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The Secrets of Hearing

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ABSTRACT

The first part presents a brief history of hearing theory and highlights only some of the issues of the still recognized hearing theory of travelling wave by Bekesy. The second part presents a new vision of hearing, in line with current knowledge. It deals with the reception, processing and transmission of auditory information. The most important processes involved in the transformation of the energy of a sound wave take place at the molecular and electron (submolecular) level. Particular attention is paid to the signal path to the receptor and the mechanism of intracellular amplification.

REMARKS ON BEKESY'S TRAVELING WAVE THEORY

The organ of hearing is the only organ of our body not fully understood. Since the 16th century, interest in hearing has increased due to the knowledge of the anatomy of the ear. In the 17th century, Galileo Galilei described the phenomenon of wave resonance. In 1863, Helmholtz announced the first resonance theory of hearing, referred to as the harp theory. New theories were developed, viz.: Hurst's moving wave theory - 1894, stationary wave theory, time theory, theory of place, volley principle, theory of travelling wave by Bekesy, Schouten's residuum theory, 1940, or volley theory of Wever, 1949. The longest recognized theory is Bekesy's travelling wave theory, awarded with the Nobel Prize in 1961 [1,2].

This theory, based on early 20th century assumptions, contains many uncertainties. The basis of this theory is cochlear fluid hydrodynamics, wave amplification in the middle ear, resonance of the longitudinal wave in the cochlear fluid with the transverse wave of the basilar membrane, and cochlear fluid flows deemed to encode a frequency, amplitude, harmonics, phase shifts and vowel length. In the 1970s, an amplification of the sound wave caused by OHC [outer hair cells] contraction, was incorporated into this theory [3].

Stirrup rocking movements at high frequencies do not correctly transmit information to the cochlear fluids. The resonance of the longitudinal wave of the cochlear fluid with the transverse wave of the basilemma does not transmit 100% of information. No resonance of this wave in creatures receiving frequencies up to 100 kHz is possible due to the incompatibility of the frequencies, respectively, of the forcing and forced waves.

There is no free vibration of the basilemma loaded with the organ of Corti, vibrating in a fluid with high attenuation. The speed of the travelling wave depends on the frequency of the wave. It varies from 50 m/s near the base of the cochlea to 2.9 m/s near the cupula. The wave velocity - 1450 m/s - in the fluid is constant and higher than the travelling wave velocity by from 29 to 500 times. Such a variable compression of information is supposed to transmit information to the cochlear fluids. An amplification of quiet waves by 40-50 dB due to OHC contraction amplifies extraneous waves on the basilemma. Quiet, but amplified sounds separated from loud ones are transmitted with a delay to the center. The amplitude of the wave on its way through the cochlear fluids decreases by several hundred times [4,5]. A threshold wave with an amplitude of 8 picometres, will not induce a travelling wave on the basilemma and cannot tilt or bend the hairs of the auditory cells, whose diameter is a million times greater than the amplitude of the wave. Pulling at the tip-links between the auditory cell hairs cannot account for the regulation of the mechanism responsible for gating the potassium mechanosensitive channels on the auditory cell membrane. Immobilization of the basilemma will not interrupt information flow to the receptor [6]. After stapedotomy surgery, high-frequency transmission to the receptor is absent [7]. Numerous ambiguities of Bekesy's theory, analyses of the mechanisms of hearing, and experimental research at various centers around the world,

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have given impetus for the creation of a new theory of hearing called 'Submolecular theory of hearing' [8]. The most important transformations of the energy encoding auditory information take place at the molecular and electron (submolecular) level [9].

SUB-MOLECULAR THEORY OF HEARING

A sound wave incident on the auricle is partially reflected. A part of its energy is absorbed, conducted through the soft tissues and cartilage of the auricle to the temporal bone. The energy of this wave combines - via constructive interference - with the energy of the waves transmitted from the middle ear ossicles. The largest part of the wave energy is transmitted from the stirrup plate performing rocking movements during high frequencies. A simultaneous promotion caused by rocking movements and exerted upon the advancing and retrograde movements of the fluid in the vestibular canal either hinders or prevents the transmission of the energy which is a wave that forces a resonance with the intrinsic vibrations of the basilemma. No proper travelling wave is formed, and therefore, the information is fully received by the receptor via the direct pathway through the cochlear housing bone. There is another possibility of travelling wave formation in the helically twisted cochlea, where sound waves are reflected from concave surfaces, concentrated, and when reflected they fall on the basilemma where the energy is absorbed. Earlier, short waves are reflected. Longer waves are reflected farther and farther away, and the summation thereof causes a wave growth at the basilemma while moving away from the oval window.

Sound waves up to about 2,400 Hz are easily transmitted by vibrations of the middle ear elements, cochlear fluids and the bone - without the involvement of the basilemma. A barn owl can hear sounds when the amplitude of the wave has 1 picometer - it is 100 times smaller than the atoms in the basilemma. In such a case, the travelling wave that excites the cochlear fluid flow cannot be generated. An owl can hear very well. A human can hear sound waves at the hearing threshold (0 dB) - whose amplitude is equal to 8 picometres.

High-frequency waves are conducted without any change in the position of the environment mass - viz. there is either no vibration of the sound-conducting mass or flows of the cochlear fluid. The inertia in wave motion, proportional to the square of the frequency, plays a significant role. A sound wave, for having no mass, is not subject to the law of inertia, conducts high frequencies with quantized energy encoding the information transmitted. This energy acts upon the receptor's sound-sensitive molecules which transmit the information to the gating mechanism of mechanosensitive potassium channels in the membrane of the auditory cell. All the molecules and atoms of the sound wave molecules, as well as the molecules and atoms that make up the receptor's sound-sensitive molecules, are in constant motion. This motion is translatory - oscillatory, rotational or constitute a combination thereof.

Associated with the motion is the kinetic energy of the molecules [9]. In addition to this energy, the molecule has as well potential energy in the form of chemical bonds, electrostatic attraction and electromagnetic interactions. The sum of those energies forms the internal energy of the molecular body. A supply of external energy from a sound wave to the auditory receptor molecule results in an increase in the internal energy of the molecule. An increase also relates to the electron energy by contacting the electron clouds of the atoms of the two molecules. Reception of a new energy creates an excited state of the molecule, which is impermanent. The natural law causes an immediate return to the ground state, by emitting - transferring to another molecule a quantum of energy or a multiple of a quantum when more energy is involved. One quantum of energy is transferred when the change concerns the transition of 1 electron up to a higher orbit. The number of such changes depends on the number of atoms in the molecule. A 10-atom molecule has 10^{10} possibilities for conformational changes. A 20-atom molecule has 10^{20} possibilities for such changes. The time of change for small molecules is 10^{-14} s. For large molecules, the time is 1000 times longer, but it is still 10^{-11} s. This gives unlimited possibilities for transferring the quantized information contained in the sound wave to the hearing receptor molecules which have a genetically determined ability to receive sound waves at given frequencies.

The energy received, encoding the information, is transferred to successive molecules which change their conformation due to the energy gained. The change in the conformation of the molecule gives the gating mechanism of the mechanosensitive potassium channels an opportunity to do its work. The activation and inactivation gates, according to the information in the sound wave, regulate the influx of potassium ions from the endolymph into the auditory cell, initiating depolarization of the auditory cell and the formation of a receptor potential.

Molecular changes in the auditory cell itself will lead to the production and secretion of a transmitter to synapses at the lower pole of the cell, where a postsynaptic excitatory potential is formed, conducted then to the spiral ganglion nerve cells. Once the information from the interneurons has been attached and the nerve cell depolarized, an action potential is formed and then conducted via the auditory nerve to the center, where it is analyzed and compared with information previously stored in permanent memory – and so, an auditory image is formed. Associated with the perception of auditory information are the mechanisms of temporal summation, spatial summation, as well as presynaptic and centrifugal inhibition, as well as auditory adaptation. A very important component of intracellular transitions is an intracellular signal amplification [10]. A

received signal - whose energy is too low to reach the center - is amplified.

Intracellular amplification constitutes a whole complex of molecular factors such as phosphorylation and defosphorylation of ion channels responsible for cell membrane conductance, ATP concentration, cAMP levels, cGMP, cell pH, osmotic pressure, and the presence of ligands. Important is the regulation of calcium levels in the cell, the work of calcium-binding proteins, where calmodulin plays an important role by influencing the production and breakdown of cAMP and cGMP, activating protein kinases and phosphatases, regulating the calcium pump, affecting the contraction of muscle and non-muscle cells through activation of cAMP-independent myosin light chain kinase. Calmodulin influences exocytosis. Saturation of the 4 domains of calmodulin increases its action up to 1,000-fold. Calmodulin, together with calcium, influences the so-called key enzymes. An interaction of all cell organelles 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 produced in connection with an increase in calcium levels or activated by G protein. The stage of second messenger production is one of several mechanisms of intracellular amplification. One enzyme molecule can produce several hundred second messengers. The mechanical energy of the sound wave, which is just the trigger language for the cascade of intracellular reactions, triggers constitutive and regulated processes in the cell. Their intensity is proportional to the energy of the external signal. Activated are intracellular information transfer pathways. Second messengers are water-soluble and have an ability to move rapidly within the cell. Information processing and transmission are associated with the reversible formation and hydrolysis of phosphate-ester bonds. Kinases are responsible for bond formation, while phosphatases are responsible for hydrolysis. Each cell has a large set of kinases and phosphatases numbering around 1,000.

The synapses of afferent and efferent innervation at the lower pole of the auditory cell play a major role in the transmission of auditory information. The efferent innervation has an inhibitory effect at excessive sound intensities. It supports the inhibitory, centrifugal action through the trigeminal and facial nerves, acting on the stirrup and tympanic tensioning muscles.

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