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Modeling Working Mechanisms of Human Cochlea

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Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Table 1

Table 1

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Abstract

To keep healthy people from auditory dysfunction such as hearing loss, tinnitus et al, it is significant to understand the working mechanisms of the cochlea. Bekesy discovered the physical mechanism of stimulation within the cochlea about 70 years ago. Since then, many topics of the researches have been continued experimentally and theoretically. Most of them are involved in: how do sound waves travel in the cochlea? Do they propagate along the basilar membrane as slow waves or through biological fluids as fast and compressional ones (similar to the sound speed in water)? To the best of our knowledge, such questions have not been fully answered and the working mechanisms of the cochleae, otoacoustic reception and emission are still unclear today, in a perspective of biomedical and biochemical infophysics.

In this study, based on Newton's laws, Shannon information theory and our previous published mathematical model relating the characteristic/natural frequencies (in time domain) and the spiral angles of human cochlea, we further develop biomedical and biochemical infophysics models to investigate working mechanisms how a human cochlea filters sound waves to obtain and transmit the signals, for both normal auditory senses and abnormal hearings, such as tinnitus, aural response obstruction or aural hindrance (loss).

We believe our models of biomedical and biochemical infophysics will help us to prevent healthy people from, or to assistant the patients to recover from the diseases, or to improve the patientsâ€™ hearing ability or quality as well as to understand the working mechanisms.

1 Introduction

It is well known, for human, the ears and (or) hearing system, yield only to the eyes and (or) visioning system, are the second most important sensory organs to acquire external information. However, about 2 to 3 out of every 1,000 children in the United States are born with a detectable level of hearing loss in one or both ears. Approximately 15% of American adults (37.5 million) aged 18 and over report some trouble hearing [1].

Cochlea is the most delicate, complex and important component in the auditory system. Cochlear dysfunction is one of the most incidence of ear diseases. There are about 600 thousands cochlear implant users in the world. There are about 14 thousands implant users in the UK, and about 700 adults and 550 children are implanted each year [2].

Musician, who have exposure of symphonic orchestra, pop, rock, or jazz, are believed to have higher probability than other people to suffer from noise-induced hearing loss (NIHL) [3]. We consider an aural hinder as a hearing loss.

Tinnitus is a hearing disease and a perception of sound without external source. The exact etiology of tinnitus is not fully understood, although some researchers believe that the condition usually starts in the cochlea [4]. An aural response obtuse is a hearing disease too.

Therefore, it is significant to understand the working mechanisms of human auditory system, especially to find out the frequency filtering principle of human cochlea, to keep healthy people fromÂ hearing loss, tinnitus and other auditory dysfunction or to assistant the patients to recover from the disease or to improve their hearing ability or quality.

To understand the mechanism or to find out the acoustic principles of cochleae, Bekesy performed significant experimental studies about 70 years ago [5]. Since then, many topics of the research have been continued experimentally [6 - 10] and theoretically [10 - 14]. Most of them are involved in: How do sound waves travel in the cochlea? Do they propagate along the basilar membrane as slow waves or through biological fluids as fast and compressional ones (similar to the sound speed in water)? To the best of our knowledge, the working mechanisms of cochlea, otoacoustic reception and emission are still unclear in a perspective of biomedical and biochemical Â infophysics.

To figure out how a human cochlea selects or tunes a frequency, based on Ohm second (acoustical) law and published data [15 - 16], we originally proposed our mathematical and informative models in a polar coordinates system to plot the cochleogram?we also investigated 12 equal temperaments and perfect frequency ratios and 11 octaves in our previous research [17].

In this investigation, we continue our previous study, and propose our modeling equatios of vibration, oscillation or progression of sonic motion in human auditory system to address the working mechanisms of cochlea, otoacoustic reception and emission in a view of biomedical and biochemical infophysics, based on published data [5 - 10, 18 - 23] and theories [17, 24 -32].

2 Models

Equation 1 describes our published mathematical model relating the characteristic/natural frequencies (in time domain by default) and the spiral angles of human cochlea. For Equation 2, 2048 Hz is in the most sensitive frequency range (from 1000 to 4000 Hz) [18]. Fig. 1 illustrates Equation 1 in a top view of the human cochlea [17]. The bold data, i.e. 64 Hz < frequencies < 8192 Hz, are the most musically effective [18].

Equation 3 is our previously proposed and normalized informative model of temporal (default) characteristic (natural) frequencies and spiral angles of human cochlea [17], based on Shannon well known communication theory. In this paper, our follow-up comments for the equation are: frequencies are equivalent to probabilities; the unit of the information (Equation 3) is bit; the information (amount) is a relative concept just like that of the pitch; if the natural frequency is the same as the most sensitive frequency, the information amount is 0 (reference value); if the natural frequency is far away from the most sensitive frequency, i.e., very high or very low natural frequencies at the two ends of the cochlea, the (absolute) information amount is great, either positive or negative; the great positive or negative information are correspondent to our different extreme feelings.

Analogously, we consider Equation 3 as pitch (frequency) levels in classic sound theory, there are total 132 sound pitch levels, and the most sensitive frequency is a reference value.

Equation 4 is our model of defined local characteristic/natural angular frequencies. We model the relationship between the geometric radiuses and spiral angels of the cochlea as Equation 5 based on physiological data [18 - 23]. The relationships in Equation 5 and Fig. 2 are the same as those in Equation 1 and Fig. 1: a base 2 logarithmic spiral function that plots a human cochleogram [17]. Equation 5 is a bridge that correlates our previous mathematical model to infophysical models in this paper.

In this study we newly define a term "spiral encoding angle" as part of information theory; in our previous study [17], we defined an equivalent term in physics "spiral resonating angle". The both terms describe a spatial angular location where a peak or maximum resonance (complex frequency response) approximately occurs when an external driving frequency is approaching the local characteristic/natural frequency. For example, according to our modeling Equation 1, a frequency of 1024 HZ is encoded at -90 degree or - half pi in the spatial angular domain (Fig. 1) and it represents a pitch C5 between 6th and 7th octaves [17]. A peak or maximum resonance occurs at a spiral resonating angle of 90 degree when an external sound signal with this driving frequency of 1024 Hz at low/moderate amplitude excites the cochlea.

Our models relate movements of two objects within a system. The first object is a resonator consisting of a combination of a basilar membrane covered with connective tissue (cells), (inner and outer) hair cells (sensors or receptors) and supporting cells in organ of Corti [18 - 23]. The second object is a tectorial membrane (mechanical trigger of stimulator), see Fig. 3.

Fig. 4 illustrates our model of the dominant path of sound signals propagating in a normal inner ear (cochlea). The sonic mechanic waves from the middle ear are coupled by the oval membrane window into scala vestibuli (perilymph fluid). The longitudinal, transverse and/or mix of both travel in the vestibuli perilymph fluid and transmit/reflect from the Reissner membrane. Then, the waves are coupled into scala tympani (perilymph fluid) by reflecting at the helicotrema, a transparent window. After the waves attenuate through the vestibuli and helicotrema, they continue to the tympani perilymph fluid and carpet bomb a series of resonators at the basilar membrane covered with the connective tissues (cells). The remaining wave energies are coupled out of the inner ear by the round membrane window. The waves reflected from the cochlear wall are much stronger than those transmitted into it. The hydrodynamics principles such as the wave equation and Fermat law of reflection and transmission can be used to depict these wave movements [25, 30].

The vestibuli fluid waves are also coupled into scala media (endolymph) by the Reissner membrane: these waves travel in the endolymph fluid and carpet bomb the tectorial membrane. Therefore, the tectorial membrane acts at the hairs/cells. However, the bombing forces/actions from the vestibule fluid waves are much weaker than that from the tympani fluid waves, based on published experimental data [18 - 23].

In transverse z direction, force $F_{z,b}$ mostly comes from tympani perilymph fluid and acts at the basilar membrane covered with the connective tissue/cells; another force $F_{z,t}$ mostly comes from the tectorial membrane and reacts at the cells/hairs (Fig. 3 and Fig. 4). The sources of the forces can come from the internal and external of the cochlea.

According to Newton's third law, $F_{z,t}$ involves an action and a reaction between the combination and tectorial membrane. $F_{z,t}$ (related shear force) bends the hairs of the cells and excites (mechanical and electrical with a phase interval [10]) peak or maximum resonances at or near a particular encoding angle when the driving and natural frequencies are (almost) equal.

The resonances are involved in a section of the first object /combination in a short angular range [17], see our models Fig. 3 and Fig. 4. The resonating energies or forces can be beyond the thresholds of most ion (K+ and Na+) channels of the cells depending on whether they are within or without the range. The mechanical and electrical oscillators or resonators are organically united together.

The cell hairs/probes and tectorial membrane make up multiple probing triggers/couples. The mechanical and electrical vibrations or oscillations are coupled or triggered by the cell hair probes. The electrical (mostly transverse wave) signals are originated from the hair cells and related synapses of the spiral ganglions at particular spatial angles. These signals are transmitted to and decoded in specific spatial sites in the brain auditory cortex.

Table 1 shows our models of waveguides, resonators and triggers in the human auditory system based on the acoustical [25, 30] and electromagnetic [31] theories and published data [5 - 8, 18 - 23]. Fig. 3 and 4 are the related illustrations of the inner ear (cochlea).

The scalae and membranes have different jobs that cooperate with each other. The scalae vestibuli, tympani and media mostly play roles in transporting the sound waves and building up K+ concentration differences within the perilymph and endolymph fluids; the basilar membrane covered with the connective tissues/cells plays a role in constructing a series of resonators with the hair and supporting cells alongside the waveguide transportation paths.

Theories and models have been thoroughly developed for the vibrations, oscillations or propagations in the outer ear canal (roughly like a brass or wind instrument), middle ear ossicles (roughly like drumsticks or beaters), and inner ear membranes [24 - 30]. Therefore in this article, we mostly focus on investigation of human cochlea tuning or filtering of a frequency. In other words, how a combined element of basilar membrane covered with the connective tissues, hair and supporting cells resonates at a particular angle, see Fig. 3 and 4. To do so, we describe dominant traveling waves in the cochlear fluids, using a perspective of biomedical and biochemical infophysics.

Based on published physiologic data [18 - 23], we consider the distributed mass (density), friction or resistance coefficient (density) and tangent tension as the only functions of the variable angle to simplify our models to obtain analytic solutions. The densities are the related physical quantity per length, see Equations 6, 7 and 8 respectively (Fig. 3 and 4).

Equation 9 shows the force from scala Tympani (Fig. 3). To obtain analytic solution, we simplify the force as a function of the angle and time only. $F_{z,b}$ is a component of the wave in z direction. The wave is a travelling and (or) damping function, radiating from the oval membrane window, passing through scalae vestibuli and tympani perilymph fluids, then carpet (saturation) bombing the basilar membrane covered with the connective tissues (cells), see Fig. 3 and 4.

According to Newton's third law, the tectorial membrane will react at the hairs while the hair cells act at the membrane (Fig. 3). We assume the distributed reacting force at the hairs from tectorial membrane is synchronized with that in Equation 9, see Equation 10; and the net forces is shown in Equation 11. We believe the force in Equation 10 is weaker than that in Equation 9.

Applying Newton's second law to an element in the combination in the z direction (Fig. 3), we derive Equation 12 as our global model of the movement of a combination element, for all angles along the whole cochlea. We neglect the higher order items and couplings between or among different dimensional vibrations, to obtain analytical solutions, because we assume the vibrations or interactions are minor, weak or moderate [5 - 15, 18 - 23].

Based on the published data [6]; we speculate the attenuating or damping procedure will finish in a very short angular range around an external excited, initial triggered or other disturbed location.

Also, based on the physiological data that human have almost no hearing senses at the apex end, very low frequency (e.g., < 20 Hz) and at the base, very high frequency, (e.g. > 38000 Hz) [16 - 23], we assume almost no vibration occurs at the both ends. The boundary and initial conditions are shown in Equations 13 to 16.

Because Â we have not found any methods of classical mathematical physics [24 - 30] to analytically solve the complex Equation 12 with variant or distributed mass, tension, viscosity or resistivity and to obtain closed-form solutions, we have to approximate our equations to fit the published experimental data [18 - 23] as well as to obtainÂ estimated (qualitative or semi quantitative) solutions.

We assume the distributed external exciting force (Equation 11) Â acting at the combination from scala tympani and related solution (Equation 17) are separable to obtain analytic solutions [25, 26]. Bernoulli separation approximation are demonstrated in Equations 17 to 20.

2.1 Resonating Models of the Combination in Temporal Domain

When resonances occur (nearly) at an encoding angle (Equation 21), we do hear a sound correspondent to the frequency. In this case, we assume the impedances of mechanical waves of the combination in angular directions are very large compared with that of the organ of Corti in z direction, especially the mechanoreceptor (hair cells); the waves can penetrate the basilar membrane covered with the connective tissues and the organ of Corti. The waves will not propagate and the external force will not excite any travelling waves along the membrane in angular directions. The most external energy will be absorbed or exchanged at the local angle, e.g., it exchanges the maximum energy with the combination.

To estimate the solution in time domain, we also consider the angle in Equations 18 to 20 as a parameter rather than a variable, assume the damping or attenuating term is much large in the spatial angular domain.

We also assume our modeling equations satisfy the superposition principles [26]. The complete solution is the sum of the non-homogeneous and the homogeneous.

2.1.1 Homogeneous (Natural) Models Determined by Temporal Conditions

Equation 22 is our local free resonating (parameter) model, a homogeneous or natural (transit state) differential equation in time domain, at a particular encoding angle (Equation 21).

After a simplification of Equation 22, we obtain a characteristic Equation 24 and a related natural frequency (Equation 25) that has the same form as that of Equation 1. Therefore, our infophysical model (Equation 26) in this paper is consistent to our mathematical model (Equation 1) in our previous article for the natural frequency [17].

From Equations 24 and 25, we obtain a standard characteristic Equation 28, a viscous damping factor (Equation 29) and a general solution (Equation 30).

Analyzing different cases of the viscous damping factor, we respectively mapping the cases between the factor and aural, such a normal hearing, aural response obtuse, aural hinder and tinnitus (See Equations 31 to 36).

2.1.2. Non-Homogeneous Models Determined by External Forces from Scala Tympani in the Temporal Domain

A distributed external exciting force acting at the combination from equation is assumed as Equation 37. Using Equations 18 and 20, in a similar way to section 2.1.1, we can get a local non-homogeneous solution by the external force. It is well known that the peak (maximum) value of complex frequency response, quality factor Q occurs at a resonating angular frequency and angle, see Equations 38 and 39. Therefore, the results are similar to that in section 2.1.1.

2.2. Non-Resonating Progressing Models of the Combination in Spatial Angular Domain

When no resonance occurs at an encoding angle, we do not (almost) hear any sound with the correspondent driving frequency. In this case, we assume the impedances of mechanical waves of the combination in angular directions are minor compared with that in transverse direction, therefore the (slow) progressing or travelling waves cannot penetrate the resonators (combined elements) in z direction; the (slow) waves can only travel or progress in the combination, within a very short range, in angular direction, or does not exist at all [6], see Fig. 3 and 4.

2.3. Quasi Plasma Oscillator and Electromagnetic Models of the Hair Cells

Our previous theoretical models describe how cellular vibrations mechanically stimulate ion channels [34, 35]; how the effective radiuses of the channels changes only 13%, but the effective channel currents will change 10 thousand times [34, 36, 37] and how electromagnetic fields interact, propagate and transport in biological cells [34, 38].

From our modeling Equations 23, 25 and 26, we can see, the resonating frequencies are directly affected by the tangent tension variation rates with respect to the spiral angles. We think the opening or closing the channel currents must change the hair cell's conformation or shapes, therefore, directly change the tension and indirectly change the resonating frequencies and the complex frequency responses.

In this paper we consider the hair cells as quasi (physics) plasma oscillators (resonators) [34, 35]. We analogue them to (but, respond faster than) crystal oscillators [29], see Fig. 5, where biological energy ATP is used to power the circuit. The cochlea works like a plasma (or crystal) microphone: transferring sound waves to electromagnetic signals; or a plasma speaker: transferring the electromagnetic signals to sound waves. The plasma oscillators work in a similar way as that of piezoelectric effect of quartz crystal oscillators: energy transformation between the mechanical and electromagnetic.

We also analogue cochlear dominant waves to brain and cardiovascular waves; cochlear hair cells to brain neurons and heart muscles. All of the waves are the combination of electromagnetic and hydrodynamic ones; all of the cells are easily excited to maintain oscillations or resonances. Our model provides another mechanism of the cochlear receiving and emitting sound waves. The oscillation or wave functions and solutions are the same or similar to that in the following Section 2.4 (more general).

2.4. Models of the Dominant Travelling Waves in Human Cochlea

Our model of mechatronics and electromagnetic equivalent circuit of quasi plasma oscillation in the cochlea is the same as or similar to that in the hair cells (information receptors), see Fig. 5. The main flows of information and energy come from the oval window to the receptors and the round window; the main flow of matters involves cardiovascular and meridian channel systems [34, 35, and 39].

We consider the perilymph, endolymph and cellular plasma as biological electrolytes, quasi physics plasma of K+, Na+, Cl-, Ca++, Mg++, OH- and H_3O+ [34 - 35], see Fig. 3, 4 and 5.

Because disturbances, internal excitations or external stimulations always exist, the charged components are often displaced from their equilibrium positions or distances, the redistribution of charges and masses will respectively set up forces, tensions or pressures at the components. The forces, the tensions or the pressures will restore the components back to their original equilibrium positions or distances and could initiate a vibration (oscillation), even a resonance. Under some conditions, the vibration (oscillation), even the resonance continues as long as an internal excitation or an external stimulation is powerful enough and retained [35].

Based on Newton second law, Equation 40 is our modified hydrodynamic equation embedded with Lorentz force, in conjunction with Maxwell equations of electromagnetism [32, 35], to describe the plasma oscillating or travelling in this study. The both mechanical and electromagnetic (internal) forces are included in this equation. The term at the right side of the equation denotes a net force.

The convective acceleration has been neglected because it is usually much smaller than the local acceleration (first term at the left of Equation 40) and others [32]. The pre-sheath and sheath plasma boundary effects have been neglected either because +/- ions are in the quasi plasma rather than electron and + ions [33], or we assume the effects are minor compared with the other factors (terms) in the equation. The annihilation and production of ions have been ignored too since we assume they are minor compared with other items in the equation.

After some approximation (Equations 41 and 42 [25]), we propose our model of dominant wave Equation 43 for the sound propagation in human cochlea. The equation includes terms of oscillations and attenuation in both temporal and spatial domains as well as in both hydrodynamic and electromagnetic terms. In natural physiological states, the magnetic fields are produced by motion of the electrical charges or electrical field variation, the electrical force is usually thousands times stronger than that of the magnetic one [34]. Therefore, we can naturally neglect the magnetic force to simplify our models. The methods to resolve Equation 43 have been developed [25] as same as or similar to that in section 2.1. Though the solution is a sum of that from all particles, we think the dominant solution is usually the external forced one.

The plasma is much easier than regular water fluids to be excited to oscillate or wave spontaneously or externally. Therefore, even there is not any external sound (force), the right side term in Equation 43 is 0, the spontaneous excitation of the plasma in scala tympani (the second or third term at the left side of Equation 43) can trigger natural (homogeneous) oscillation. We think this is another source of tinnitus or acoustic emission.

3 Discussion

Our informative modeling Equation 3 is mathematically similar to intensity levels of classic sound theory, see Equations 44 and 45. If we define I_0 as a normal or/and moderate sound intensity, Equations 44 and 45 are informatively similar to Equation 3. The intensity is equivalent to the probability. The stronger or weaker the intensity, the more the information. The extreme intensity levels (information) are correspondent to our different extreme fillings.

We also speculate the sound intensity level could be proportional ion channel currents of the hair cells, the currents are related to the cross membrane voltage [36 - 37], and the voltage is modeled with Goldman equation of logarithm function of ion concentrations. We think this could one of reasons why the sound intensity levels are logarithm equations too.

Our models are more suitable to the low or moderate amplitude signals than the high ones, because at low sound levels the tuning curve is impressively narrow. For high amplitude signals, the tuning curve becomes much wide, especially for frequencies below characteristic frequency [19]. Although our models are more suitable to low-amplitude signals, they also explain this high-amplitude situation, see Fig. 3: the louder the sound, the more hair cells are triggered and the wider the tuning curve. We believe, loud sounds hurt the hair cells as well as the windows, membranes or/and eardrums. Therefore, it is important to keep our ears from loud sounds to maintain our auditory system at a high quality level.

We speculate that the source of tinnitus could be abnormal interactions between the inner hair cells' hairs (IHCH) or outer hair cells' hairs (OHCH) and the tectorial membrane. The probing triggers of the hairs and tectorial membrane could stimulate an abnormal resonance as long as an excited component frequency is approaching a local natural frequency (Equations 25 to 27), or Â vibrations/oscillations could occur when the viscous damping ratio is (almost) 0 (Equation 36).

IHCH are not embedded into the tectorial membranes and they can move freely; OHCH are embedded into the tectorial membranes and they cannot move freely. Moreover, about 95% of the spiral ganglion fibers (SGF) innervate IHC, whereas only about 5% of SGF innervate OHC. This innervation plan strongly suggests that IHC and the related SGF mostly play roles in selecting the frequencies and OHC and the related SGF play roles in amplifying the loudness [18 - 23]. Therefore, we hypothesize that in the auditory cortex, neurons that respond only to frequency variation are mostly linked to IHC and neurons that respond only to amplitude variation are mostly linked to OHC. We believe that the complex response patterns of the cortex neurons depend on the neural network linkages between the central-peripheral nervous systems, the central-central, and the peripheral-peripheral; the cortex response pattern also fits other nervous systems, such as the vision and somatic.

We think the scala media (endolymph) plays at least two important roles in the human auditory system. One role is to store high concentrations of K+ ions to make the receptors or sensors (hair cells) very sensitive to depolarization and polarization via electromagnetic or electrochemistry principles [18 - 23]. Another role is to separate the hair cells from scala vestibuli, therefore protecting the hairs from direct intensive mechanical stimulation that may damage the hairs/cells if the carpet (saturation) bombing is too strong. This may be one of reasons why and/or how nature selects the sound waves to resonate a combination of the basilar membrane covered with connective tissue (cells), hair and supporting cells (that are in the scala tympani rather than scala media).

Additionally, we think scalae tympani, media and vestibuli work like big quasi plasma oscillators (or resonators).

Based on our models in this paper, when an external (low or moderate amplitude) sound with an appropriate driving frequency comes into the human cochlea, it Â can either excite the combined basilar membrane elements at all angles near the peak or excite maximum resonating angle. The spatial angular resolution of the human cochlea is about 7.5 degree or 1/24 pi and this resolution corresponds to note differentiation in the human auditory frequency (pitch) domain [16 - 17]. Our model in this paper answers the question: why humans or well trained musicians can only identify/differentiate a maximum of 12x11= 132 notes rather than tens of thousands of temporal frequencies/pitches, when humans can perceive sounds in a frequency/pitch range from 20 to 30 thousands Hz [19 - 24].

According to the Equations 25 to 27, we see that local homogeneous characteristic/natural angular frequencies depend on local physical properties or attributes. These physical properties include the tangent tension variation rates with respect to the angle, mass density and radius. The more the tension variation, or the less the mass density, the higher the frequencies are, and vice versa. Hair stiffness is included in the tension variation. Our models fit the physiological data [18 - 23].

Our modeling equations could also answer the question of why humans feel that the frequency decreases when the sound intensity increases [11, 15, 18 - 23]: the tangent tension variation rates with respect to the angle could increase when the intensity increases. Therefore, the natural frequency increases while combined resonator elements shift to the low frequency end (apex), see Fig. 2. In effect, we feel a red shift in the sonic frequency. Using the same analysis, humans can feel a violet (purple) shift under different conditions.

Our modeling equations provide another way to explain the physiological question of how frequencies respond to excitation: we describe the complex frequency response as dependent on the distributed friction coefficient, mass, radius, tangent tension variation rates with respect to the angle.

Human cochlea works like a band pass filter of the temporal frequency where the band is between 20 Hz (apex) and 38000 Hz (base) [16 - 23]; the sensitivity of frequency is high in the middle section and low at the ends.Â We think the friction/resistance plays a very important role for the hearing sensitivity. At both the base and apex, we assume the resistance or friction to be high so that the vibration amplitude is low. Therefore, humans need a stronger intensity of frequencies on the external/ending sections of the cochlea band to get a similar auditory experience as those in the middle range of frequencies. Therefore, our models qualitatively explain in formulae why and how human auditory sensitivity is low at the both ends and high in the middle range of the cochlea [18 - 23]. Other parameters and variables that play roles can be subjects of future papers.

Our models describing the relative movements of a two objects system, in principle, fit experimental data that the outer hair cells respond to the stimulation by altering their lengths (elongation and contraction) [19].

It was shown experimentally that the motion of the tectorial membrane is resonant at a frequency of 0.5 octave (oct) below the resonant frequency of the basilar membrane and polarized parallel to the reticular lamina [8].Â It was also found that the mechanical response characteristics of the Reissner's membrane differed considerably from the cochlea [9]. We think the two experimental results are reasonable according to our models in this paper. The resonant frequency of the basilar membrane determine the mechanical response characteristics of the cochlea; the structures/components of the three membranes are different; and the different the structures/components have different response characteristics.

Hair cells are strongly involved in both electrical and mechanical resonances [10]. Alternatively, opening and closing of ion channels oscillate the electrical currents and voltages of the cells. The cells also play roles in determining the local mechanical natural/characteristic frequencies by contributing towards tension variation, mass and friction resistance Â distribution in the resonators (Equations 25 to 27). Therefore, we cannot and do not have to separate the mechanical and electrical oscillators or resonators. For biological systems, we must often simultaneously work mechanically, electrically and chemically because the mechanisms are organically entangled together.

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Illustrations

Illustration 1

Fig. 1

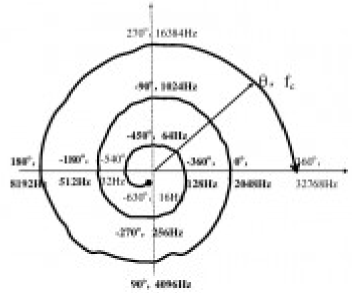


Fig. 1. Cochlear spiral angles and correspondent characteristic frequencies represented in Equation 1. The draw is not to scale.

Illustration 2

Fig. 2

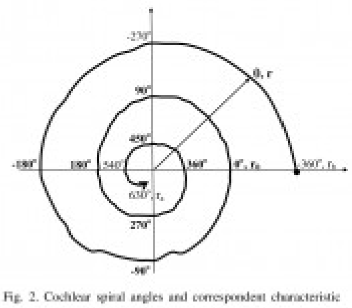


Fig. 2. Cochlear spiral angles and correspondent characteristic radius represented in Equation 5; subscript a = apex, b = base. The draw is not to scale.

Illustration 3

Fig. 3

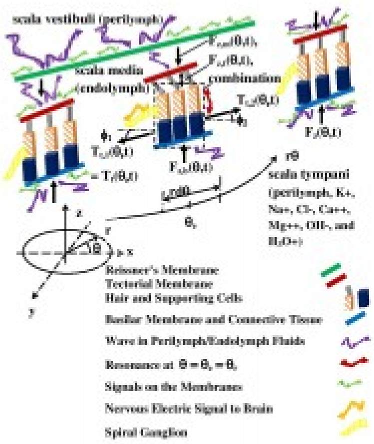


Fig. 3. External forces (the thicker, the stronger) and tension of elements of reissner's, tectorial and basilar membranes; receptors: hair cells in organ of Corti and spiral ganglion. See the text. The draw is not to scale.

Illustration 4

Fig. 4

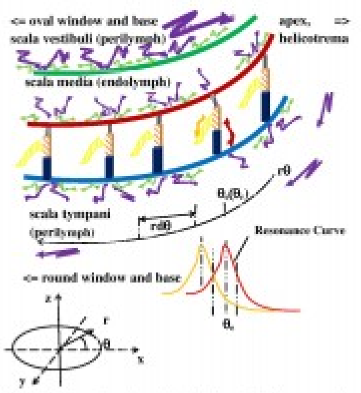


Fig. 4. Auditory signals and discrete elements in human cochlea along the spiral angles in a cylindrical coordinates system. The perilymph and endolymph are electrolytes or plasma (physics) of K+, Na+, Cl-, Ca++, Mg++, OH- and H_3O+. The explanations of components are the same as that in Fig. 3. See the text. The draw is not to scale.

Illustration 5

Fig. 5

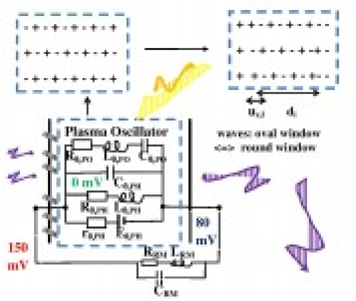


Fig. 5. Mechatronics and electromagnetic equivalent circuit of quasi plasma oscillation of the hair cells. E: biological power; R(r): resistor; C: capacitor; L: inductor; + and - : positive and negative charges; Plasma Oscillator (PO): Hair Cell Plasma; PH: Plasma Holder (cell membrane); RM: Reissner's Membrane. Spiral ganglions carry assumed output electric signals from the cells to the brain; assumed input signals are electromagnetic and mechanic waves from scalae tympani to the cells. Components or circuits of Scalae Media and Tympani are assumed to be minor and not shown here, to simplify our modeling illustration. The others are the same as that in Fig. 3 or 4. See the text. The draw is not to scale.

Illustration 6

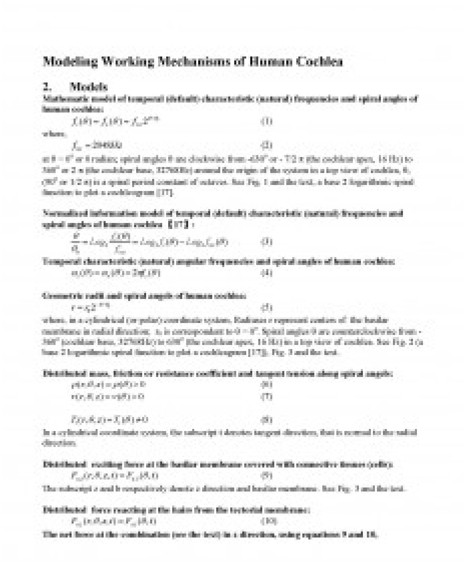
Table 1

Table 1 Wave Guides, Resonators and Triggers of Human Auditory System

Ear/Nerves /Brain	Wave Guide[1] /Resonator[2]/Trigger[3]	Coupling of Energy and Information	Media	Most vibration direction
Outer Ear	Ear canal[1,2]	Ear drum (tympanic membrane) to middle ear.	Air, N_2, O_2, ...	Longitudinal
Middle Ear	Auditory ossicles[2]	Ear drum (tympanic membrane) to outer ear, oval and round membrane window to inner ear.	Solid, bone.	Longitudinal
Inner Ear (Cochlea)	Scala vestibuli[1]	Oval membrane window to middle ear; transparent window to scala tympani; membrane to scala media.	Liquid (plasma), perilymph.	Longitudinal and transverse
Inner Ear (Cochlea)	Scala tympani[1]	transparent window to scala vestibuli; round membrane window to middle ear; membrane and cells to scala media.	Liquid (plasma), perilymph.	Longitudinal and transverse
Inner Ear (Cochlea)	Scala media[1]	Membrane to scala vestibuli; membrane and cells to scala tympani.	Liquid (plasma), endolymph.	Longitudinal and transverse
Inner Ear (Cochlea)	Basilar membrane[1,2], hair and supporting cells[2]; a temporal frequency is encoded at a spatial angle.	Hair probing to tectorial membrane and scala media; synapses to spiral ganglion; membrane to scala tympani.	Liquid (plasma); solid, membrane.	Longitudinal and transverse
Inner Ear (Cochlea)	Tectorial membrane[1,2] and hairs[3]	Membrane to scala media; hair probing to hair cells.	Solid, hair, membrane.	Transverse and Longitudinal
Inner Ear (Cochlea)	Spiral ganglion[3]	Synapses to hair cells (receptors or sensors).	Liquid (plasma).	Transverse
Auditory Cortex	Neurons[3]; a cochlear angle is decoded at a cortical location.	Synapses to auditory radiations.	Liquid (plasma).	Transverse

Illustration 7

Equations Page 1



Modeling Working Mechanisms of Human Cochlea

2. Models

Illustration 8

Equations Page 2

Illustration 9

Equations Page 3

Illustration 10

Equations Page 4