

Analysis of Bekesy's Travelling Wave Theory

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Abstract

This paper presents an analysis of the foundations of the travelling wave theory that pertain to the pathway a sound wave takes to reach the receptor. A critical assessment of the resonance of the longitudinal wave in the cochlear fluid with the transverse wave of natural vibrations of the basilar membrane is included. Amplification in the middle ear and the inner ear are subjected to analysis. Attention is drawn to energy conversions on the way to the receptor and the coding of information on each section of that pathway. A description of the mechanisms for receiving and transferring the information on a molecular and electron levels has not been included.

Keywords: datura stramonium; atropine; anticholinergic syndrome; devil's apple; pipe flower

Introduction

A sound wave does not hit the inner ear fluid directly; 99.9% of the energy of the wave that hits the tympanic membrane is not reflected. The assumption of the energy loss above has been adopted for calculating amplification in the middle ear [1]. On the boundary between these mediums, the sound wave is reflected, refracted, diffracted, dispersed, and absorbed. The resistance of the wave propagation in the medium is the product of density and speed of sound in the medium. The speed is 340 m/s for air, 1,450 m/s for water, 1,540 m/s soft tissues, and 3,800- 4,800 m/s for bone. Density in kg/m³: 1.2 for air, 1,000 for water, 1,060 for soft tissues, 1,912 for bones. Laser vibrometry shows that a 1,000 Hz 90 dB wave with the amplitude of 500 nm, that hits the tympanic membrane on the side of the tympanic cavity is ca. 80 dB with the amplitude of 100 nm. This wave is transmitted via the auditory ossicles to the stapedial footplate. On the stapedial footplate on the side of the inner ear its amplitude is 11.5 nm – ca. 60 dB [2,3]. Throughout the pathway of the sound wave from the external auditory canal to the cochlear fluid, sound wave amplification is not observed compared to the wave that hits on the tympanic membrane.

The difference in the active surface of the tympanic membrane of 55 m² and the 3.2 mm² surface of the stapedial footplate, the lever mechanism and the funnel shape of the tympanic membrane is claimed to increase the wave amplitude by 44 times, by 33 dB compared to the wave on the tympanic membrane [4,5].

The surface of the piston of 0.4 mm in diameter in stapedotomy is 100 times smaller than the surface of the tympanic membrane – does not increase the wave amplitude. The surface of a piston that is 0.6 mm in diameter is 50 times smaller than the surface of the tympanic membrane, and likewise, does not increase the wave amplitude in the vestibule. The lever mechanism decreases the wave amplitude at the ratio of 1.3 to 1. The energy of the wave is proportionate to the wave amplitude squared. At high frequencies, there is no vibration of the ossicles as a mass. The acoustic wave transferred via the ossicles has no mass and cannot be amplified by means of the lever method. According to Huygens' principle, "each point of the medium reached by a wave becomes a source of a new elementary spherical wave".

Following this principle, the energy absorbed by the tympanic membrane is partly transferred to the temporal bone. Likewise, the energy transmitted via the auditory ossicles is transferred onto the bony capsule of the tympanic cavity [6]. The majority of the sound wave energy is transferred onto the bony labyrinth of the cochlea by means of rocky motion of the stapedial footplate. The wave energy of the same frequency is transferred from the auricle, the tympanic membrane, the auditory ossicles of the middle ear with the stapedial footplate are subjected to constructive interference and is transmitted via the bony labyrinth of the cochlea to the hearing receptor at the speed of up to 4,000 m/s.

The adequate stimulus of the hearing organ is the sound wave that encodes auditory information.

The bony stapedial footplate is separated from the vestibular duct fluid by a layer of connective tissue that provides an additional border separating the media that has an effect on the lowering of the transmitted wave energy. Part of the energy is reflected, absorbed and dispersed. The largest part of the energy is transferred to the cochlear fluid Bekesy proposed a "straight-pipe cochlea" that forms a straight narrowing cochlear duct. This alters the laws of physics – there is no wave reflection, reflective damping, absorption damping, or interference damping. Additionally, Bekesy proposed that the Reissner's membrane be omitted in calculations and that there is a connection between the vestibular duct and the cochlear duct. The aim of this combination is to allow the sound wave to propagate on both sides of the basilar membrane and generate a travelling wave by means of creating a difference in the pressure on both sides of the basilar membrane [7,8]. In that case, resonance between the wave and the basilar membrane is possible. If allegedly, the wave runs on the side of the basilar membrane from the side of the cochlear duct, then first, it has to go across the Reissner's membrane – then, the cochlear fluid, lamina tectoria and reaches the auditory cells, the receptor. It does not transfer information because it is claimed to generate a running wave? A running wave allegedly generates flows of liquids and bends hair cells. Piston motion transfers sound wave energy to a certain frequency level undistorted [9]. Above a certain sound level, the stapedial

footplate is generating rocky motion. This motion is possible owing to the ball-and-socket incudostapedial joint. This motion is generated by means of high frequencies acting on the tympanic membrane, thus causing it and the incus to move in a way that generates motion that causes the incus and then the stapes to rock.

The rocky motion of the stapes in the transverse axis or in the longitudinal axis of the stapedial footplate cause disruption in the sound wave energy transmission. When one part of the footplate is generating a forward wave, at the same time, the other part of the footplate is generating a regressive wave. The opposing wave streams cause wave friction or destructive interference. A wave in the opposite direction cannot be in resonance with the natural vibrations of the basilar membrane. A travelling wave cannot be generated; consequently, high frequencies are not transmitted to the receptor via this pathway. In stapedotomy, the piston transmits low frequencies to ca. 6,000 Hz. Low frequencies transmitted to the cochlear fluid are well-transferred via fluids, soft tissues and bone.

The rocky motion of the stapedial footplate generates incorrect waves in the vestibular duct fluid that are inconsistent with the natural vibrations of the basilar membrane. It cannot generate a travelling wave encoding auditory information.

An additional problem pertains to the natural frequencies of basilar membrane in mammals that hear frequencies up to 100 kHz. At low frequencies, a correct wave can be formed in the cochlear fluid. However, it is questionable if there is resonance with the transverse wave of the basilar membrane heavy with the organ of Corti and embedded in the cochlear fluid that has significant damping properties. If damping is greater than the energy of the incident wave, no resonance takes place. The energy of threshold tones and tones of a slightly higher energy is lower than the damping of the reflected wave, and these tones are audible regardless. This proves that information is heading to the receptor via a different path.

Assuming that resonance is generated and a transverse travelling wave will be formed, there is an enormous disproportion between the speed of the longitudinal wave in the fluid and the transverse wave on the basilar membrane. The speed of the longitudinal wave in the cochlear fluid is 1,450 m/s, whereas the speed of the travelling wave on the basilar membrane varies from one frequency to another, estimated at 50 m/s in the area of the oval window and decreasing to 2.9 m/s in the area of the cupula.

The thesis that the speed of a travelling wave is from 29 to 410 times lower depending on frequency is untenable. Assuming the speed of a travelling wave of 10 m/s, on 1 mm of the travelling wave there is information recorded, densely packed on a 145 mm wave in the cochlear fluid. This information compression fails to ensure precise transmission of frequency, intensity, harmonics, phase shifts or quantitative. It is impossible for natural frequencies of basilar membranes in mammals to be consistent in terms of resonance with very high frequencies that they can hear. How do the data that are so densely packed and resonance-inconsistent able to code auditory information, move the cochlear fluid and the auditory hair cells?

How do they transfer the information to the receptor? Are cadherin fibres capable of coding and transmitting all the information?

Another problem pertains to amplification of soft tones ranging from 40 to 50 dB [10], by means of OHC contractions where each tone is transmitted in a different time. Multi-tones that contain soft and loud sounds that contain aliquots and phase shifts. Are soft tones are separated from loud sounds for amplification? Loud sounds are received and transferred to the centre. Are soft tones amplified by means of OHC contractions and transmitted separately to the centre? Such amplification is time-consuming and lasts several milliseconds. In that time, there is a completely different wave on the basilar membrane. This wave whose amplitude is unknown overlaps with a wave amplified by the pulling of the basilar membrane. This model of amplification is untenable. There is a molecular-level intracellular

amplification [11,12]. It is difficult to explain how the tip-links mechanism works with the basilar membrane immobilized in the cochlear implant surgery due to partial deafness. The information provided via the hearing aid in post-surgical recovery reaches the receptor. The signal reaches the receptor via the bony labyrinth of the cochlea [13].

Conclusions

Bekesy's travelling wave theory fails to explain the simultaneous depolarization and contraction of the entire auditory cell with account of the frequency of cell contractions determined by the activity of ion channels of the lateral and lower wall of the auditory cell. The operating cycle of a tension-dependent ion channel is limited to 3-4 ms. A local limited depolarization of the auditory cell is likely. Testing the frequency of OHC contractions cannot be done by teasing the cell with electricity. Cell contraction is determined by ion channels [14].

This theory lacks descriptions of processes on a molecular and electron levels. No explanation as to how a hearing receptor and the gating mechanism of the mechanically-activated potassium ion channel has been provided. No explanation has been offered for all the conversions inside the auditory cell itself has been offered either.

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