

Questions for Proponents of Bekesy's Theory

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ARTICLE INFO

Received: 📅 February 21, 2024

Published: 📅 March 01, 2024

Citation: Jan Myjkowski. Questions for Proponents of Bekesy's Theory. Biomed J Sci & Tech Res 55(3)-2024. BJSTR. MS.ID.008692.

ABSTRACT

The theory of hearing called Bekesy's traveling wave theory, announced in 1928 by a young engineer from Budapest, Georg Bekesy (1899-1972), was revised and supplemented many times. In 1961 it was awarded the Nobel Prize. It still contains several ambiguities that require analysis. The most important points requiring clarification include:

1. Sound wave resonance in the cochlear fluids with the transverse wave of the basilar membrane.
2. Own vibrations of the basilar membrane.
3. Frequency resolution associated with the basilar membrane.
4. Transmission of information through the cochlear fluid.
5. Tip-link mechanism.
6. Amplification of quiet sounds by OHC contraction.
7. The pathway of auditory information conducted to the receptor.

Keywords: Sound Wave; Basilar Membrane; Own Vibrations; Resonance

Abbreviations: Hz: Hertz, kHz: 1000 Hz, nm: Nanometer, dB: Decibel, OHC: Outer Hair Cell, CNS: Central Nervous System, s: Second, ms: Millisecond, Å: Angstrom = 0,1 nm

Questions About the Traveling Wave Theory

1. How the resonance of a longitudinal sound wave in the fluid of the atrial canal, acting in the frontal plane with transverse waves of the basilar membrane in the sagittal plane, works? Is it possible to transmit 100% of energy when a 100 Hz sound wave has a wavelength of 14,500 mm and the length of the basilar membrane is 35 mm in humans, but in small mammals and birds - 2-5 mm [1]? Moreover, a pigeon can hear loud sounds from 3 Hz upwards, and normal sounds from 5 Hz [2]. How does the resonance of wave with the basilar membrane come about? Another problem is that some mammals perceive frequencies up to 100 kHz [2]. There is a lack of compatibility with own vibrations of the basilar membrane. If excited wave is suppressed, the amplitude of the excited wave is smaller. High frequencies are attenuated to a greater extent. The vibrations of the basilar membrane are strongly attenuated by the massive organ of Corti, which is intimately attached to the basilar membrane. Even if a resonance of a longitudinal wave with a transverse wave occurs, which is doubtful, there is no possibility of precise transmission.
2. It is assumed that own vibrations of the basilar membrane in humans range from 16 Hz to 20,000 Hz. Vibrations were determined for a very thin strip of connective tissue of the basilar membrane. Not included is the organ of Corti, which lies on the basilar membrane, that cannot vibrate on its own, without the organ of Corti, which has a much larger mass. The reception of frequencies up to 100 kHz by mammals having the same hearing organ is not considered. Moreover, the 2-5 mm long basilar membranes of small mammals and birds also receive all frequencies. It is difficult to imagine a wave traveling on basilar membrane of an owl hearing sounds at a level of -10 dB [2], when the input wave amplitude is 0.001 nm and in the cochlea the wave amplitude decreases by about 100-200 times [3]. A wave 10 times smaller than the diameter of a hydrogen atom can't produce a traveling wave on the basilar membrane. Such a sound wave fading in the cochlear canal

is not able to move the cochlear fluid by acting through the organ of Corti located on the basilar membrane. A 0.001nm wave fading about 100 times on its way to the cap can't tilt or bend hairs of hair cells, 4000 nm long and 200 nm in diameter. Besides, studies on the natural vibrations of human tissues have shown that the results range between 2 Hz and 100 Hz [4].

3. Bekesy's theory relates frequency resolution to the resonance of the sound wave with the basilar membrane. When the frequency of the sound wave and own vibrations of the basilar membrane match, the resulting wave peak transmits wave energy encoding auditory information [5]. Is it possible that the natural vibrations of the basilar membranes in mammals reach 100 kHz? Where on the basilar membrane does the peak of the wave form when the wavelength is many times greater than the length of the basilar membrane?[6] How does the wave on the basilar membrane originate and travel in the case of polytones? The frequency is recognized with cochlear implantation due to partial deafness, when the basilar membrane is immobilized. Frequency resolution is related to tonotopy.
4. The vibrations of the basilar membrane are supposed to move the fluid of the cochlear duct according to the frequency of the sound wave [7]. The wave energy is conducted through the elastic structure of the organ of Corti, which has damping properties. The fluid has mass, is in constant motion, has positive and negative acceleration in accordance with the wave frequency. A non-inertial system is formed with the possibility of inertia action. As the frequency increases, the acceleration in wave motion increases rapidly. The attenuation of the sound wave increases.
5. The energy of the sound wave is quantized, which makes precise transmission possible [8]. Does the tilting or bending of the hairs of the hair cells take place in a staggered manner? Or continuously, which interferes with the transmission of information. A similar problem relates to cadherin filaments connecting adjacent hairs of hair cells. Their tension and release of tension, which determines the regulation of the gating mechanism of mechano-dependent potassium channels, does not occur in steps.
6. The contraction of the OHC after depolarization of the OHC is supposed to be responsible for the amplification of quiet sounds by 40 dB [9]. Quiet sounds below the auditory threshold cannot be amplified because they are unable to excite the OHC - so there is no OHC contraction. Sounds above the threshold are received and the signal is transmitted via the afferent pathway to the CNS. Outer hair cells have afferent innervation and the signal can be transmitted to the brain. Traveling wave theory holds that OHCs serve solely as amplifier of quiet tones. The following question arises: For what purpose do OHCs possess afferent innervation if they do not use it? If we assume that the contraction of the OHC amplifies the quiet tones by OHC contraction, then the question arises:

What waves does it amplify? After the 0.2 ms needed to amplify wave, there is already another wave on the basilar membrane. In addition, in the case of polytones, when we hear loud and quiet tones at the same time, the loud tones are received and information is sent to the brain. In contrast, quiet tones are separated and routed through the time-consuming signal amplification pathway of OHC contractions. But those waves that have been separated from the loud ones can't be amplified, because the pull of the basilar membrane disrupts the new traveling wave existing on the basilar membrane at that time. Such splitting of a polytone wave is unacceptable. There is an intracellular signal amplification at the molecular level, not interfering with the reception of polytones.

7. Traveling wave theory assumes that the auditory signal pathway leads from the middle ear through cochlear fluids, basilar membrane, then through cochlear fluid, tilting or bending of hairs of hair cells, and tip-links mechanism [10]. The transmission of energy is in accordance with the frequency and amplitude of the sound wave. Pulling cadherin "strings" acts on the mechanism responsible for gating mechano-dependent potassium ion channels. Myosins, which do not have the ability to operate the channel opening and closing to 200 kHz, are supposed to be involved in the regulation of the closing of ion channels. This described pathway is energy-consuming, time-consuming, and highly prone to distortion of the conducted information.

Final Question

If there are so many theoretical and practical problems with the accurate transmission of information via the route adopted by the traveling wave theory, the possibility of a pathway that is fast, simple, energy-saving and ensures precision in the transmission of auditory information should be considered. This path leads from the middle ear through the bony casing of the cochlea directly to the hearing receptor. Sound waves are transmitted from the eardrum, incus and plate of the stapes to the bony casing of the cochlea. Bone conducts sound waves at a speed of approximately 4000 m/s. It is very close from the crista spinalis to the hair cells. The sound wave carries the quantized mechanical energy to the receptor of the auditory cell. The difference in the portions of energy contained in a sound wave must be a multiple of 1 quantum of energy.

New Theory

The new, sub molecular theory of hearing differs significantly from the traveling wave theory in several points. The basis of the new theory of hearing is the reception and transmission of quantized energy encoded in a sound wave to the centers of the brain while maintaining proportions, regardless of molecular changes at the atomic and electronic levels along the way. The adequate stimulus for the hearing organ is the mechanical energy of the sound wave, previously properly formed, which reaches a specific receptor in the form of molecules sensitive to the energy of the sound wave, called sound-sensi-

tive molecules. These molecules have their own basic energy, which depends on several variable factors [11]. The length of their atomic bonds is constantly lengthened and shortened due to the normal atom vibrations. Atoms reach their maximum deflections at the same time. They perform constant oscillatory and rotational vibrations and vibrations around their equilibrium positions. The vibration frequency is between 1013 Hz and 1014 Hz. The vibration period is on average 1012 s. The oscillation deflections are 10% of the bond length. For the hydrogen molecule H₂, it is about 0.1 Å. Each molecule has its own basic energy. The mechanical energy of the sound wave causes a change in the potential energy of the receptor; rotational excitation, a change in bond length, a change in covalent and torsion angles, a change in the total energy of the molecule, and finally a change in the conformation of the receptor molecule, which transfers energy to the next molecule [8].

The kinetic energy of the molecule is associated with motion. In addition to kinetic energy, the molecule has potential energy, which is represented by chemical bonds and forces of electrostatic attraction and electromagnetic interactions. The sum of these energies creates the internal energy of the molecule's body. The internal energy still depends on the temperature and on the mass of the molecule. The transmission of the sound wave external energy to the receptor molecule causes the internal energy of the receptor to increase at a given moment. Particles transfer energy to the next particle through the energy of molecular collisions and the merging of the electron clouds of these particles. Each atom has electrons that form an electron cloud around the nucleus of the atom. The size of this cloud depends on the number of orbitals in which the electrons are distributed. If an atom in a molecule receives energy from another atom, molecule or sound wave, the electron jumps to an orbital closer to the nucleus - its internal energy increases - in a quantized jump. The so-called excited state of the atom is formed, which, unlike the ground state, is unstable. Such state is unstable and there is an instantaneous attempt to return to the ground state by emitting 1 photon of energy — when 1 orbital transition of an atom is concerned. If, in the transfer of information to the next molecule, we have an innumerable number of such transitions, or at least 2 orbital transitions, there are 1020 possibilities of transmitting different types of quantized energy.

This provides an endless amount and variety of transmitted auditory information. The molecule that received the information from the sound wave has an increased total energy. According to the law of entropy, there is a tendency to return to the lowest free energy state possible the obtained energy, which is in excess, is transferred to the adjacent molecule, which changes its shape through its conformational changes. These physical changes of the molecule are the driving force for the mechanism regulating the openness of the mechano-dependent potassium channel of the hair cell membrane. The openness of the potassium channel from 0.3-1.0 nm at the frequency of the sound wave allows for the flow of 6 million/s of potassium ions from the endolymph to the interior of the hair cell. The influx of pos-

itive ions into the negatively charged cell interior initiates the depolarization of the hair cell. A change in the cell membrane potential of approximately 5-10 mV activates voltage-gated calcium and sodium ion channels. Cell depolarization increases rapidly. Once the equilibrium for the sodium ions is achieved, the sodium channels close and the repolarization of the hair cell begins. The influx of calcium during depolarization causes the release of calcium from intracellular stores - the endoplasmic reticulum of mitochondria and the nucleus. Calcium binds with proteins whose activity is dependent on calcium.

A typical protein that increases its activity many times over is Calmodulin, which, together with other mechanisms, plays an important role in the intracellular amplification of the signal received, but too weak to reach the brain. In the hair cell, processes related to cell life rapidly accelerate. But in the hair cell, the most important are the processes associated with the reception and processing of auditory information. The so-called second relays, molecular motors, are produced, a transmitter is produced, transported from the Golgi apparatus to the cell membrane in the vicinity of the synapses and secreted into the synapse. At the synapse, a postsynaptic excitatory potential is created and conducted to the spiral ganglion nerve cells, where, after integration with other dendrites, the signal is encoded and transmitted via the auditory nerve as an action potential to the brain [12].

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ISSN: 2574-1241

DOI: [10.26717/BJSTR.2024.55.008692](https://doi.org/10.26717/BJSTR.2024.55.008692)

Jan Myjkowski. Biomed J Sci & Tech Res



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