials. Therefore, piezoelectric phenomena have been included in the modeling of the OHC operation. Other observations provide also an evidence that movements of electrical charges within the OHC walls are directly coupled with mechanical elongation and shortening of the OHC structure. At the top of sensory cells (OHCs and IHCs) a tuft (called hair bundle–HB) of a few tens to a few hundreds of stereocilia is located.

Existing so far theories of the amplification in a single OHC and in the entire cochlea do not describe all the phenomena experimentally observed, or they are entirely phenomenological theories, not related to actual physical (physiological) processes occurring in a single OHC and in the entire inner ear. Similarly, the previously published electromechanical models of a single OHC and the whole cochlea only reflect their external characteristics and not the physical processes in them.

A characteristic feature of the OHC is the presence of the piezoelectric effect. Electric voltage applied across the walls of the cell membrane of the OHC results in a change (increase

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or decrease) of its length (inverse piezoelectric effect). Similarly, change in the length of the OHC generates electrical voltage across the walls of the cell membrane of the OHC (direct piezoelectric effect). Thanks to the piezoelectric effect, amplified in the OHC (on the electric side) acoustic signal is transferred to the tectorial membrane (TM) and subsequently to the inner hair cells (IHCs).

In summary, OHCs as elements of the cochlear amplifier provide:

1. power amplification,
2. frequency selectivity,
3. dynamics, and
4. generation of otoacoustic emissions.

2.1. What is the power amplification?

In order to verify whether a given system or device, such as the cochlea, is passive or active it is necessary to determine the balance of power flowing in and out of the device. To this end, the device should be surrounded by a closed surface with its normal vector $\vec{n}$ pointing outwards. Then, one has to identify all power components (electrical and mechanical) flowing through the surface and calculate the corresponding fluxes of the power density. A negative value of the total flux (power) is the signature of the fact that the system is a passive one, in which the power is dissipated (more power is flowing into the system than outflows from it). An example of such a system can be an electrical network consisting of resistors, inductors, and capacitors. A positive value of the total flux (power) indicates that the device is an active element, i.e., more power is flowing out of the device than flowing into the device. An example of such a system (device) can be either a bipolar transistor or a field effect transistor (MOS) operating in the amplifier circuit.

Simply speaking, if the output useful power exceeds the input signal power, then the device amplifies the power.

2.2. What is the frequency selectivity?

The frequency selectivity of the system is its ability to unambiguously discriminate between two signals with very close frequencies. This property occurs, for example, in narrow band resonant circuits with quartz resonators. High frequency selectivity of the cochlear amplifier is an evidence that the frequency characteristics of the cochlea can be tuned to a narrow frequency band, e.g., from 1000 to 1002 Hz. This frequency selectivity is essential for comprehension of speech and music perception.

2.3. What is the dynamics?

The dynamic range (dynamics) of the device is the ratio P_2/P_1 of the maximum P_2 and minimum power P_1 of the input signal, which can be handled properly by the device (cochlea). For convenience, the dynamics is represented in a logarithmic scale, i.e., $Dynamics = 10 \log$

(P_2/P_1), measured in decibels (dB). Here, the symbol "log" stands for the logarithm to base 10. For example, if power density $P_2 = 1\ W/m^2$ and $P_1 = 10^{-6}\ W/m^2$, then the dynamics equals $10\ \log(1/10^{-6}) = 60$ dB. The dynamics of the cochlear amplifier can reach 120 dB. Colloquially speaking, the dynamics tells us about the difference between the loudest and the weakest sound that we can still hear.

3. Role of the electric currents flowing in the structure of the cochlea

It is generally accepted that most important processes of acoustic signal processing (power amplification and frequency selectivity) occur in the inner ear. In the outer ear and the middle ear, the power of the received sound is not amplified, since the outer and middle ears are passive devices. In the middle ear there is only a mechanical impedance matching, whereas the power of travelling sound is not amplified.

3.1. What is the impedance?

In general, the impedance is a measure of opposition displayed by mechanical (damper, spring, mass) or electrical (resistor, capacitor, inductor) elements to external driving forces (mechanical stresses or electrical voltage, respectively). In case of an electrical excitation the electrical impedance is defined as the ratio of voltage applied to the electrical element to the current flowing through the element. On the other hand, the mechanical impedance is defined as the ratio of force applied to the mechanical element to the velocity at which the element moves. For harmonic (sinusoidal) excitations, the electrical and mechanical impedances can be conveniently described by complex number quantities. The above definitions for mechanical and electrical impedances are valid only for so-called lumped elements, i.e., the elements without spatial dimensions. Lumped elements are subject of the circuit theory. Somewhat different definitions of the impedance are introduced for acoustic and electromagnetic waves propagating in the three-dimensional media. However, in case of the cochlear amplifier the wavelength of the acoustic waves reaching the OHC (1.5 m at a frequency of 1000 Hz) is much higher than physical dimensions of the OHC (90 μm). Therefore, the circuit theory description holds [12].

The incoming acoustic wave passes through the outer ear to the middle ear, where it causes vibrations of the bones (hammer an anvil and stapes). Vibrations of the stapes through the oval window excite acoustic waves in liquids contained in the cochlea of the inner ear. This acoustic wave motion generates a transverse acoustic wave propagating along the basilar membrane. This mechanical wave travelling in the BM excites to vibration OHCs that are located between the BM and TM, see **Figure 1**.

Mechanical displacement of stereocilia, located on top of the OHCs, opens ion channels which provokes the flow of ionic current (K+ cations) in a closed circuit starting from the stria vascularis (DC voltage source) to the body of the OHC and then back to the stria vascularis. Sinusoidal deflection of stereocilia produces a sinusoidal in time flow of electric current (ions K^+) in this circuit. Produced in this way (AC) current source pumps energy into the

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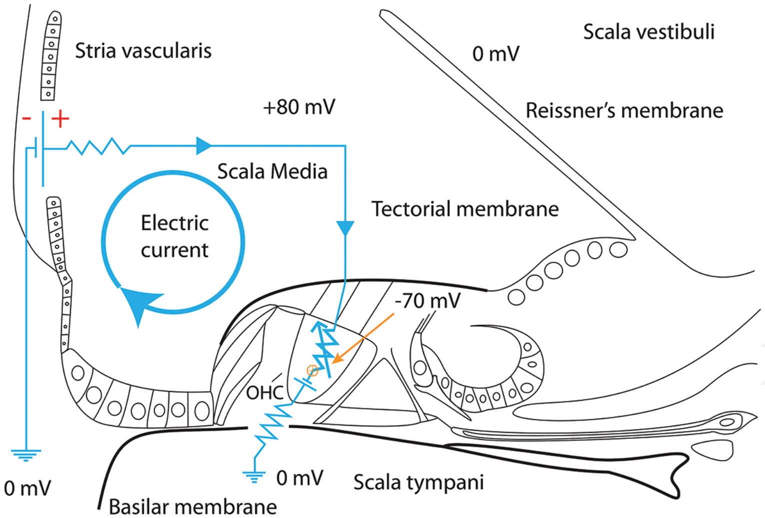

Figure 1. The flow of ionic currents (K^+) in a closed circuit including a DC voltage source (stria vascularis), scala media (+80 mV), OHC (-70 mV), and scala tympani (0 mV). Demonstratively, only one OHC is shown in the figure. Stria vascularis powers the activity of the cochlear amplifier.

nonlinear capacitance, which constitutes a part of the cochlear parametric amplifier. The existence of this nonlinear capacitance was confirmed experimentally [13]. This parametric amplifier provides the necessary selectivity of the frequency characteristics of the cochlear amplifier that is based on a single OHC. The above mentioned problems will be explained in more detail in Sections 9–11.

3.2. Electric currents in the cochlea

Presence of natural (physiological) sources of a DC voltage (stria vascularis) and conductive liquids (electrolytes) in the cochlea creates favorable conditions for flow of electrical currents. It should be emphasized that ionic currents in the cochlea must flow in a closed circuit, according to the classical circuit theory. **Figure 1** shows an example of an ionic current flowing through one of the 20,000 OHCs in the cochlea. This ionic current (K^+ cations) flows from the positive pole of the stria vascularis voltage source (battery), through the scala media (SM; +80 mV) and ion channels at the top (apical) part of the OHC, into the bulk of the OHC (-70 mV). Then, through channels in the lower (basolateral) part of the OHC to perilymph, which has a zero (0 mV) electric potential (right grounding in **Figure 1**). The current loop closes in the negative pole of the stria vascularis battery (grounding in the left side of **Figure 1**).

3.3. Zero of electric potential

It should be remembered that the value of an electric potential at any point is measured with respect to the potential at a reference point, assumed to be zero. As a result, we can only measure the potential difference (voltage). In the cochlear structure in **Figure 1** we assume as zero potential (grounding), the potential of perilymph in scala vestibuli and scala tympani (0 mV). With respect to this reference point, the potential in scala media (SM) is +80 mV and the potential inside the OHC is equal to -70 mV. As it will be shown later in this chapter, the flow of electric currents in the cochlea plays a primary role in the phenomena of power amplification and frequency selectivity, which occur in the cochlea.

4. Stria vascularis

4.1. Direct current (DC) voltage source in the cochlea

A fundamental role in the cochlear amplifier, besides the OHCs, is played by the stria vascularis, which produces a source of DC voltage between endolymph and perilymph. This potential difference, resulting from difference in ion concentrations in endolymph and perilymph, is sustained by metabolic processes occurring in the cochlea. This source of a DC voltage stores energy in the form of an electrical (potential) energy. In fact, the cochlear amplifier draws energy from the stria vascularis battery to amplify power of an incoming acoustic wave. The stria vascularis battery will play a key role in the generation of electrical signals and currents (both direct and alternating) flowing in the cochlear amplifier. In the circuit model of physical phenomena in the cochlea, the stria vascularis is represented by a (DC) voltage source, see the upper left part of **Figure 1**.

5. The cochlea as a set of nonlinear oscillators

The cochlea is characterized by tonotopic organization, i.e., its resonant properties are a function of the longitudinal position (a given stimulus frequency corresponds to a given location) and vary along the cochlea from base to apex. Structurally, the cochlea can be modeled as a series of radial sections [cochlear partitions (CPs)] starting at the base and ending at the apex. Each section of the CP is considered to be a highly resonant structure, which can vibrate preferably at only one frequency named as characteristic frequency (CF). The resonant frequency of each section of the CP is governed by the average mass, stiffness, and damping of the corresponding elements, e.g., basilar membrane, OHCs, and tectorial membrane constituting this section.

The elements responsible for the active processes occurring in the cochlea are OHCs. Manifestations of this active process are high sensitivity and frequency selectivity with respect to week stimuli, nonlinear compression of input stimuli with small and large amplitudes, and spontaneous otoacoustic emissions [14].

From a mathematical point of view, all this features are consistent with the operation of a set of nonlinear oscillators within the inner ear that are tuned to different frequencies [15].

In other words, the cochlear amplifier can be treated as a set of nonlinear electromechanical oscillators, represented by CPs with the corresponding OHCs, with the fundamental

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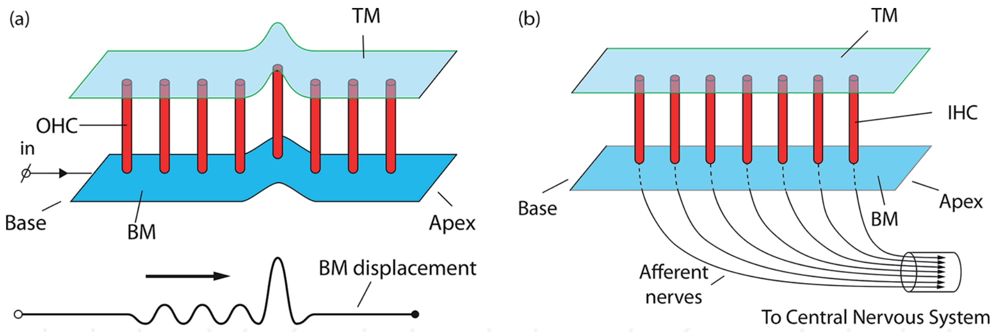

Figure 2. (a) Cochlea as a set of nonlinear oscillators (represented by OHCs), (b) a set of IHCs in the cochlea acts as a sensor. It should be noted that the OHCs and IHCs operate in a liquid environment, not air.

frequencies of vibrations extending approximately from 20 Hz to 20 kHz. The nonlinear electromechanical oscillators are stimulated to vibrations by transverse acoustic waves traveling along the basilar membrane, see **Figure 2a** and **b**.

Mechanical input signal that stimulates the wave traveling in the BM (see **Figure 2a**) represents the input acoustic signal, which reaches the inner ear through the oval window. Vibrations of the oval window excite acoustic waves in liquids (perilymph, endolymph) filling the cochlea. This wave motion in turn generates a pressure distribution that induces mechanical transverse waves propagating along the BM. This transverse acoustic (mechanical) wave traveling in the BM, when moving from base to apex, stimulates to vibrations OHCs, which rest on the BM. The OHCs which are located in the vicinity of the partition with CF (characteristic frequency) that corresponds to the frequency of the input acoustic signal are excited to oscillate.

In **Figure 2a** we can see the OHC, which is located at the area where the BM displacement is maximal. It is this OHC (with a natural frequency of, e.g., 1000 Hz) which will be excited to vibration. The vibrations of this OHC amplify deflection of BM and TM. Mechanical energy forwarded by this OHC to TM is transferred through TM to the stereocilia of the IHC (see **Figure 2b**) with a proper frequency (i.e., 1000 Hz). In this IHC, transformation of mechanical energy into electrical energy occurs, which stimulates afferent nerve endings that produce a series of electrical impulses transmitted to the central nervous system.

If the frequency of the input acoustic signal is, for example, 1000 Hz, then this wave stimulates vibrations of the oscillator with a natural frequency equaled also to 1000 Hz. These vibrations are further amplified actively in this resonant circuit, see **Figure 2a**. The resonant curve of the nonlinear oscillator can be quite narrow (high selectivity) and can be therefore characterized by a high quality factor. For weak acoustic signals, the electrical and mechanical power at the output of the oscillator may exceed many times (e.g., 500 times) the power of the input acoustic wave. In this manner, in the nonlinear (active) electromechanical oscillator (represented by the OHC), phenomena of power amplification and frequency discrimination occur.

6. State of the art

Hermann von Helmholtz was the first who created mechanical model of the cochlea in 1863 [16]. In his model the BM is represented as a system of harmonic oscillators tuned to different frequencies. In this model, the cochlea is treated as a kind of a spectrum analyzer. Next significant cochlear model was proposed by Georg von Békésy in 1928 [17]. In his model the mechanism of hearing is described in terms of the traveling wave propagating in the passive BM (*in vitro*). Position of the maximum of the wave depends on the frequency. In other words, the basilar membrane was found to be tonotopically organized: a given stimulus frequency corresponds to a given location. However, the theory of Bekesy was not able to explain the phenomenon of power amplification and frequency selectivity as well as other actual properties of the cochlea in living humans.

In 1948, Gold [5] concluded that the inner ear cannot act only passively. Only the active element can provide amplification and experimentally observed selectivity. As a model of such an element Gold introduced a valve regenerative amplifier. But these were suggestions, purely hypothetical, and not supported by any physical and physiological data. Therefore, they were not accepted at that time. Thirty years later Kemp experiments [18] concerning otoacoustic emissions and works of Davis [6] confirmed the existence of active processes in the organ of Corti. For many years, discussions continued on what is the physical mechanism of this phenomenon. It is now widely accepted that the active component is the cochlear amplifier. Still, the controversy raises a mechanism of action of this amplifier [19, 20].

7. Deficiencies of the existing models of the OHC and whole cochlea

So far the existing models (theories) of the amplification in a single outer hair cell (OHC) and the entire cochlea do not take into account all the physical phenomena experimentally observed. They are phenomenological theories, not related to actual physical (physiological) processes occurring in a single OHC and in the entire inner ear. In recent years a theory has gained popularity, which attributed the phenomenon of the cochlear amplification to Hopf bifurcations [21]. This theory, however, raised many doubts among others concerning the problem of stability [22]. Many authors of papers published very recently stated that in the theory of the cochlear amplification many unresolved problems still exist and work on it must be continued [14, 23–27].

A similar discussion applies considering electronic models of a single OHC and the entire cochlea. These models to a greater or lesser extent, describe the characteristics of a single OHC and the whole cochlea, but do not reflect their physical structure.

In conclusion, one can state that none of the existing theories of hearing explains satisfactorily the mechanism of the signal processing phenomena occurring in the cochlea.

8. Contemporary models of the cochlear amplifier

Below, we present an overview of recently developed models of operation of the OHC and the entire Cochlea.

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(1) Model presented in Ref. [21]

In this model the operation of an individual OHC is described in terms of a Hopf bifurcation. The cochlear amplifier (based on an individual OHC) has the dynamical characteristics of a Hopf bifurcation. This model can explain the nonlinear effects, selectivity, and resonance phenomena.

Critique: there is no description of power amplification, it is a purely phenomenological model, not a physical one. Electrical phenomena are not taken into account. There is no explanation of the role of ionic currents in the processes of power amplification and sharpening of the frequency characteristics.

(2) Model introduced in Ref. [28]

This model describes the resonant effects in a single OHC and the entire cochlea. The phenomenological parameters are introduced to match the theoretical and experimental curves.

Critique: there is no description of power amplification, it is a phenomenological model.

(3) Model presented in [29]

This model describes the behavior of a single OHC and the entire cochlea. The mechanical aspects of the model are characterized by using the concepts from hydrodynamics. Resonant characteristics of the cochlea are obtained by superposition of acoustic waves propagating in fluids inside the organ of Corti.

Critique: there is no description of power amplification, it is a phenomenological and a purely mechanical model. Electrical phenomena are not considered. The explanation of resonant phenomena is very complicated. To this end, an exotic concept of so-called squirting waves is employed. There is no explanation of the role of ionic currents in the processes of power amplification and sharpening of the frequency characteristics.

(4) Model introduced in Ref. [30]

This model interprets the nonlinear resonant phenomena in a single OHC in terms of a Hopf bifurcation. To obtain proper resonant curves two phenomenological parameters are introduced.

Critique: There is no description of the power amplification, this is a purely phenomenological model. There is no analysis of electrical phenomena.

(5) Model presented in Ref. [31]

This model describes acoustic, mechanical, and electrical phenomena in a single OHC and the entire cochlea. The phenomenological parameter is introduced to match the experimental and theoretical curves. Some nonlinear effects are discussed.

Critique: there is no description of power amplification. The presence of nonlinear capacitance is ignored.

(6) Model introduced in Ref. [32]

This model gives an electrical equivalent circuit of an individual OHC. Elements of an equivalent circuit have their counterparts in the actual structure of the cochlea. The model is a physical model. Nonlinear phenomena are modeled by the nonlinear stiffness and capacitance.

Critique: there is no description of power amplification. The theory is incomplete.

(7) Model presented in Ref. [33]

The model analyses the electromechanical phenomena in a single OHC using black boxes and flow chart diagrams. Amplitude responses to sine wave and random noise excitations are given.

Critique: there is no description of power amplification, this is a purely phenomenological model. No correspondence between physical elements in an actual OHC and model elements.

(8) Model introduced in Ref. [34]

This is an experimental, piezoelectric, and hydrodynamic model of the cochlea operation. Theoretical analysis is performed for motion of BM along with surrounding liquids. Resonant characteristics of the cochlea are obtained.

Critique: there is no description of power amplification, it is a phenomenological model. There is no description of ion currents flow. Nonlinear analysis is not carried out.

(9) Model presented in Ref. [35]

In this model the role of HB motility and electromotility is presented. Resonant characteristic of the cochlea are given.

Critique: there is no description of power amplification, incomplete theory.

(10) Model introduced in Ref. [36]

The model comprises finite element method analysis of the mechanical part of the cochlear partition. Electrical representation of the OHC is given. Responses of an isolated OHC to electrical stimuli are analyzed.

Critique: there is no description of power amplification, it is an incomplete theory. The presence of nonlinear capacitance is ignored.

(11) Model presented in Ref. [37]

Time domain and resonant characteristics of the cochlea are obtained by solving a set of nonlinear partial differential equations.

Critique: there is no description of power amplification, it is a phenomenological model, a purely mechanical model. Electrical phenomena are not considered.

(12) Model published in Ref. [38]

The macromechanical and micromechanical model of the cochlea is presented. Electrical model of a single OHC and the organ of Corti is given. Time domain and frequency domain analysis of electric signals in the cochlea structure is performed.

Critique: in the model there is no description of power amplification. The theory is incomplete.

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(13) Model published in [39]

The author formulated an original theory of cochlea functioning using a concept of a laser. The theory is interesting; however, it seems to be rather nonphysical.

Critique: there is no description of power amplification, incomplete theory, theory is rather qualitative.

(14) Model published in Ref. [3]

The macromechanical and micromechanical model of the cochlea is presented.

Critique: the theory is only mechanical. There is no description of power amplification. The theory is incomplete.

In summary, it is evident that the existing models of hearing processes exhibit numerous deficiencies. The physical (mechanical and electrical) processes occurring in the cochlear amplifier are not well understood.

In the following of this chapter, the author presents his new and original concepts and physical models for the phenomena of power amplification and sharp frequency tuning occurring in the cochlea.

9. Power flow in the OHC

9.1. Introduction of the concept of an electromechanical transistor

A single OHC element represents one of 20,000 active elements in the cochlear amplifier. The most important feature of the active element is its ability to amplify the power of an input acoustical signal. It is amazing that by analyzing power flow in the OHC, the author arrived to the new concept of an electromechanical transistor.

The analysis performed in this section is based on the phenomenon of forward mechano-electric transduction that occurs in the apical part of the OHC.

9.1.1. Power amplifier

Here, we will present the conditions which must be fulfilled by the system (device) to be a power amplifier. Such a system must include the following components:

1. a source of potential energy
2. a valve that controls the flow of the power from the source to the load (controlled element)
3. input circuit
4. output circuit

The principle of operation of the amplifier is based on the control of a higher output power by a lower input power. In our case, see **Figure 3a** and **b**, the low power P_{in} in the mechanical

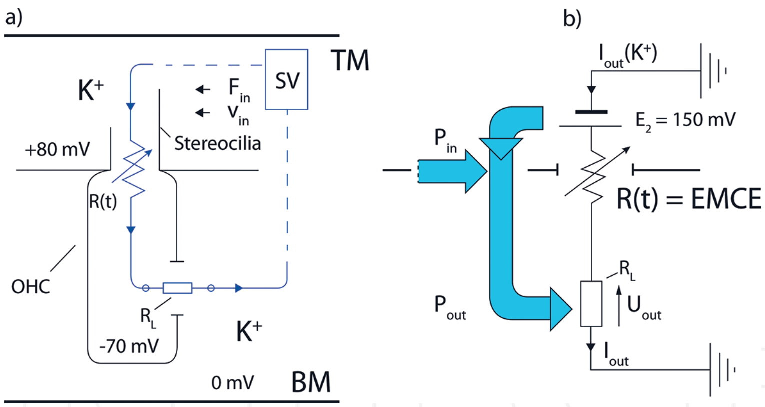

Figure 3. (a) Structure of the proposed electromechanical biological transistor, built around a single OHC. Arrows indicate the flow of K^+ ionic electric current in the electromechanical transistor (amplifier), $R(t)$ is a time-varying channel resistance, which represents the electromechanical control element (EMCE), and R_L is a load resistor. BM is the basilar membrane, TM is the tectorial membrane, and SV denotes the stria vascularis, (b) electrical equivalent circuit of the OHC's electromechanical transistor, electromotive force E_2 = 150 mV represents the difference of an endocochlear potential and intracellular potential inside the OHC.

input circuit (stereocilia of the OHC) controls the high power flow from the stria vascularis battery to the output electrical circuit, P_{out}. As it will be seen later, all of the above conditions are satisfied by the system composed of the following elements:

1. Stria vascularis
2. Stereocilia + ionic channels located in the apical part of the OHC
3. Ionic channels located in the basolateral part of the OHC

9.1.2. Electromechanical amplifier

The active electromechanical device, presented in **Figure 3a**, is composed of the initial part of the OHC and the entire amplifying tract of the cochlear amplifier that begins with BM deflection and terminates in IHC, where the amplified mechanical signal is transformed into an electrical signal stimulating the afferent nerves.

Figure 3a presents schematic view of the proposed electromechanical (biological) transistor, built around a single OHC. To illustrate the principle of operation of the new amplifying device, dimensions of channels at the upper (apical) part and in the lower (basolateral) part of the OHC in **Figure 3a** are greatly exaggerated. Operation of the channels at the apical part and at the basolateral part of the OHC is modeled by one resultant (effective) channel, i.e., one effective channel for the apical part and one effective channel for the basolateral part. The flow of potassium ions K^+ is of crucial importance for electrical phenomena occurring in the OHC. The current of potassium ions K^+, see **Figure 3a**, flows in a closed circuit starting from the stria vascularis (DC voltage source) to the body of the OHC and then back to the stria vascularis. The top apical channels play a role of a controlled (time-varying) resistance $R(t)$.

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9.1.3. Electromechanical control element (EMCE)

The time-variable resistance $R(t)$ in **Figure 3a** and **b** is controlled by a time-varying input acoustic signal, i.e., particle velocity $v(t)$ and/or mechanical force $F(t)$. As a consequence, the current flowing through the load resistance R_L varies in time unison with the changes of the input acoustic signal. This time-variable resistance $R(t)$ can be identified as an electromechanical controlled element (EMCE), see Ref. [40].

9.1.4. Load resistance

The basolateral channels in **Figure 3a** are modeled by a load resistance R_L, which represents the output power receiver. The power dissipated on the load resistance R_L is not a lost power, but in contrary constitutes a useful power, which pumps energy into the parametric electromechanical amplifier, based on the nonlinear capacitance of the OHC. This will be shown in more details in Sections 11–13 of this chapter.

Figure 3b shows an equivalent circuit model of the amplifying electromechanical device presented in **Figure 3a**. In this circuit model we can identify a source of potential energy (DC battery), an active control element (electromechanical transistor) represented by a controlled (time-varying) resistance $R(t)$, and finally a load resistance R_L.

9.1.5. Power flow in the electromechanical amplifier

Power flow in the electromechanical amplifier, based on the phenomenon of the forward mechano-electrical transduction, which is triggered by the movement of the OHC stereocilia, is as follows:

1. The electric power from the stria vascularis battery flows through ion channels in the apical part of the OHC to the body of the OHC. Then, through the interior of the OHC the electric power flows into the output circuit, where it is dissipated on the load resistance R_L.
2. The power of the input signal is transmitted to the control circuit formed by the stereocilia of the OHC. The amount of power from the stria vascularis battery, which flows to the output circuit, depends on the power level of the input control signal.
3. The signal in the output electric circuit varies in time synchronously with changes of the input acoustic signal in the control circuit. The signal in the output circuit reproduces the characteristics of the input signal. However, the power of the signal in the output circuit can surpass many times the power of the input control signal. Thus, power amplification phenomenon takes place.

The physical foundation of operation of the proposed electromechanical transistor is the phenomenon of forward mechano-electrical transduction, taking place in the apical part of the OHCs (stereocilia + ion channels).

9.1.6. Input and output circuits

The input circuit of the proposed electromechanical transistor is a mechanical circuit consisting of the OHC's stereocilia. Input control signal is the particle velocity and/or the mechanical force exerted on the stereocilia. The output circuit is an electrical circuit, see **Figure 3a** and **b**. Electrical output controlled signal is the current and/or the voltage across the load resistance R_L. The electric circuit in **Figure 3a** and **b** closes through the structures lying outside the OHC (back to the stria vascularis).

9.1.7. Electromechanical transistor (EMT)

The electromechanical amplifying system in **Figure 3a** and **b** satisfies four necessary conditions for power gain to occur, namely:

1. There is a source of potential energy (voltage source E_2).
2. There is a device (electromechanical controlled element – electromechanical transistor) to control the flow of energy from the voltage source E_2 to the load resistance R_L, i.e., $EMCE = R(t)$. The value of the resistance $R(t)$ is controlled by the input mechanical (acoustical) signal (velocity and/or force). Ion channels in the apical part of the OHC play the role of the controlled resistance $R(t)$.
3. There is a mechanical control input circuit (stereocilia of the OHC).
4. There is an electric controlled output circuit (ion channels in the basolateral part of the OHC).

Thus, this electromechanical controlled element $EMCE = R(t)$ represents an electromechanical transistor. This transistor is a close analog of the electronic unipolar field effect transistor (FET), see **Figure 4a** and **b**.

9.2. Analogy between the proposed EMT type transistor and the FET type transistor

The proposed electromechanical transistor is analogous to the classical field effect transistor (FET). Certainly, the proposed electromechanical transistor resembles also a vacuum tube or a bipolar transistor, but according to the author, similarity in this case is less direct (explicit). This is due to the following reasons:

a. In the proposed electromechanical transistor, similarly as in the field effect transistor (FET), the process of electric current conduction involves only monopolar carriers of the same sign. Therefore, like in case of the classical FET electronic transistor, the electromechanical transistor is a "unipolar" transistor, since the process of current conduction in the electromechanical transistor employs only positive potassium cations K^+.

b. In the proposed electromechanical transistor, similarly as in the FET transistor, channel resistance is modulated. These channels exist physically in the structure of the OHC, i.e., they have definite dimensions, spatial positions, and play the role of the controlled resistor $R(t)$.

c. In case of the FET transistor, the channel is formed in the semiconductor material, which is sandwiched between two electrodes (source and drain). Resistance of this channel is modulated by changing voltage applied to the gate. This results in a change of channel's cross-section and its conductivity.

d. In case of the electromechanical transistor (EMT), the role of the channel is played by ion channels existing in the apical part of the OHC. Their resistance $R(t)$ varies depending on the degree of opening or closing of the channels (deviation of stereocilia). This resistance exists physically and could be measured using an ohmmeter. The resistance $R(t)$ is modulated by an input acoustic (mechanical) signal reaching OHC.

e. By contrast, the resistance which is modulated in the vacuum tube or in the bipolar transistor is rather an effective resistance (a phenomenological concept). This resistance is not located in a definite site. For example, in the vacuum tube (triode), the resistance which is modulated by the grid voltage is an apparent resistance of the region distributed between the cathode and anode.

Therefore, we can state that the proposed electromechanical transistor is a close analog of the classical electronic field effect transistor (FET), see **Table 1**.

The principle of operation of the proposed EMT transistor and the classical FET transistor is presented below in **Figure 4**.

Transistor type	**EMT**	**FET**
Carrier type	K^+ ions	Electrons or holes
Input circuit	Stereocilia (mechanical circuit)	Gate + input source (electrical circuit)
Output circuit	OHC walls + ionic channels in the basolateral part of the OHC	Drain + load resistance R_L
Channel type	Ionic channels in the apical part of the OHC	Semiconductor channel
Controlled element	Variable resistance $R(t)$ of the ion channels in the apical part of the OHC	Variable resistance $R(t)$ of a semiconductor channel
Mechanism changing channel resistance	Deflection of stereocilia	Change of the gate voltage
Power amplification	Yes	Yes

Table 1. Comparison of the features of the electromechanical transistor (EMT) and the field effect transistor (FET).

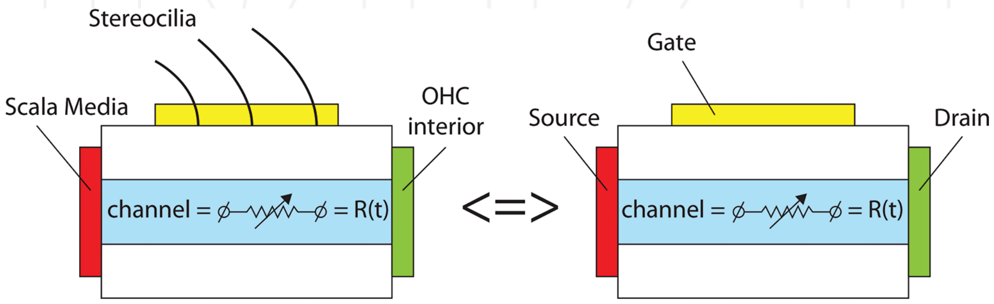

Figure 4. Physical models of (a) proposed electromechanical transistor EMT, and (b) classical field effect transistor FET.

It is not surprising that the structures of both transistors presented in **Figure 4a** and **b** are almost identical. In case of the proposed EMT transistor, movement of the stereocilia modulates the conductivity of ion channels. On the other hand, in the classical FET transistor, the voltage applied to the gate modulates the conductivity of the semiconductor channel. Thus, the proposed EMT transistor and classical FET transistors are controlled, correspondingly, by mechanical and electrical signals.

The channels in the EMT and FET transistors exist physically and can be modeled by a time-varying resistance $R(t)$. It is worth noticing that the transistor itself does not generate any energy. In fact, its essential function is to control (according to changes in the input modulating signal) the flow of energy from an external "high" energy source (such as a DC voltage battery) into the output circuit (load resistance).

9.3. Small signal linearized electric equivalent circuit of the EMT

Operation of the proposed EMT transistor can be presented in the form of an equivalent electrical circuit.

9.3.1. Small-signal electrical equivalent circuit

The input circuit of the proposed electromechanical transistor EMT is represented by two mechanical quantities, i.e., the velocity v_1 and mechanical force F_1 on the cilia. The output circuit of the proposed electromechanical transistor EMT is represented by two electrical quantities, i.e., output voltage U_2 and current I_2. In general, the relationships between $(F_1, \; v_1)$ and $(U_2, \; I_2)$ are described by complex nonlinear functions. However, for small signal amplitudes, the link between $(F_1, \; v_1)$ and $(U_2, \; I_2)$ can be linearized, i.e., described by linear functions framed in a matrix form.

Classical circuit theory allows modeling of the transistor in the form of an equivalent circuit composed of passive admittances and active current sources. In this way, instead of investigating a large number of complex 3D physical phenomena occurring in the actual spatial structure of the transistor, operation of the transistor can be satisfactorily described using a combinations of lumped circuit elements, such as admittances and controlled sources. The resulting circuit constitutes a small-signal equivalent circuit of the transistor. Influence of these elements on the operation of the transistor can be calculated by applying the laws of the current flow, known from the classical circuit theory [12].

Figure 5 shows small signal equivalent circuit of the proposed electromechanical transistor for small values of the output AC electric signals (voltage and current) and input mechanical signals (velocity and force on stereocilia).

The matrix equation linking together the input mechanical and output electrical signals in **Figure 5** can be presented using the concept of a hybrid matrix $[h]$, as follows:

$$\begin{bmatrix} F_1 \\ I_2 \end{bmatrix} = \begin{bmatrix} h_{11} & h_{12} \\ h_{21} & h_{22} \end{bmatrix} \cdot \begin{bmatrix} v_1 \\ U_2 \end{bmatrix} = \begin{bmatrix} Z_{in} & 0 \\ g_{em} & g_{22} \end{bmatrix} \cdot \begin{bmatrix} v_1 \\ U_2 \end{bmatrix} \qquad (1)$$

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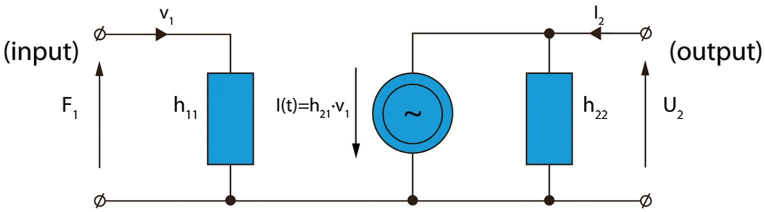

Figure 5. Linearized electromechanical equivalent circuit of the electromechanical transistor that uses a phenomenon of forward mechano-electric transduction occurring in the apical part of an OHC (hair bundles + ionic channels).

The elements of the matrix [*h*] have the following physical interpretation:

$h_{11} = Z_{in}$ is a mechanical input impedance,

$h_{22} = g_{22}$ is an electrical output conductance, and

$h_{21} = g_{em}$ is a coefficient of electromechanical transduction.

9.3.2. Occurrence of the alternating currents (AC) in the cochlea

In Sections 3 and 4 of this chapter, we found that (DC) voltages and currents are present in the cochlear structure. In the following, the problem of occurrence in the structure of the cochlea (AC) voltages and currents will be analyzed in more detail.

From the analysis presented formerly by the author it follows that the transistor effect (based on the phenomenon of forward mechano-electric transduction) generates alternating electric current (AC) in the cochlea. This current is represented in **Figure 5** by an active current source.

This analysis can serve as a theoretical description of the (AC) voltages and currents in the structure of the cochlea. These (AC) voltage and current sources are produced in the circuit: DC voltage source + time variable resistance $R(t)$, see **Figure 3b**.

The output circuit has the properties of the controlled current source. Output current I_2 is generated by the controlled current source $I(t) = h_{21} v_1(t)$, which depends linearly on the input velocity $v_1(t)$. This is a characteristic feature of active elements (in this case electromechanical transistors).

As it will be presented later, the controlled (AC) current source, shown in **Figure 5**, will act as the electrical signal that pumps energy into the parametric amplifier established on the basis of the nonlinear capacitance of the OHC, see **Figure 7**. More details concerning the operation of this electromechanical transistor can be found in the work of the author [40].

9.3.3. Otoacoustic emission

Discovered in 1978, phenomenon of otoacoustic emission (OAE) relies on the generation of sound waves in the inner ear. Acoustic waves generated in this way travel into the middle and outer ear [41, 42]. To explain the phenomenon of the OAE, we can examine the properties of the active elements constituting the cochlear amplifier, which in certain conditions can produce sustained “undamped” vibrations. The active elements in the cochlear amplifier, such as the proposed electromechanical transistors and parametric amplifiers based on the nonlinear capacitance of the OHC, can be responsible for the generation of periodic self-sustaining vibrations in the inner ear. Under certain conditions any amplifying element can become a generator.

Generation of the OAE signals in the OHCs occurs on the electric side. Subsequently, these signals through the inverse piezoelectric effect are transformed on the mechanical side. These mechanical (acoustic) signals leave the inner ear and can be received in the outer ear. The occurrence of the OAE phenomenon is an evidence that active processes in the cochlea do exist. The measurement of the OAE is now routinely employed for the detection of hearing impairment in newborns (in newborn hearing screening).

The phenomenon of the OAE can be treated as a side effect of operation of the cochlear amplifier.

10. Nonlinear capacitance of the OHC

Between the inner and outer cell membrane of the OHC, there is a linear (static) capacitance and nonlinear capacitance. The linear capacitance has a constant value (~30 pF), which does not depend on the applied voltage u. The nonlinear capacitance $C(u)$ depends on the voltage applied between the inner and outer wall of the OHC. The shape of this function resembles a bell curve, with a maximum value of approximately 25 pF. It is assumed that the nonlinear capacitance $C(u)$ is produced by the movement of confined charges in walls of the OHC.

This nonlinear capacitance of the OHC $C(u)$ will be used as an active element in the proposed parametric cochlear amplifier based on a single OHC. In classical electronics, nonlinear voltage-dependent capacitance is called “varactor.” By driving a nonlinear capacitance $C(u)$ with a the time-dependent voltage $u(t)$, we obtain the capacitance $C(t)$ which is a function of time.

11. Parametric-piezoelectric model of the cochlear amplifier

In general, parametric amplification can be achieved in a resonant circuit, when one of its reactive elements (capacitance $C(t)$ or inductance $L(t)$, see **Figure 6**) changes in time. The variations of $C(t)$ and $L(t)$ will supply energy to the resonant circuit.

Figure 6 shows the layout of a serial (electrical) resonance circuit whose capacitance $C(t)$, formed by two parallel plates, varies sinusoidally in time. The capacitance of this planar capacitor is modulated by moving up and down the upper plate of the capacitor. Here, the lower plate of the capacitor is fixed. Setting the upper plate of the capacitor into motion requires an additional external source of energy, which is called the pumping source (pump).

In the circuit of the electronic parametric amplifier (where the variable in time capacitance $C(t)$ is the varactor), this external energy is delivered from an electrical (AC) pumping signal

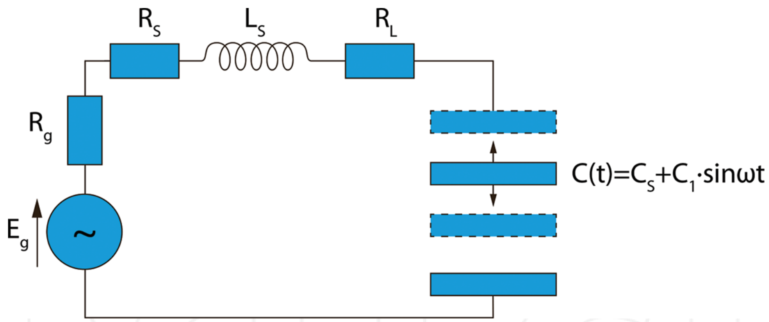

Figure 6. Illustration of the idea of a parametric amplifier that uses a time-variable capacitance $C(t)$. The inductor L_s = const.

source of appropriate frequency, in relation to the frequency of the input signal E_g. Nonlinear (variable in time) capacitance (varactor) transfers energy from the pump circuit into the input signal circuit (R_s, L_s, C_s). In this way the energy (power) of the input signal (represented by E_g) is amplified and dissipated on the load resistance R_L. At the same time, sharpening of the frequency characteristics (resonance curve) of the parametric amplifier occurs. These are characteristic features of the parametric amplifier.

11.1. Proposed parametric: piezoelectric model of the OHC

A new physical (parametric-piezoelectric) model of the OHC cochlear amplifier was proposed by the author in 2013 [43]. This model explains the mechanisms of power amplification and frequency selectivity that occur in the cochlear amplifier. The proposed model is a direct consequence of the idea of Gold. In the following a physical interpretation of the active element is given. The active element is related to specific physical (physiological) components of the cochlea. The model proposed by the author removes most of the deficiencies of the existing models, presented in Sections 6–8.

Below, the proposed parametric amplifier model of the cochlea will be briefly described.

One OHC element is represented by a piezoelectric tube, see **Figure 7**. The left side of the OHC shown in **Figure 7** is the region of the OHC adjacent to the basilar membrane (BM). The right side of the OHC in **Figure 7** displays the apical part of the OHC in the vicinity of tectorial membrane (TM). Nonlinear capacitance $C(u)$ between the inner and the outer wall of the OHC is a key component of the proposed cochlear parametric amplifier.

11.2. Operation of the proposed OHC parametric-piezoelectric amplifier

Force source $F(t)$, on the left side of **Figure 7**, represents an input acoustic signal, which acts on the OHC from the BM side. Through the direct piezoelectric effect this force source $F(t)$ is transformed into the electric side as an alternating current (AC) voltage or current source. The cylinder, which represents the structure of the OHC exhibits piezoelectric properties. On the right side of **Figure 7**, one can see OHC stereocilia located at the apical part of the

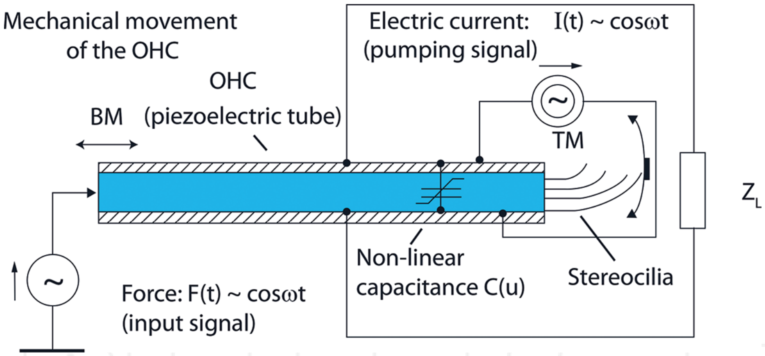

Figure 7. Simplified electromechanical diagram of a single OHC operating as a parametric amplifier. $F(t)$ represents the input acoustic signal, Z_L is the electrical load impedance, $C(u)$ is the nonlinear capacitance of the OHC, and u is the voltage between the inner and outer walls of the OHC.

OHC. Movement of stereocilia causes the flow of ionic currents (through the ion channels) into the bulk of the OHC. Taking place here, the phenomenon of forward mechano-electric transduction produces a transistor effect. As shown in **Figure 5**, the operation of the electromechanical transistor generates an alternating current source (AC). This variable current source $I(t)$, which is also visible at the top right in **Figure 7**, acts as a pumping signal that pumps power to the nonlinear capacitance of the OHC $C(u)$, which is visible on the right side of **Figure 7**.

This nonlinear capacitance $C(u)$ operates in a parametric amplifier circuit. Transformed, on the electric side, the input acoustic signal is amplified in this parametric amplifier circuit. Apart from the power amplification, the phenomenon of the sound sharpening (sharp tuning) occurs here. This enhanced (on the electrical side) acoustic input signal is subsequently transformed into the mechanical side (inverse piezoelectric effect), where it performs useful work on the TM and BM. The work carried out on the mechanical side represents, on the electrical side, the power that dissipates in the output circuit on the load resistance R_L. The electric power which is dissipated on the resistance R_L is not a lost power, i.e., it is not transformed to heat. On the contrary, this is the useful power that represents the amplified (on the electrical side) power of the input acoustic signal.

Sequence of the physical phenomena that occur in an individual OHC is as follows:

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

2. The movement of BM acts on a corresponding OHC and causes its motion with respect to TM. As a consequence, deflection of the OHC stereocilia occurs, which triggers operation of the proposed electromechanical transistor. In this stage, the transformation of mechanical energy into electric energy occurs.

3. Subsequently, nonlinear capacitance of the OHC is charged (pumped) by an AC current source $I(t) \sim \cos\omega t$, generated at the output of the proposed electromechanical amplifier

(EMT transistor). In fact, in the EMT transistor, the changes in the mechanical deflection of stereocilia are transformed to changes in the channel conductance and consequently to changes in the ion channel current (K^+ ions) flow, see **Figures 3a**, **b** and **4**. Power to the nonlinear capacitance $C(u)$ is supplied by an AC electric pump signal represented by the variable current source $I(t)$. The mechanism of power gain in the EMT transistor is similar to that occurring in the electronic field effect transistor, with a modulated channel conductance [40].

4. The input driving signal is an acoustic (mechanical) signal (represented by the force $F(t)$ and/or velocity $v(t)$) acting on the piezoelectric tube (OHC) from the basilar membrane (BM) side (see left side of **Figure 7**). Through the direct piezoelectric effect, this input (acoustic) mechanical signal is transferred to the electrical side as a voltage source $E(t)$ and then is amplified in the parametric amplifier based on a nonlinear capacitance $C(u)$. Power to the nonlinear capacitance is supplied by an AC electric pump signal represented by a variable current source $I(t)$.

5. The electric signal amplified at the output of the proposed parametric amplifier is dissipated (performs useful work) at the electrical load impedance Z_L. The output electrical signal is then transferred to the mechanical side by an inverse piezoelectric effect.

6. The output useful signal from the OHC amplifier is therefore a mechanical signal (force, velocity, or displacement) acting on the basilar membrane (BM) and tectorial membrane (TM) and as a consequence on stereocilia of the inner hair cells (IHCs). Finally, IHCs sensors transform mechanical signals into electrical signals (electric pulse trains) in afferent nerves connected to the central nervous system.

The power of the output mechanical signal in the OHC amplifier can surpass many times the power of an input acoustic signal. Since the parametric amplifier is a highly selective system, it can get a very narrow frequency characteristic (sharp tuning). More details concerning the operation of the proposed cochlear parametric amplifier can be found in the author's paper [43].

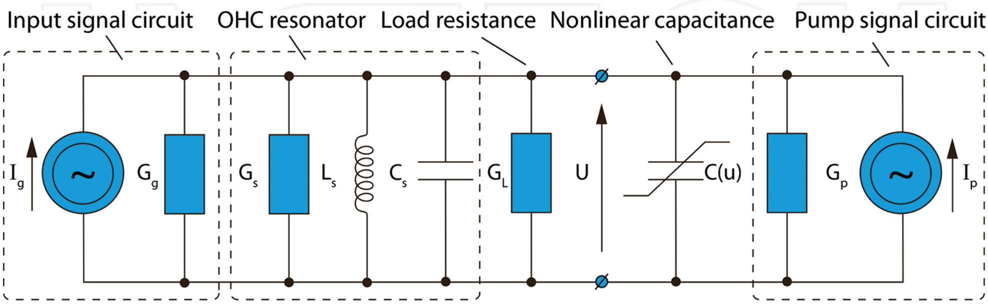

Figure 8. Nonlinear electrical equivalent (Norton) circuit of the proposed parametric cochlear amplifier built around a single OHC. $I\,g$ is the input signal current source, $G\,g$ is the source conductance, G_L is the load conductance, G_S is the loss conductance, L_s is the inductance of the OHC's resonator, $C(u)$ is the nonlinear capacitance, $I\,p$ is the pumping current source, and $G\,p$ is the pumping source conductance.

11.3. Nonlinear Norton equivalent circuit of the proposed parametric cochlear amplifier

The operation of a nonlinear oscillator resulting from the proposed model of the parametric cochlear amplifier can be described using the concept of a parallel (Norton) electrical equivalent circuit, see **Figure 8**.

The input electric signal, represented by the current source I_g with an admittance G_g (see left side of **Figure 8**), corresponds to the input acoustic signal transformed into electrical side by the direct piezoelectric effect. The input electrical signal I_g is subsequently amplified in the proposed parametric amplifier (formed with the nonlinear capacitance $C(u)$). The electric power is supplied to the circuit by the pumping current source I_p, which is generated by the forward mechano-electric transduction effect (see right side of **Figure 8**). After amplification, the electric signal is dissipated at the output load conductance G_L. The dissipated power is a useful output power of the proposed parametric amplifier.

It is noteworthy that mathematical description of the operation of the electrical circuit presented in **Figure 8** is a nonlinear ordinary differential equation of the second order. This equation results from Kirchhoff's laws applied to the circuit in **Figure 8**. The solution of this nonlinear equation describes nonlinear properties of the OHC amplifier for an arbitrary level of signals (small and large). For low-level signals, the solution of this equation should display an enhanced value of the quality factor and therefore higher value of amplification of the input signal.

11.4. Negative conductance

To explain the power amplification phenomenon in the parametric amplifier the concept of negative conductance was introduced. Negative conductance $-G_a$ occurs in parallel to the nonlinear capacitance $C(u)$ that represents an active element in the parametric amplifier. Positive conductance (resistance) dissipates electric power. By contrast, negative conductance supplies energy to the circuit. The negative conductance represents energy transfer from an external source to the circuit of the resonator, thereby the reduction of attenuation (undamping) of the resonant circuit occurs. In this way, the negative conductance characterizes an active element in the parametric amplifier circuit (e.g., the nonlinear capacitance of the OHC). The resultant conductance of the parallel OHC resonant circuit decreases ($G = G_s - G_a$) which increases the quality factor of the resonant circuit, see right side of **Figure 9**. As a result, a sharpening of the resonance curve of the resonant circuit occurs. This leads to higher sensitivity and selectivity

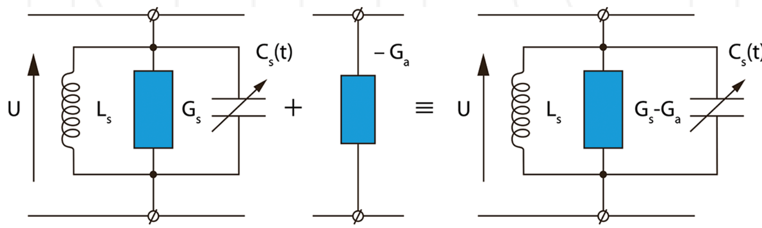

Figure 9. Operation of the active element, based on the nonlinear (time-varying) capacitance of an OHC, produces a negative conductance $-G_a$, which reduces the loss of the OHC resonant circuit and increases its quality factor.

(i.e., the ability to distinguish two tones with nearly the same frequencies, e.g., 1000 and 1005 Hz) of the proposed cochlear amplifier, as well as its power gain.

It is known from the classical circuit theory that parametric effect introduces an effective negative conductance (resistance) to the resonant parametric circuit, see **Figure 9**.

In summary, electromechanical parametric amplifier built with 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 cochlear amplifier (larger quality factor Q), and
4. improves the sensitivity of the OHC's cochlear amplifier.

12. Interplay between HB motility and electromotility in the OHC

In previous theories of the cochlear amplification and selectivity sharpening the following hypotheses, about which type of motility is the prime mechanism of operation, were considered:

1. In active processes of power gain and sharpening of frequency selectivity involved is only HB motility.
2. In active processes of power gain and sharpening of frequency selectivity involved is only electromotility.
3. Both HB motility and electromotility are necessary for the operation the cochlear amplifier.

From the theoretical analysis performed by the author it follows that the correct choice is the third hypothesis, i.e., both mechanisms (HB motility and electromotility) are necessary to provide high sensitivity and sharp frequency selectivity in the mammalian cochlea. HB motility and electromotility in isolation cannot provide simultaneously power amplification and selectivity sharpening.

13. Role of the electrical phenomena

Remarkable properties of the hearing human organ (cochlea) are due to the presence in the cochlea of the sensory hair cells, i.e., OHCs and IHCs.

Electrical and mechanical phenomena occurring in the cochlea are mutually coupled. It is amazing that the flow of ionic currents (e.g., K^+ ions) in the cochlea is governed by the same laws as the flow of electric currents in conventional electronic circuits (i.e., Ohm's and the Kirchhoff's laws). Therefore, it was possible to establish an equivalent electrical circuit for the cochlear amplifier. Moreover, to model the operation of the cochlea (cochlear amplifier) we can employ elements well-known in the classical circuit theory, such as resistors, capacitors, inductors, voltage sources, and current sources both direct current (DC) and also alternating current (AC). In fact, the capacitors, inductors, and resistors in the equivalent electrical circuit of the cochlear amplifier are built of biological materials. In addition, these elements in the electrical equivalent circuit of the cochlear amplifier are lumped elements.

As it was shown in previous sections the role of electrical phenomena in the hearing process is enormous, since signal processing, power amplification, and frequency selectivity takes place on the electric side of the cochlear amplifier. The energy necessary to amplify the power of an input acoustic signal is drawn from the stria vascularis (DC voltage battery). Power amplification occurs in a circuit that consists of the following elements: input electromechanical transistor (formed by hair bundle stereocilia and ion channels), body of the OHC, and stria vascularis.

The fundamental element of the proposed cochlear amplifier is a parametric amplifier using the nonlinear capacitance of the OHC and its piezoelectric effect. The cochlear parametric amplifier is pumped by an electrical current source formed by ionic currents triggered by deflection of stereocilia (input electromechanical transistor). In the cochlear amplifier, a DC electric power is converted to an AC electric power. Moreover, the transformation of electrical to mechanical energy and vice versa occurs due to direct and inverse piezoelectric effect. In this parametric amplifier the sharpening of frequency selectivity occurs.

Operation of the cochlear amplifier can be compared to the operation of an "old fashioned" analog "straight" radio receiver (i.e., a receiver with a direct amplification, without frequency mixing). In a classical analog transistor, "straight" radio receiver, one can enumerate the following elements:

1. antenna,
2. selective amplifier,
3. detector,
4. power amplifier, and
5. loudspeaker.

Similar elements and associated processes can be found in the human cochlea. Namely, the role of the antenna in the cochlea is played by the outer ear and middle ear, the role of the selective and power amplifier is played by the cochlear amplifier, and the main components of the cochlear amplifier are OHCs. The role of loudspeaker is played by afferent nerves endings.

13.1. Novelty of the proposed parametric-piezoelectric model

Novelty of the model proposed by the author relies on the use of well-known electronics idea of parametric amplification. Exploration of this concept was motivated by the existence in the actual structure of the cochlea and the nonlinear electrical capacitance of the OHC. It is worth noticing that in existing models of the cochlear amplifier, the presence of nonlinear capacitance is ignored.

The model proposed by the author is able to explain in a logical, natural, and complete way the following so far unresolved physical processes occurring in the cochlear amplifier: (1) power amplification, (2) selectivity of acoustic signals reception, and (3) nonlinear phenomena.

13.2. Physical (physiological) model

The model proposed by the author is a physical and a not phenomenological model. The main element of the model is the parametric amplifier providing adequate gain, sensitivity, frequency selectivity, and dynamics. Elements of the model are uniquely linked to the actual physical (physiological) components that are present in a single OHC and in the entire cochlea. Moreover, these elements are directly related 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 membrane, nonlinear effects, generation of electrical potentials by metabolic processes in the stria vascularis, etc.). The model is internally coherent, consistent with experimental data published in the literature and it describes comprehensibly (qualitatively and quantitatively) the phenomena of the cochlear amplification.

13.3. Results of numerical simulations with the new model

The results of numerical calculations (simulations) with the new model have been presented previously by the author in his two former papers [40, 43]. Here, we will repeat briefly some results showing increased frequency selectivity due to the parametric effect occurring in the OHC parametric amplifier.

Applying the Kirchhoff's laws to the linearized equivalent circuits (series and parallel), describing the operation of the parametric amplifier built around a single OHC, gives rise to linear ordinary differential equations of the Mathieu and Ince types [43]. The resulting differential equations of the second order with variable in time coefficients were solved numerically (for various values of frequency) using a Scilab software package. In the numerical simulations the resonant frequency of the resonant circuit (OHC oscillator) was assumed as $f_0 = 1000$ Hz.

The following values of the parameters of the equivalent (parallel Norton) circuit were applied:

1. Conductance of the input signal source G_g, conductance of the resonant circuit G_s, and the load conductance G_L are in the range from 7.5 to 23 nS.
2. The linear capacitance of the OHC is about 30 pF. Maximum of the nonlinear capacitance is 25 pF.
3. The value of the input signal current source is $I_g = 30$ pA.

The above numerical values of the elements of the equivalent circuit are compatible with the physiological data [8, 24, 35, 44–46].

The results of numerical calculations with the Scilab package show that using the above parameters, the parametric effect increases the quality factor of the OHC resonator from $Q = 12$ to $Q = 120$ (10 times). It is noteworthy that the passive OHC resonator with the quality factor 12 has an effective frequency bandwidth of 80 Hz (8%), for example, from 960 to 1040 Hz. On the other hand, the active OHC resonator with the quality factor 120 has an effective frequency bandwidth of 8 Hz (0.8%), for example, from 996 to 1004 Hz. The latter case represents a remarkable frequency selectivity (0.8%) enabling for frequency discrimination much narrower than one semitone in modern musical scales (6%).

13.4. Consequences resulting from the author's model

1. Power amplification of the acoustic signal occurs in the circuit of the input electromechanical transistor formed by stereocilia of an outer hair cell (OHC), ion channels, bulk of the OHC, and the stria vascularis. Selectivity of the reception of acoustic signals is realized by a parametric amplifier based on the nonlinear capacitance of the OHC and the piezoelectric phenomenon.

2. Electromechanical transistor (based on the forward mechano-electric transduction) supplies (pumps) the power to the nonlinear capacitance (parametric amplifier), producing a negative resistance in the resonant circuit.

3. The parametric amplifier is realized with a reactive element (nonlinear capacitance), not on a resistive element (like laser amplifier or tunnel diode amplifier). It is worth noticing that a source of noise is mostly resistive elements. From that reason, the parametric amplifier exhibits a very good noise characteristics.

4. By the inverse piezoelectric effect (electromotility), amplified acoustic (on electric side) signal is transformed into the mechanical side where it stimulates the tectorial membrane (TM).

5. Both mechanisms (HB-motility and electromotility) must operate simultaneously in order to achieve the power amplification and selectivity in the cochlear amplifier.

6. TM stimulates mechanically stereocilia of the IHC. Thus, the mechanical energy from the TM is delivered to the IHC stereocilia and transformed by the IHC into electrical ion currents. These currents excite the afferent nerves, which generate a series of electrical impulses that are transmitted into the central nervous system.

14. Conclusions

The new theory of the hearing processes, proposed by the author, links together the concepts emerged in former theories of hearing, such as a resonant theory, travelling wave theory, and Gold's theory of active amplification (cochlear amplifier). The new model of the phenomena occurring in the cochlea is a physical (physiological) model (not phenomenological), in which the role and operation of individual elements of the actual cochlea are explained qualitatively and quantitatively.

To initiate the research on the mechanism of hearing the author was motivated by incompleteness of the existing models of the hearing process. In fact, the existing theories of hearing are phenomenological in nature and do not directly correspond to the physical components in the

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cochlea. Another stimulus was a potential importance for various possible applications, such as hearing aids, digital sound coding, perception of music, etc.

Full physical model of the cochlea is described mathematically by nonlinear ordinary differential equations (ODE). Linearized physical model of the cochlea is described by linear ODE of Mathieu and Ince's type. In the established model of the cochlea new concepts from electronics (e.g., parametric amplification and electromechanical transistor) are applied. This goes significantly beyond the range of methods and concepts used so far in the existing theories of the hearing.

The model proposed by the author explains the process of power amplification and frequency selectivity that take place in the cochlear amplifier. By contrast, existing models of the cochlear amplifier are incomplete and do not describe satisfactorily the physical processes that occur in the organ of Corti. Furthermore, in scope of the author's model, the phenomenon of an otoacoustic emission can be described.

The new model of a single OHC, developed by the author, conforms qualitatively to the existing experimental data. A novel refined theory of the hearing processes, based on the piezoelectricity and parametric amplification, can open new horizons for research including deeper understanding of the physical phenomena underlying auditory processes, new phenomena in musical and speech acoustics, etc. This may create a possibility to design new musical instruments as well as new audio codecs that could outperform the existing MP3 codecs.

The author hopes that the results of this study (which relate to the validity of crucial electrical phenomena occurring in the cochlea) can also be useful in the construction and design of a new generation of hearing aids. Today, most hearing aids are based on power amplification of the input audio signals at specific frequencies without increasing the selectivity (the ability to distinguish between signals of different frequencies).

Therefore, the future hearing aids should be more closely based on the knowledge of complicated electrical and mechanical phenomena occurring in the cochlea. In these devices, in addition to the power amplification of the input acoustic signal, adequate selectivity of acoustic signal reception (sharpening of the receiving characteristics of the receiver—the cochlear amplifier) should also be ensured.

Glossary of technical terms	
Acoustic waves	Pressure disturbances propagating in gases, liquids, and solids. Acoustic waves rarely propagate along straight lines, but can be easily reflected, refracted, diffracted, or guided
AC signal	A signal which is variable in time
Active element	An element, which can deliver more (useful) active energy than it consumes
Admittance	An element, defined as the inverse of impedance. Electrical admittance is a measure of how readily the circuit or device allows a current to flow
Actuator	A component of a device which is responsible for moving or controlling a mechanism or system

Glossary of technical terms	
Ampere (A)	The SI unit of electric current intensity. If the current flowing through a cross-section of a conductor has intensity of 1 A, then within 1 s the charge of 1 C flows through this cross-section, namely: 1 A = 1 C/s, where C stands for the coulomb and s for the second
Anions	Negatively charged ions
Bandwidth	A difference between the maximum and minimum frequencies handled by a device
Bipolar transistor	A transistor that uses both negative electrons and positive holes, in contrast to unipolar FET transistors
Capacitor	A passive electrical element, which can store electrical energy. Capacitance of the capacitor is measured in farads (F) to honor English scientist M. Faraday (1791–1867). 1 F = 1 C/1 V, where C stands for the coulomb and V for the volt. Typical capacitance may vary from about 1 pF (10^{-12} F) to about 1 mF (10^{-3} F)
Cations	Positively charged ions
Charge	A measure of the amount of electricity. The electric charge is measured in coulombs to honor French physicist C.A. Coulomb (1736–1806). 1 C = 1 As, where A stands for the ampere and s is the second. There are positive and negative charges. The electric charge is a discrete quantity. The smallest electric charge is carried by the electron. An electron has a charge equal $1e = 1.602 \times 10^{-19}$ coulombs
Circuit theory	A set of techniques, definitions, and mathematical tools used to describe the flow of currents and voltage distribution in electrical networks composed of lumped passive and active elements. The theory includes Ohm's law, Kirchhoff's laws, and theorems (Thévenin, Norton), which are based on first physical principles, such as conservation of energy, conservation of electrical charge, etc.
Conductance	A resistive electrical element defined as an inverse to the electrical resistance
Coulomb (C)	The SI unit of electric charge, defined as the charge carried by a constant current of intensity of 1 A that passes through a cross-section of a conductor in one second. Therefore, charge $Q = It$, where I is the current and t is time
Current source	An active electrical element providing DC or AC electric current on its terminals
DC battery	A source of potential electrical energy
DC signal	A signal, which is constant in time
Decibel (dB)	A logarithmic unit used to express the ratio of two values of a physical quantity. For example, the device dynamics, measured in dB, equals 10 $\log_{10}(P_2/P_1)$, where P_2 and P_1 correspond, respectively, to the maximum and minimum input power, which can be properly handled by the device
Differential equation	An equation for an unknown function, e.g., $y(t)$ containing sum of derivatives up to a certain order. For example, a differential equation describing harmonic oscillations contains derivatives up to order two

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Glossary of technical terms	
Direct piezoelectric effect	A generation of net electrical charges (voltage) in the material subjected to a mechanical stress (direct piezoelectric effect). Direct piezoelectric effect was discovered in 1880 by French physicists brothers Jacques (1855–1941) and Pierre (1859–1906) Currie
Dynamic range (dynamics)	The ratio P_2/P_1 of the maximum P_2 and minimum power P_1 of the input signal, which can be handled properly by the device. Dynamics is often expressed in a logarithmic scale in dB as $10\log(P_2/P_1)$. If power density $P_2 = 1\ \mathrm{W/m^2}$ and $P_1 = 10^{-6}\ \mathrm{W/m^2}$ then the dynamics equals $10\log(1/10^{-6}) = 60$ dB
Equivalent circuit	An electrical circuit with lumped elements, providing precise, but often simplified description of complex phenomena occurring in a physical device or system
Electric current	A stream of electrically charged particles flowing in a medium. The intensity of the electric current is measured in amperes (A) to honor French physicist A.M. Ampère (1775–1836). 1 A = 1 C/s, where C stands for the coulomb and s for the second
Electrical impedance	The ratio of the voltage applied to an electrical element (capacitor, resistor, inductor) to the electrical current flowing through the element. Electrical impedance is measured in Ohms (Ω) to honor German physicist G.S. Ohm (1789–1854). 1 Ω = 1 V/1 A, where V stands for the volt and A for the ampere
Electrical side	The electrical port of a multiport electromechanical device + an electric circuit connected to this port
Electrolyte	A substance that produces an electrically conducting solution, when dissolved in a polar solvent, such as water. The dissolved electrolyte separates into positively charged cations and negative anions
Electromechanical control element (EMCE)	A time variable electrical resistance $R(t)$ controlled by a time-varying input mechanical (e.g., acoustic) signals
Electromechanical transistor	A device to control mechanically the flow of electrical energy from a DC voltage source to the load resistance. This device can amplify an input acoustic signal and transform it into the output electrical signal with enhanced power
Energy	The ability of a system to perform work. Energy is measured in joules (J) to honor English physicist J.P. Joule (1818–1889). 1 J = 1 Ws, where W stands for the watt and s for the second
Field effect transistor (FET)	A transistor that uses an electric field to control the shape and hence the electrical conductivity of a channel with one type of charge carriers (electrons or holes) in a semiconductor material. FETs are also known as unipolar transistors as they involve a single carrier (negative or positive) type operation
Frequency selectivity	An ability of the device (system) to discriminate between two signals with close frequencies. It is an analogue of spatial resolution in optical devices
Hopf bifurcation	An advanced mathematical concept from the theory of nonlinear differential equations, gained popularity in some mathematical models of the cochlea

Glossary of technical terms	
Inductor	A passive electrical element, which can store magnetic energy. Inductance of the inductor is measured in henrys (H) to honor American scientist J. Henry (1797–1878). 1 H = 1 Wb/1 A, where Wb stands for the weber and A for the ampere
Inverse piezoelectric effect	An occurrence of a mechanical stress or deformation in the material subjected to the electrical voltage. Inverse piezoelectric effect was predicted from thermodynamic considerations in 1881 by French scientist and inventor G. Lippmann (1845–1921)
Joule (J)	The SI unit of energy. 1 J = 1 Ws, where W stands for the watt and s for the second
Kirchhoff's voltage law	It states that, an algebraic sum of all voltages on lumped elements in an arbitrary closed loop in a circuit is always zero. The law was discovered in 1845 by German physicist G. Kirchhoff (1824–1887). Kirchhoff's Voltage Law is a direct consequence of the principle of conservation of energy
Kirchhoff's current law	It states that, an algebraic sum of all electric currents flowing into and out of a node in an electric circuit equals zero. Kirchhoff's Current Law is a direct consequence of the principle of conservation of charge
Longitudinal waves	Acoustic waves with particle vibrations parallel to the direction of propagation (called sometimes compressional waves)
Lumped element	A mechanical (spring, dashpot, mass) or electrical (capacitor, resistor, inductor) element with no spatial dimensions. Lumped elements are adequately described by circuit theory
Mechanical displacement	A difference in the positions of a mechanical particle e.g., a particle that is stimulated to vibrations by an acoustic wave
Mechanical impedance	The ratio of the force applied to a mechanical element (spring, dashpot, mass) to the velocity at which the element moves. Mechanical impedance is measured in Ns/m, where N stands for Newton, m for meter, and s for the second
Mechanical side	The mechanical port of a multiport electromechanical device + mechanic elements connected to this port
Mechanical stress	The force per unit area. Mechanical stress is measured in pascals (Pa) to honor French scientist, mathematician and philosopher B. Pascal (1623–1662). 1 Pa = 1 N/m^2, where N stands for Newton and m for the meter
Micrometer (μm)	One millionth part of the meter (10^{-6} m)
Millivolt (mV)	One thousandth part of the volt (10^{-3} V)
Noise	Any unwanted signal, random or coherent
Nonlinear capacitance	An electrical capacitance, which value depends on voltage on its terminals. The constitutive equation for the nonlinear capacitance $C(u)$ is given by $Q = C(u)u$, where Q stands for the electrical charge and u for the electric voltage on the nonlinear capacitance
Nonlinear oscillators	An oscillator containing at least one nonlinear element
Nanometer (nm)	One billionth part of the meter (1 nm = 10^{-9} m)
Nanosiemens (nS)	One billionth part of the siemens (1 nS = 10^{-9} S)

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Glossary of technical terms	
Norton equivalent circuit	Any network of linear sources and impedances at a given frequency can be presented as an equivalent current source connected in parallel with an equivalent admittance. This equivalent circuit was proposed in 1926 by Bell Labs Engineer E. L. Norton (1898–1983)
Negative conductance	A resistive electric element supplying energy to the circuit, by contrast to a positive resistance (conductance) which dissipates energy into heat
Ohm's law	It states that, the current flowing through a conductor is directly proportional to the voltage across the conductor terminals. Therefore, the current $I = U/R$, where U is the electric voltage and R is the resistance of the conductor
Picoampere (pA)	One trillionth part of the ampere (1 pA = 10^{-12} A)
Parametric oscillator	A harmonic oscillator containing at least one reactive element with a value varying in time
Parametric-piezoelectric amplifier	A parametric amplifier employing the nonlinear OHC capacitance to achieve power amplification and frequency selectivity. Direct piezoelectric effect transforms an input acoustic signal into the electrical side (sensor). Subsequently, an inverse piezoelectric effect transforms the enhanced output electrical signal on the mechanical side (actuator)
Passive element	An element, which can only store or dissipate energy, but cannot generate energy
Picofarad (pF)	One trillionth part of the farad (1 pF = 10^{-12} F)
Phenomenological model	A set of mathematical expressions that relate several different empirical observations of phenomena to each other, in a way which is consistent with fundamental theory, but is not directly derived from theory. In other words, a phenomenological model is not derived from first principles
Potential energy	An energy stored in the system. The notion of potential energy was introduced by Scottish engineer W. Rankine (1820–1872). Potential energy is measured in joules (J) to honor English physicist J.P. Joule (1818–1889). 1 J = 1 Ws, where W stands for the watt and s for the second
Power	The rate at which energy is generated or consumed. Power is measured in watts (W) to honor Scottish engineer and inventor J. Watt (1736–1819). 1 W = 1 J/s, where J stands for the joule and s stands for the second
Power amplification	Property of the device (system), in which more (useful) power is flowing out of the device than into the device
Pressure	The force applied perpendicular to the surface of a medium per unit area. Pressure is measured in pascals (Pa) to honor French scientist, mathematician and philosopher B. Pascal (1623–1662). 1 Pa = 1 N/m^2, where N stands for Newton and m for the meter
Quality factor	A quantity characterizing sharpness of the resonant circuit. It is defined as the ratio of the resonant frequency to the bandwidth of the resonant circuit
Resistor	A passive electrical element, which dissipates energy. Resistance of the resistor is measured in Ohms (Ω) to honor German physicist G.S. Ohm (1789–1854). 1 Ω = 1 V/1 A, where V stands for the volt and A for the ampere

Glossary of technical terms	
Resonant circuit	A passive electrical or mechanical circuit with two different type of reactive elements (capacitor and inductor or spring and mass), connected in series or in parallel. It displays a natural, preferred frequency of oscillations
Sensitivity	The lowest level of the input signal, applied to the device, resulting in an output signal of an acceptable quality (signal-to-noise ratio)
Sensor	A device which provides a usable output in response to a specified physical stimulus. Sensors are more general than transducers, since their input and output energies may be different, like in transducers, or the same
Siemens (S)	The SI unit of the electrical conductance. 1 S = 1/Ω, where Ω stands for the ohm. Siemens was introduced to honor German inventor and industrialist E.W. von Siemens (1816–1892)
Signal frequency	Number of cycles per second for a sinusoidal signal. Frequency is measured in hertz (Hz) to honor German physicist H. R. Hertz (1857–1894). 1 Hz = 1/s, where s stands for the second
Tonotopy	A property of the device (system) in which different signal frequencies are processes in different locations within the device. Tonotopy was introduced by German physicist and physician H. von Helmholtz (1821–1894)
Transducer	A device which converts one form of energy to another. For example, piezoelectric transducer converts mechanical signals to electrical signals (sensor) and vice versa (actuator)
Transverse waves	Acoustic waves with particle vibrations perpendicular to the direction of propagation (called sometimes shear waves)
Vacuum tubes	Electronic devices used to process and amplify electric signals, before appearance of transistors
Varactor	A nonlinear (time-varying) capacitor which capacitance depends on voltage applied to its terminals. By contrast, capacitance of a linear capacitor is constant and does not depend on voltage across its terminals. Varactor constitutes the main component of the parametric amplifier
Volt (V)	The SI unit of voltage. 1 V = 1 W/1 A, where W stands for the watt and A for the ampere
Voltage	The difference between an electrical potential at two points. Voltage is measured in volts (V) to honor Italian physicist A. Volta (1745–1827).
Voltage source	An active electrical element providing DC or AC electric voltage on its terminals
Watt (W)	The SI unit of power. 1 W = 1 J/s, where J stands for the joule s for the second

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