Review Article

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Problems with Bekesy's Traveling Wave Theory

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ABSTRACT

Keywords: Sound Wave, Basilar Membrane, Natural Vibrations, Resonance

Abbreviations: EAC: External Auditory Canal; nm: Nanometer; OHC: Outer Hair Cell; kHz: 1000 Hz nm; nanometer = 10^{-9}m; mm: Millimeter = 10^{-3}m; dB: Decibel; ms: Millisecond

Introduction

The theory of hearing under the name of traveling wave theory was announced in 1928 by Georg Bekesy, a 29-year-old engineer from Budapest. In 1961, it was awarded the Nobel Prize [1]. It has been revised and supplemented many times. The progress of science over the century has been much faster than the evolution of this theory. Many years of analysis and consideration of the logic of what is assumed to be a mechanistic theory of hearing indicate the need for a new discussion on a seemingly already closed issue. New studies and experiments not previously known have emerged [2]. Processes at the molecular and electron levels are coming to the fore [3]. Less important is the mechanics and hydrodynamics, which so far was the center stage. Some fundamental assumptions of the theory need to be verified. In effect of the analysis of countless works originating from numerous specialties and consultations with specialists in many fields of science, a picture of hearing has emerged that is significantly different from that presented in textbooks and publications related to hearing. For 20 years now, there have been voices of criticism of the current philosophical system of our hearing [4]. Today, despite the censorship of orthodox reviewers, increasingly more is heard about the frailty of the traveling wave theory. But it is still impossible to think about the possibility of making a mistake in the assumptions of the theory of hearing almost 100 years ago.

Thanks to advances in science, this is becoming more and more apparent. A consequence of this is the need to introduce new information related to hearing theory into textbooks. This is met with some significant resistance from potent decision makers, accustomed to the existing state of affairs, despite contradictions with current knowledge and the logic of Nature. There have been signals about the problems of the traveling wave theory for a long time, but they are certainly too weak because they do not stimulate even the slightest discussion on this topic. It seems to be a forbidden topic; it is forbidden to challenge a Nobel Prize-winning theory. As evidence pointing to the need for discussions and analysis, I present some of the most important issues related to hearing theory.

Problems of Hearing Theory for Discussion

1. Human threshold hearing needs to be clarified, where the hearing threshold of 0 dB means a sound wave in EAC with an amplitude of 0.008 nm. This is a pressure of 2.0 x 10-5Pa - the amplitude of this wave = 8 x 10-12 m [5]. This wave, approx. 0.01 nm, fades several hundred times on its way to the cap. It does not have enough energy to induce a wave traveling on the basilar membrane, to move the fluid mass according to the amplitude and frequency of the sound wave. It has no energy to tilt or bend the hairs of the hair cells. Thus, it has no ability to induce OHC depolarization.

Despite this, such a signal is detected along the auditory nerve. According to the logic, there is another simple signal path to the receptor.

2. The main pillar of Bekesy›s theory is the resonance of the sound wave with the basilar membrane. The problem arises: how does the longitudinal wave resonate with the transverse wave of the basilar membrane? Bekesy assumed, based on simple studies, that the natural vibrations of the basilar membrane are between 16 Hz and 20,000 Hz. Studies of natural vibrations of human tissues have shown that the results range from 8-100 Hz [6]. In addition, Bekesy assumed false dimensions of the basilar membrane for his calculations. The width of the vestibular duct at the oval window is 4.3 mm. In contrast, the width of the basilar membrane at this location taken for calculation is 0.1 mm. In a narrowing cochlea, the width of the vestibular canal near the cap is 1.7 mm, while the width of the basilar membrane increases to 0.5 mm. The thickness of the basilar membrane increases from 0.025 mm at the oval window to 0.075 mm at the cap region. According to Bekesy, this membrane, occupying only 1/42 of the width of the septum between the canals, with an average thickness of 5 micrometers, houses the entire organ of Corti with Deiters cells, Hensen cells, Claudius cells, phalanx cells, external and internal hair cells, Nuel›s space, internal tunnel of Corti, reticular membrane, nerves and vessels, and a layer of connective tissue on the lower surface of the basilar membrane. By itself, the anatomical basilar membrane is only a small part of the entire vibrating mass. It should be added that these vibrations take place in the fluid of the two cochlear ducts, which have high vibration damping capabilities. The transmission of accurate auditory information through this route is very questionable, even impossible. Consider that small mammals and birds have basilar membranes 2-5 mm long and can hear sounds up to 100 kHz [7]. There is no explanation of how resonance is created for a 100 Hz wave when this wavelength in the cochlear fluid is 1450 cm, and the basilar membrane is 5-32 mm. There is no explanation of how the resonance of a wave lasts a tenth of a ms. is formed when the wave has only 1 or 2 wave periods? [8]. The significance of the difference in the speed of the longitudinal wave in the cochlear fluid - 1450 m/s - and that on the basilar membrane - a traveling wave of 8-100 m/s depending on the frequency and location on the basilar membrane - has not been explained. The wave traveling on the basilar membrane grows from the oval window toward the cap. On what principle, since the energy of the sound wave decreases rapidly and, besides, low frequencies cannot resonate in the initial section of the basilar membrane due to the incompatibility of the forcing vibrations with the forced ones. How does resonance arise in small mammals and birds that have a basilar membrane of 2-5 mm, hearing sounds with a frequency of 10 Hz (a pigeon hears sounds of 5 Hz), when the wavelength in the cochlear fluid is 145 m?

3. The sound wave transmits not only energy, which encodes auditory information. How are polytones with aliquots, phase shifts, and accent transmitted? The same is true for cochlear fluid moved by a traveling wave. The same information is supposed to be conveyed by the tilting of auditory cell hairs and the tightening of cadherin filaments, connecting neighboring hairs and the gating mechanism of the potassium mechanosensitive channel. The energy of the sound wave encoding the information is quantized [3]. The mechanisms described above do not have the ability to quantize the energy transferred.

4. Signal amplification, according to theory, is typically mechanical amplification by contraction of the OHC and pulling up the basilar membrane in the appropriate place. Quiet sounds are amplified by 40 dB, i.e. their amplitude increases 10,000 times. It is difficult to understand that we still hear them as quiet sounds. In addition, for loud sounds, OHC contraction after depolarization and basilar membrane pull-up occur, all the same. Doesn›t it interfere with the wave at that time traveling along the basilar membrane? Tones that are below the auditory threshold cannot be amplified because they do not cause depolarization and contraction of the OHC. There is a problem of amplifying polytones, containing quiet and loud tones with harmonic tones. Mechanical amplification is time-consuming. Loud tone information is sent to the brain, while quiet tones are separated and amplified. Information cannot be transmitted along with loud tones. Besides, amplification of quiet tones interferes with extraneous new waves existing on the basilar membrane. Such mechanical amplification could only exist for a continuous harmonic tone. The sound wave does not meet such conditions. Intracellular amplification has no such problems.

5. To simplify calculations, Bekesy assumed that the cochlea is a straight pipe narrowed in half. This changes the mechanics of the cochlea. In the coiled cochlea, wave reflections from the wall surfaces of the double concave ducts play an important role, resulting in a concentration of reflected rays. There is absorption attenuation, reflection attenuation and interference attenuation. Additionally, the dispersion of the wave on the fluid contents of the cochlea and the increasing distance from the oval window cause a dramatic decrease in the energy of the sound wave, which makes it difficult to transmit information to the brain.

6. The fading of wave energy on its way to the receptor: Laser Doppler vibrometry studies have shown that the amplitude of the 90 dB (500 nm) and 10 kHz wave in the EAC, examined on oval window, has an amplitude of 0.5 nm [2]. The path to the oval window is not the path to the receptor, but the greatest energy loss occurs on the way to the cap. Please note that the input is 90 dB. A human hears a tone at an input of 0 dB = 0.01 nm. If such a wave amplitude fades on its way to the cap several hundred times, how is the wave traveling on the basilar membrane formed? This is a

size 10 times smaller than the diameter of the atoms that make up the basilar membrane. Is such a wave capable of bending the hairs of hearing cells 10,000 times thicker? And if it is assumed that these hairs are connected to the covering membrane, they must be bent to change the tension of the cadherin filaments. If this is impossible, then inducing OHC depolarization is impossible, mechanical amplification is impossible. We hear it! So there is another signal pathway to the receptor.

7. Cochlear Implant Surgery for Partial Deafness: The electrodes inserted into the tympanic canal immobilize the basilar membrane, but this does not change the hearing of tones heard before the surgery. The signal must go to the receptor by another route.
8. Stapedotomy surgery improves hearing only of low and medium frequencies [9]. The piston prosthesis mimics only the movements of the piston. It does not imitate the physiological movements of the stapes plate in the transverse axis at high frequencies, or movements in the longitudinal axis of the stapes plate during the highest frequencies. The absence of these rocking (oscillating) movements is the reason for the lack of improvement in high frequencies after surgery.
9. The incudostapedial joint is a spherical joint. It allows the stapes plate to move in various planes, which allows you to hear high frequencies by transmitting them from the middle ear bones to the cochlear bone casing. In the case of rocking movements, half of the staples generate fluid movement in the direction of the cap, while the other half of the plate generates fluid movement in the opposite direction. Adjacent fluid and wave streams with opposite directions are formed. The transmission of information through this route is disturbed. And precise information reaches the receptor. It is believed that it takes a different route - through the bone housing of the cochlea.
10. The signal travel time from the EAC to the auditory nerve according to electrophysiological studies is 1.5 - 1.9 ms. On the other hand, the signal travel time, including all sections of the path through the basilar membrane, cochlear fluids and the tip-links mechanism, is approximately 5 ms. This indicates that there is a path twice as fast. The bone conducts sound waves at a speed of 4,000 m/s.
11. Bekesy incorrectly assumed that the sound wave resonating with the basilar membrane travels on both sides of the membrane. For this purpose, for calculation purposes, he removed Reissner›s membrane from the ear and connected the vestibular duct with the cochlear duct, regardless of the difference in electrolyte concentrations of these fluids. In this way, he obtained a different (artificial) path of sound wave along the basilar membrane. However, he neglected the important facts that along the way the sound wave encounters the tegmental membrane with very low natural vibrations, then crosses the subtegmental endolymph layer to pass through the organ of Corti with receptors in the form of hair cells. It passes through these cells, without transmitting information, and heads for the basilar membrane, where it is supposed to induce a traveling wave, which is supposed to activate the cochlear fluids to tilt the hairs of the hair cells. This resulting movement of the cochlear fluid due to the traveling wave has a direction opposite to the direction of the wave heading to the basilar membrane. Nature could not accept such an illogical solution, incompatible with anatomy. The auditory receptor receives a relevant stimulus, which is the energy of the sound wave. So the hair cell = receptor receives information from the sound wave that reaches it. In Bekesy›s concept, the sound wave passed through the auditory cells without passing information to the receptor. This goes against the logic of Nature.
12. A sound wave has no mass and is not subject to the law of inertia, possessing motion and acceleration. In contrast, the vibrating elements of the middle ear (ossicles) and the vibrating elements of the inner ear - the basilar membrane, inner ear fluids, OHCs and hairs of hair cells - have mass and are subject to positive or negative motion and acceleration in wave motion. There is a formula for acceleration in wave motion. (2π x frequency)2 x amplitude. Acceleration times mass = inertia g/mm/s2. The higher the frequency and amplitude of vibrating element, the higher the inertia. This issue is not analyzed in the traveling wave theory, because it indicates the difficulty of transmitting high frequencies through the basilar membrane and cochlear fluids. On the other hand, there is no problem with signal transmission through the bone housing of the cochlea.
13. The tip-links mechanism, with the pulling of cadherin links acting as the molecular mechanism of channel gates, is supposed to be responsible for the opening of mechanosensitive potassium channels in the hair cell membrane. J. Hudspeth announced that myosin is responsible for closing potassium channels. None of the entire range of myosins are able to operate this mechanism during high frequencies. They are too slow to act.
14. The basilar membrane, according to the traveling wave theory, is supposed to be responsible for frequency discrimination. The length of the human's basilar membrane = 32 mm. A trained musician recognizes 3,000 frequencies. That is, for 1 frequency with the maximum wave deflection on the basilar membrane, there is 0.0106 mm of the basilar membrane. What do these waves look like in the case of polytones with harmonic components? How do these waves traveling on the basilar membrane determine frequency resolution in mammals or birds having basilar membranes 2 - 5 mm long? Birds are very musical.
15. The hair cell is an excitable cell [10]. A supra-threshold stimulus in the form of a sound wave knocks the cell out of a state of

dynamic equilibrium, starting its depolarization, followed by repolarization. During these phases, the hair cell is insensitive to new stimulation. This is an absolute refraction, lasting about 1-2 ms. Assuming that all ion channels work at the same time, the cell cannot be depolarized and thus contract more often than 1000 /s. It is not possible to transmit high frequencies while depolarizing the entire cell at the same time. Only limited depolarization gives the possibility of high-frequency transmission. A problem arises with the mechanical amplification of low intensities of high frequencies if depolarization and contraction of the OHC cannot occur.

16. Directional hearing is determined by the difference in the time it takes for the signal to reach both ears. The difference in the interaural distance in humans results in a difference in the received signal time of 0.6 ms in air and 0.5 ms in water. This 0.1 ms difference means that in water, directional hearing does not work. The interaural distance in birds is much smaller, yet they have excellent directional recognition, even in the case of quiet sounds, which, according to the traveling wave theory, require time-consuming amplification and travel to the receptor in a roundabout way through time-consuming resonance, basilar membrane, cochlear fluids and the inclination of hairs of hair cells. The survival of many animal species on Earth depends on the speed of auditory reactions, the ability to recognize directions and judge distances.

17. The traveling wave theory does not clearly describe the conversion of the quantized mechanical energy of a sound wave into electrochemical energy of the auditory cell membrane [11]. There is no description of the biochemical processes inside the hair cell, intracellular amplification, or the importance of calcium in the transmission of information. These processes are described in the paper: «Processing and Transmission of Auditory Information» from 2004 and in the paper: «Submolecular Theory of Hearing» from 2022.

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