

Perspective Article

New comments on the theory of submolecular theory of hearing

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The explanation of hearing mechanisms dates back to antiquity. It was the Greek philosopher and poet Empedocles (483-423 BC) who claimed that air was responsible for the hearing process. Aristotle (384-322 BC), in his work 'De anima', presented his own views, which survived for 2000 years. Thousands of scholars over 25 centuries have failed to fully explain the mechanisms of our hearing. Learning about the anatomy and physiology of the ear contributed to new theories of hearing. In 1841, Weber announced the harp theory. In 1863, Helmholtz presented the resonance theory. The remaining theories were: standing wave theory, traveling wave theory, Rutherford's telephone theory, place theory, volley theory, and eventually, Bekesy's traveling wave theory reported in 1928 and awarded the Nobel Prize in 1961. The cellular resonance theory constitute a modernization of Helmholtz's theory and Bekesy's traveling wave theory.

The latest theory of hearing is the 'Submolecular Theory of Hearing'. It is based on the knowledge of many scientific disciplines, has irrefutable evidence, and is confirmed by experimental studies performed in many scientific centers around the world.

This theory differs significantly from the hitherto existing theories of hearing on a number of points. The main difference consists in the recognition of the signal pathway to the receptor via the cochlear housing bone. A limitation of the role of the basilemma in the reception, encoding and transmission of information to the receptor. The disappearance of sound wave energy on its way to the fenestra cochleae has been described, which may play a role in the degradation of energy constantly flowing into the ear, heading for the fenestra cochleae rather than to the receptor. The sound wave encodes and conducts auditory information directly to the receptor, without involvement of a travelling wave on the basilemma and without encoding information in the cochlear fluid flows, and without the tip-links mechanism in operation. The information contained in the sound wave is received directly by the receptor. Submolecular theory casts some doubt on the possibility of the OHC contracting as a whole cell simultaneously up to 100 kHz. Local depolarization is possible. Amplification of quiet sounds takes place in the auditory cell. Processes in the receptor and auditory cell take place at the submolecular - atomic and electron - level. There is no continuous transmission of wave energy. The energy transfer of a sound wave is consistent with quantum physics.

According to submolecular theory

A sound wave is a longitudinal wave; it transmits energy through pressure changes throughout the environment, without changing the displacement of the environment. The energy encoded in the wave is transmitted in packages which are full multiples of a unit of energy in the form of a quantum of energy. The packages are separated one from another by a minimum gap, just as in writing words are separated by spaces. This means that the energy of a sound wave is quantized and transmitted without continuity of change, as in classical physics.

The incident wave on the auricle in humans is reflected to a small extent and directed into the external auditory canal. The primary role of the auricle is to absorb the energy of the sound wave. A law of physics states: 'every point in the environment reached by a wave will become a source of a new spherical wave'. The energy of the wave absorbed by the auricle is transferred to the cartilage of the auricle, and further on, viz. to the temporal bone. A cat has 32 ear muscles that allow her to change the position of the auricle by 180°; the wave energy from the auricle is not directed into the ear canal. The energy received by the auricle is used to quickly recognize the direction from which a sound is coming. In the animal world, this feature is very important. Basset hounds and spaniels have long dangling ears covering the external acoustic meatus. They are excellent at hearing and recognizing the directions of incoming waves.

A sound wave falling through the external auditory canal onto the eardrum, is reflected approximately in 20 per cent [1], and its remainder will be absorbed and transmitted to the ossicles. Some of this absorbed energy is transferred to the temporal bone through contact between the eardrum and temporal bone. The wave energy is conducted through the malleus and incus to the stirrup, causing thus the stirrup plate to perform piston-like or rocking movements at higher frequencies which transmit the wave energy to the cochlear fluids.

A part of the energy is transferred to the cochlear bone housing. The energy transmitted from the auricle, eardrum and ossicles is combined and amplified by constructive interference, and then conducted through the cochlear casing bone - at a rate of up to 4,000 m/s - to the hearing receptor. At high sound frequencies, the stirrup plate makes a rocking motion that facilitates the transmission of vibrations to the bone, interfering at the same time with the transmission of information to the cochlear fluids. At medium frequencies, the stirrup plate sways along the transverse axis of the plate. At high frequencies, plate vibrations occur along the longitudinal axis of the plate. Such movements cause a high conflict in the transmission of information. When a half of the plate generates forward movement, at the same time the other half of the plate generates a backward movement. It is impossible to transmit complete information [2].

Neither is it possible to generate a normal travelling wave forming on the basilemma. Regardless thereof, the full range of high frequencies is received by the receptor. This fact constitutes a piece of evidence to corroborate the thesis that there is another signal pathway to the receptor, through the cochlear housing bone, a fast pathway without further energy exchanges that can cause distortions in the transmitted information.

A second important piece of evidence for a different signal pathway to the receptor is the preservation of residual hearing after cochlear implant surgery for partial deafness. The insertion of 20 electrodes into the eardrum canal alters or excludes the travelling wave at the basilemma. It does not affect the hearing existing before the operation. Auditory information reaches the receptor via a pathway through the bony case of the cochlea [3].

Bekey's concept of the importance of wave resonance and the generation of travelling waves on the basilemma which induces cochlear fluid flows to encode information is difficult to accept for several reasons, especially for high frequencies.

It should be noted that both the resonance of waves and the great importance of the basilemma were introduced into the theory of hearing by Helmholtz in 1863, and this thesis is still accepted.

Waves disturbed due to the rocking movements of the stirrup plates travel in the vestibular canal fluid simultaneously in two directions at a speed of 1450 m/s. This results in impaired transmission of information, friction of the fluid streams and loss of energy. The speed of the travelling wave at the basilemma is variable and amounts to 50 m/s near the base of the cochlea, decreasing to 2.9 m/s near the cupula. This means that each forcing wave segment is recorded on a section of the basilemma, shorter from 29 to 500 times. Such a high compression of the transmitted information is supposed to induce a travelling wave at the basilemma, a flow of cochlear fluid for tilting the hairs of the auditory cells. A major complication of the transmission of information is the variable rate of the travelling wave, depending on the frequency of the wave, resonating at different locations on the basilemma, which leads to the maximum tilt of the travelling wave at different times. In the case of multitones and harmonics, this is unacceptable. It is difficult to accept the thesis that this mechanism conveys accurate information, viz.: amplitude, frequency harmonics, phase shifts and sound length [4].

Low tones conducted to the cochlear fluid can be conducted to the receptor through the fluid and tissues, without the mediation of a travelling wave on the basilemma. This is how a baby hears in the womb in the second half of pregnancy. Soft tissues conduct sound waves at a rate of 1550 m/s.

Another problem with traveling waves is caused by the resonance of the longitudinal wave in the fluid with the transverse wave of the basilemma's own vibrations. This resonance, where the force vectors act in the perpendicular direction, does not allow for full and rapid transmission of information. Resonance is a process that takes place over time. A 100% rapid transmission is required.

Another problem is the resonance compatibility of the forcing and forced waves. Intrinsic vibrations of human tissues are between 5-100 Hz [5]. We can hear sounds up to 20 kHz, whereas mammals having the same hearing mechanism can hear sounds up to 100 kHz. There is no resonance match. The basilemma, flaccid and loaded with the organ of Corti, without tension regulation, embedded in a fluid that has high attenuation properties, cannot account for the perception of sounds of very low intensity. A suppression greater than the energy of the forcing wave precludes the formation of resonance.

We can hear a threshold tone when the amplitude of this wave is 8 picometres. This size is about 10 times smaller than the average size of the atoms that make up the basilemma structure. A barn owl can hear tones when the amplitude of the wave is 10 times smaller – viz. 0.001 nm. No resonance is possible. The owl can hear perfectly. Its mechanism of hearing is the same as in humans. There is a different signal pathway to the receptor, leaving out resonance, travelling wave and cochlear fluids.

On the path of the signal through the cochlear fluid, the energy of the wave rapidly disappears due to 3 types of suppression and fluid dispersion. Laser Doppler vibrometry tests have shown that the waveform in the external auditory meatus is 800 Hz, 90 dB – the amplitude of 500 nm at the entrance - measured on the rotund window is 0.5 nm [6,7]. A part of this pathway, - to the cupola - is the pathway to the receptor. Assuming that there is only a 100-fold decrease in the wave amplitude, then for hearing at the auditory threshold limit, when the signal would reach the receptor via a pathway through the basilemma and cochlear fluids - the wave amplitude decreases from 0.01 to 0.0001 nm. According to Bekesy's travelling wave theory [8], such a wave, with an amplitude more than a million times smaller than the diameter of an auditory cell hair, is supposed to tilt or bend the hair. It is supposed to generate cochlear fluid flows that, in turn, are supposed to encode all the information. Can a 1 cm thick twig tilt or bend a tree with 10 m in diameter? Those sounds are audible, and they reach the receptor by a different route.

The receptor perceives sounds with a duration of tenths of a millisecond when only 1 or 2 wave periods are active in the resonance mechanism. In such a short time it is impossible for the waves to resonate and for information to be transmitted. Resonance needs time, and all the more the resonance of the longitudinal wave with the transverse wave of the basilemma [9,10].

The signal path time from the ear canal until a receptor potential in electrophysiological studies is generated varies from 1.5 - 1.9 ms. In contrast, the calculated path time through cochlear fluid, resonance, travelling wave and fluid flows is 4 - 5 ms. The submolecular theory is critical of the thesis of signal amplification in both the middle ear and amplification by pulling at the basilemma caused by the contracting OHCs after cell depolarization. Bekesy assumed that an incident wave from the air to the cochlear fluid is reflected in 99.9%. Therefore, there must be an amplification of this fading wave. The error in the assumption is that the sound wave falls on the elastic eardrum, which absorbs and further conducts about 80% of the incident energy to the eardrum. There is no need to amplify this wave 44 times, i.e. by 33 dB - according to Audiology textbooks [11]. A middle ear amplification is supposed to result from the difference in surface area between the eardrum and the stirrup plate, and from a lever mechanism created by the difference in lengths between the malleus shaft and the anvil joint in a ratio of 1.3 : 1. The third element of amplification is a funnel-shaped structure of the eardrum, which is supposed to amplify the sound wave twice.

No gains in the middle ear are confirmed by vibrometric testing. A 1000 Hz sound wave, incident on the eardrum, with an intensity of 90 dB and an amplitude of 500 nm, on the side of the eardrum cavity has 80 dB = 100 nm. The stirrup plate amplitude of this wave on the vestibular canal side is 11.2 nm = approximately 60 dB.

In stapedotomy, the active area of the piston is 100 times smaller than the area of the tympanic membrane, and no 100-fold wave amplification is observed.

In the 1980s, the effect of electric current on isolated external auditory cells was studied. They were found to be contractile. It led to an erroneous conclusion that the OHC, when depolarized, will contract and can amplify quiet sounds by 40-50 dB. In the ear, depolarization depends on the work of the ion channels of the cell wall, operating at a certain pace. This limits the possibility of contraction rates of more than a few thousands. There cannot be a one-time depolarization of the whole cell, e.g. 50,000/s. There can be local, limited depolarization. There is a paradox, however: We listen, according to the travelling wave theory, to a quiet sound of 20 dB which is amplified by 33 dB in the middle ear, then in the inner ear by an OHC contraction this already amplified sound will be amplified successively by 40-50 dB, whereas we can still hear the quiet sound - 20 dB.

The submolecular theory recognizes an amplification of quiet sounds that are picked up by the receptor but are too weak to reach the center. The amplification takes place in the auditory cell, is regulated and takes place at the molecular level [12].

In all senses there is an intracellular, regulated, molecular amplification. Most chemical reactions and energy transfer between molecules take place in 10-14 s. These reactions occur at the atomic and electron level. 'Difficult' reactions run 1,000 times slower, but it is still 10-11 s.

Intracellular amplification means a whole complex of factors such as phosphorylation and dephosphorylation of ion channels responsible for cell membrane conductance, ATP concentration, cAMP levels, cGMP, cell pH, osmotic pressure, presence of ligands, and operation of Ca^{++} ATPases pumps. These membrane-associated pumps play a major role in maintaining fluctuating calcium levels in the cell. Intracellular enhancement is related to the work of calcium-binding proteins, where calmodulin plays an important role, by influencing the production and breakdown of cAMP and cGMP. It activates protein kinases and phosphatases as well as regulates the calcium pump. Exerts an effect upon the contraction of muscle and non-muscle cells through activation of cAMP-independent myosin light chain kinase. Calmodulin also affects the transmitter's exocytosis. The binding of 4 calcium atoms by calmodulin increases its action 1000-fold. Enzyme production or the rate of enzyme degradation is regulated.

Calcium is the second messenger of information in the cell, acting faster than the other second messengers: cAMP, cGMP, DAG, IP₃ which are either produced in association with an increase in calcium levels or activated by G protein. The stage of production of second messengers constitutes one of several mechanisms of intracellular amplification. One enzyme molecule can produce several hundred second messengers. Received tones - whose energy is too low to reach the center - are amplified. Intracellular signal amplification is one of the main pillars of the 'Submolecular Theory of Hearing'.

One of the main features of the submolecular theory which distinguishes this theory from Bekesy's travelling wave theory, is the direct transmission of information from the sound wave to the auditory receptor. The energy of the sound wave encoding auditory information is perceived by proteins sensitive to the energy of the sound wave, called sound-sensitive molecules. Like in the eye, the rod cells and cones receive electromagnetic energy, the outer and inner auditory cells receive the mechanical energy of the sound wave in the ear. Auditory cells, sensitive to a specific frequency are arranged along the basilemma in the organ of Corti. From the oval window towards the cupola received are progressively lower frequencies. The ability of the auditory cells to perceive a particular frequency is genetically determined. The location of a particular frequency-receiving cell is known to the central nervous system. During the development of the nervous system, neural connections between the center and the auditory cells are formed.

The reception of information from the sound wave is not dependent on the resonance of the longitudinal wave with the transverse wave of the basilemma, nor on the vibration of the basilemma itself. These phenomena exist, are ascertained, but do not conduct especially high frequencies to the receptor. This is corroborated by the lack of high-frequency transmission after stapedotomy surgery. The flow of sound wave energy through the spiral cochlea to the rotund window may have to do with the need to degrade the excess energy constantly flowing into the ear. This energy cannot be accumulated, it cannot disappear, so it must be converted into another form of energy.

Sound-sensitive molecules, upon receiving energy, will increase their total energy and transfer the excess energy to molecules responsible for gating mechanosensitive potassium ion channels. Conformational changes in these proteins provide an opportunity to perform the work of regulating the openness of the ion channels according to the information contained in the sound wave. The influx of positive potassium ions initiates depolarization of the auditory cell probably over a limited space. A large number of ion channels means that there are potassium channels capable of activation at all times. This offers a possibility of transmitting wave frequencies up to 100 kHz, or even 200 kHz in the case of bats. A one-step depolarization of the entire cell precludes the transmission of such high frequencies. There is too little space to describe here all the processes inside the auditory cell involved in the production, transport and secretion of the transmitter into the synapse. In the synapse chemical energy is converted into electrical energy of the postsynaptic excitatory potential, conducted to the nerve cells of the spiral ganglion, where via the auditory nerve generated is an action potential, then conducted to the center

The calmodulin-related stage of transmission of information in the auditory cell leads to a splitting of the signal into different directions. The amplified signal goes further in the centripetal direction, but at the same time, calmodulin activates many so-called constitutive processes, i.e. those occurring in the unstimulated cell. Information is separated into constitutive actions associated with normal cell function and regulated actions which are associated with the production, transport and release of transmitter into the synapse. Once calcium levels have been raised and information is transmitted, there is a rapid decrease in calcium levels in the auditory cell. Calcium pumps and ion exchangers operate to eject calcium ions out of the cell and some calcium moves back into the mitochondria, endoplasmic reticulum and nucleus. The lower the calcium level in the

cell, the more sensitive the cell is to receiving a new signal. Intracellular transmitters (messengers), fluctuating calcium levels and the actions of intracellular proteins are responsible for intracellular amplification.

The second system, activated by the calcium-calmodulin complex, involves regulating the interaction of all cellular organelles. The third, relatively slow system of cell operation regime involves the regulation of production of proteins, particularly of enzymatic ones. The production of enzymes or the rate of their breakdown can be altered. The rate of reaction is also influenced by enzyme activators and inhibitors. These three systems of process regulation interact with each other, being responsible for the synergy of constitutive and regulated processes [13].

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