

Two Theories of Hearing

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Summary

Part one of this study presents a brief overview of the philosophy of Bekesy's travelling wave theory. The principles of the travelling wave theory are based on cochlear hydrodynamics. This aside, an important role is played by wave resonance, natural vibrations of the basilar membrane, travelling wave on the basilar membrane. The theory recognizes cochlear fluid flows that codes and transfers auditory information. An important element of that theory is the tip-links mechanism and the mechanical amplification of soft tones.

Part two of the paper provides a short description of the new submolecular theory of hearing. The main premise in this theory is that there is a different simple pathway of a signal to the receptor. Wave resonance, the travelling wave, the mechanical amplification of soft tones and the tip-links mechanism cease to be important. The information is transmitted to the receptor by means of a sound wave. Transformations in the energy that codes auditory information take place in the receptor and the auditory cell on a submolecular level. Signal amplification occurs inside the auditory cell.

Part three contains a brief summary and comparison of both theories of hearing.

Bekesy's travelling wave theory of hearing

Falling on the auricle, a sound wave is reflected and

directed to the external auditory canal. In the external auditory canal, it is subjected to resonance thus generating a wave amplification of 10-12 dB. The wave that falls from the air to the cochlear fluid is then reflected in 99.9% of the wave energy. Due to the amplification mechanism in the middle ear, 50% of the energy of the wave that falls on the tympanic membrane reaches the receptor. The difference in the surface of the tympanic membrane and the stapedial footplate amplify the signal 17 times. The difference in the length of the manubrium of the malleus and the long crus of the incus yield an amplification of 1 : 1.3. The funnel shape of the tympanic membrane amplified the signal 2 times. In total, the amplification in the middle ear is 44 times = 33 dB. According to the theory, it is an amplification of the wave that falls on the tympanic membrane (1).

The energy of the wave is transferred via the chain of ossicles onto the stapedial footplate in the oval window. Up to 2,400 Hz, the entire malleus vibrates as the mass of the malleus (2). At higher frequencies, vibrations of the malleus are not visible. Amplified by the stapedial footplate, the wave generates movements of the fluid in the vestibular duct in accordance with the frequency and intensity of the amplified wave. At low frequencies, the stapedial footplate acts as a piston, whereas at medium frequencies, it generates rocking motion in the transverse axis of the footplate. At high frequencies, it generates motion in the transverse axis of the footplate. The wave in the cochlear fluid propagates in the vestibular duct to the cupula and further to the round window. The theory holds that there is a difference in

the pressure on both sides of the basilar membrane (3,4).

Allegedly, the sound wave in the vestibular fluid triggers resonance with the natural frequencies of the basilar membrane. It is claimed to generate a traveling wave on the basilar membrane with the maximum displacement at a consistent wave frequency. The natural frequencies of the basilar membrane were estimated at 20 kHz in the area of the oval window, decreasing to 16 Hz in the cupula area. The speed of the sound wave in the cochlear fluid is 1450 m/s, the speed of the traveling wave on the basilar membrane is 50 m/s in the cochlear base area, decreasing to 2.9 m/s in the cupula area (5).

In the vestibular duct the pressure is higher than the pressure in the tympanic duct. Bekesy first assumed that the traveling wave is formed on the basilar membrane due to the difference in pressure. Later, he adopted a new concept, namely, that the sound wave propagates on both sides of the basilar membrane and causes a resonance of the longitudinal wave in the fluid with the frequencies of the natural vibrations of the basilar membrane. The lower the frequency, the closer to the cupula the sound wave is received. In the 1930s, tonotopy of hearing has been already known. The natural frequencies of the basilar membrane were adjusted to the frequency audible to the human.

The second foundation that the traveling wave theory is based on is the haemodynamics of the cochlea. A description of flows of fluids from the oval window to the round window is provided. The flow of fluids in the inner ear, which depends on the maximum displacement of the basilar membrane of the basilar membrane, make auditory hair cells lean down or bend them. The leaning of a hair cell towards the longest hair cell causes mechanically-gated potassium ion channels to open. The leaning in the opposite direction causes the ion channels to close. Neighbouring auditory hair cells are connected via protein fibres that become tense when the hair cells change their position (6). By becoming tense, the fibres pull the cell membrane of the neighbouring hair cell where the hearing receptor is located. Allegedly, the bending of a hair cell opens and closes the ion channel that allows potassium ions inside the cell, triggering its depolarization. Bekesy assumed that the basilar membrane, resonance, fluid flows and the tip-links mechanism are responsible for intensity and frequency resolution.

In the mid-1980s, it was found that an isolated external auditory cell shrinks under the influence of electricity. It was concluded that OHC contractions after depolarization in the case of soft tones are amplified by

the OHC contraction and the pulling by the basilar membrane. The amplification of soft tones is estimated at 40-50 dB (7).

The tip-links mechanism is claimed to transfer the information about the intensity, frequency, the harmonics, phase shifts, accent, melody and quantitative in a mechanical manner to the molecular mechanism that is gating the mechanically activated potassium ion channels.

Bekesy's travelling wave theory fails to explain the molecular transformations of the hearing receptor and the auditory cell itself.

Alternative theory

Submolecular theory of hearing

It describes the pathway a signal takes to the receptor and the sound wave energy transformations taking place on a molecular level. This description substantially differs from the travelling wave theory. In mammals, a small part of the sound waves that fall on the auricle is directed to the auditory canal. A bigger role is played by the energy absorbed by the auricle and transferred to the temporal bone and further to the receptor. The cat, which has 32 muscles of the ear and can turn the auricles 180°, does not direct the wave to the auditory canal. The received waves are directed via the bone labyrinth to the receptor, and also play a role in determining direction.

The ossicles of the middle ear the malleus and the incus transfer the sound wave energy absorbed by the tympanic membrane to the stapes. Some of the transferred wave energy is transmitted via ligament and articulation joints onto the bony capsule of the tympanic cavity and to the receptor (8).

A sound wave whose frequency is 1,000 Hz, intensity is 90 dB, amplitude is 500nm, that falls on the tympanic membrane is 80 dB = 100 nm on the side of the tympanic cavity. On the stapedial footplate on the side of the cochlea it is 11.7 nm, whereas in the vestibular fluid by the oval window it is 0.275 nm. The sound wave energy that reaches the stapes causes piston motion of the stapedial footplate at low frequencies. At medium frequencies, the footplate generates rocky motion in the transverse axis of the footplate. At high frequencies, the footplate motion occurs in the long axis of the stapedial footplate. Simultaneously, part of the stapedial footplate is generating progressive motion of the waves, while the other part of the footplate is generating a regressive wave. High frequencies cannot code and transfer auditory information with high precision in this manner. This is not only about the

amplitude and the frequency, but also about the harmonics, phase shifts, accent, and melody. These data are transferred via the sound wave directly to the receptor and received without any interference.

It is claimed that there is a different simple pathway that a signal takes to reach the receptor via the bony labyrinth of the cochlea. The impedance of the ossicles and the cochlear bones is similar. The wave speed is ca. 4000m/s.

By means of rocky motion, the stapedial footplate transfers sound wave energy onto the bony labyrinth of the cochlea straight to the receptor. The acoustic wave in the vestibular fluid generated by the rocky motion is an altered wave that cannot generate resonance with the natural frequencies of the basilar membrane. The information reaches the ECoG measurement point from the auditory canal via the bony labyrinth of the cochlea in 1.5 ms. The potential and kinetic energy that reaches the receptor forms the total energy of the sound wave. This energy, which codes auditory information and is received by sound-sensitive molecules is forwarded to the gating mechanism of mechanically activated potassium ion channels of the auditory cell membrane. In the time when a potassium channel is fully open, the cell can receive an influx of 6000 ions from the endolymph in 1 millisecond. These processes are taking place on a sub molecular level (9). Sound wave energy determines the gating of mechanically activated potassium ion channels by generating conformational changes of particles and the formed conformers fulfil their role that consists in regulating the flow of potassium ions through the canal t the auditory cell. This results in a depolarization of the auditory cell and all the consequences related to the discharge of the transmitter to the synapse (10).

Molecular transformations inside an auditory cell are addressed in a separate study. Part of these transformations is the intracellular signal amplification, which is regulated on a molecular level.

Comparison of both theories of hearing

The difficulty in accepting the submolecular theory of hearing is due to the grave difference between the two philosophies of hearing. To explain the mechanisms of hearing, this theory provides a description of the processes on a molecular an electron level.

1. The new theory postulates a pathway of the signal to the hearing receptor leading from the tympanic cavity via the bony labyrinth of the cochlea directly to the auditory cells.

Substantiation

- a. Blocking the pathway leading via the travelling wave and the cochlear fluid in the cochlear implant surgery due to partial deafness does not affect the existing hearing abilities.
 - b. The use of a hearing aid for air conductivity in rehabilitation of patients after the cochlear implant surgery shortens the rehabilitation process. The signal reaches the receptor through the hearing aid (11).
 - c. The resonance of a longitudinal wave in the cochlear fluid with a transverse wave of the basilar membrane does not transfer all the auditory information. This issue is worse in mammals that can hear sound frequency up to 200 kHz.
 - d. In the case of 1 or 2 incident wave periods, the auditory signal is received by the receptor. Wave resonance is not possible. Hearing is preserved for signal whose duration is tenth of a millisecond (12,13).
 - e. The speed of a sound wave in liquid is 1450 m/s. According to Bekesy the speed of the travelling wave is 2.9 m/s - 50 m/s. This causes the information to be compressed from 29 to 410 times on the basilar membrane. Each frequency of the incident wave triggers a different speed of the travelling wave. 410 mm of a wave in the cochlear fluid is recorded on 1 mm of the travelling wave. This is unacceptable.
 - f. The frequency of the incident wave must be consistent with the frequencies of the reflected wave - with the frequencies of the natural vibrations of the basilar membrane. Natural vibrations of human tissues range from 5 to 100 Hz. We can hear frequencies up to 20 kHz. Other mammals can hear sounds up to 200 kHz. There is no consistency in the frequencies of the two waves (14).
 - g. The basilar membrane is vibrating in the fluid with high dampening properties. If the dampening is higher than the energy of the incident wave energy, no resonance occurs. This situation takes place during listening to threshold tones and louder tones that are received by the receptor regardless of this principle.
2. On its way to the round window via the cochlear fluid, the sound wave disappears. The 8000 Hz wave, which is 90 dB – amplitude of 500 nm on entry, examined in the round window shows an amplitude of 0.5 nm. (15,16).

The pathway to the round window is not the pathway to the receptor; however, on half of that

pathway – the one that leads to the cupula – losses higher than on the pathway from the cupula to the round window are shown. The energy loss in the way to the receptor is not known. The amplitude of the wave becomes 100 to 500 times lower. We do not know that since there are no studies to prove that. What is certain is that it becomes lower.

A wave of 800 Hz and 30 dB on entry could not be detected on the round window. The wave on the pathway to the round window calculated based on Bekesy's methodology for 10 dB and 10 kHz – the frequencies that are audible for us; Amplitude of the displacement of the stapes = 0.000011757 nm, Amplitude of the wave at the beginning of the vestibule = 0.0000000874 nm, Amplitude of the basilar membrane = 0.000260 nm. One cannot hear a wave of the above amplitude.

3. A healthy young man can hear the sound of 1000 Hz, amplitude of 8 pm. This wave becomes weaker on the pathway via the cochlear fluid by 100, perhaps 200 times, and supposedly moves the fluid in the inner ear that bends or leans the hair cells that are 100 nm thick.

A wave that is about a million times smaller than the diameter of the hair cell can move it up to 200 times a second. A twig that is 1 cm thick cannot bend a tree that is 100 metres in diameter! or make a hair cell lean if it is connected to the tectorial membrane.

4. The time in which the signal covers the pathway from the auditory canal to the ECoG or BERA measurement point is 1.5 ms (17). In turn, according to Bekesy, the time for all the sections of the same pathway is 5-6 ms. Each frequency has a different time in which it reaches the receptor due to varying speed of the traveling wave after it resonates with the transverse wave of the basilar membrane. The auditory reaction time is highly important in the animal world.
5. The tip-links mechanism does not work for a blocked basilar membrane (cochlear implant) and the signal reaches the receptor.
6. If according to Bekesy, an OHC contraction amplifies soft tones then amplified soft tones are transferred to the receptor with a delay separately from loud tones. An issue arises regarding multi-tones. Sounds amplified 44 times in the tympanic cavity and amplified by 40-50 dB by the OHC

contractions are still audible to us as soft tones.

7. A sound wave transfers a chain of tightly packed data. If an OHC contraction pulls by the basilar membrane when another foreign bit of information is being transferred, perhaps a loud one, would it be amplified, too?
8. Sound wave energy codes not only amplitude and frequency but also aliquots, phase shifts, accent, melody, and quantitative. How are these values coded and transmitted by means of the travelling wave, fluid flows, the bending of auditory hair cells, or cadherin fibres?
9. Sound wave energy is quantized and in that form forwarded to the receptor. How do the travelling wave and the cochlear fluid quantize the energy that codes multi-tones with numerous harmonics that work at the same time?
10. In the middle ear and the inner ear, there are elements of the signal pathway that transfer vibrations that have mass. In wave motion, there is also speed, acceleration. If there is mass, then there is inertia that in is not accounted for in the travelling wave theory. It affects the lack of conduction of high-frequency sounds in stapedotomy. Physiologically high tones are audible since the wave heading from the tympanic cavity to the receptor has no mass and is not subject to the law of inertia. In the middle ear, the ossicles vibrate to the frequency of ca. 2,400 Hz. Above this threshold, the ossicles conduct sound waves like a bone – albeit with no shift in the mass of the environment.

The submolecular theory dismisses the mechanical amplification of a sound wave invented in in the 1970-80s by adherents of Bekesy's theory. The amplification exists on a molecular level in the auditory cell itself, after the signal is received by the receptor. Tones that are too weak to reach the central nervous system are amplified. This mechanism applies to other senses, too. The basilar membrane is not pulled by OHC contractions. The pulling without regulation in time when a completely foreign wave propagates via the basilar membrane interferes with the transfer. The soft tone that requires amplification cannot be amplified by means of this purely physical method. The information of the soft wave has been received and forwarded to the centre. A wave that has not been received cannot be amplified by means of this method. An OHC contraction is the condition in this respect. Intracellular amplification has been described in 2004 in a study called *Przetwarzanie*

i przekazywanie informacji słuchowych [Transforming and transmitting auditory informations] and another paper titled *Nanomechanizmy słyszenia* [The nanomechanisms of hearing]. Amplification of soft tones occurs also when the signal pathway is blocked by the cochlear fluid, resonance, and the travelling wave.

The submolecular theory dismisses the tip-links mechanism. It is the sound wave energy that acts directly on the gating mechanism of potassium ion channels by means of sound-sensitive molecules.

The submolecular theory explains why hearing is preserved after partial deafness is remedied by means of a cochlear implant surgery.

The submolecular theory emphasizes the meaning of sound wave energy quantization in the coding, reception, and transfer of auditory information. It describes the nanostructures and nanoprocesses related to energy transformations on the way from the external world to the central nervous system.

The submolecular theory claims that there are molecules with genetically conditioned sensitivity to receiving sound wave energy of a specific frequency. These particles are called sound-sensitive molecules back in 2003. The receptors that receive frequencies from high to low are located on the basilar membrane from the basis of the cochlea to the cupula. This thesis explains the tonotopy that has been known for 100 years that is wrongly associated with resonance and the travelling wave.

The submolecular theory provides a detailed description of the life and activity of an auditory cell. Life, since it a living cell, just like all the others. Activity, since it fulfils complex tasks related to depolarization, information processing, transmitter production and discharge to the synapse at the frequency conditioned by the activity of the ion channels of the cell.

The submolecular theory questions if a contraction of an entire auditory cell is possible. The operating cycle of ion channels is 4-5 ms. Therefore, an auditory cell as a whole cannot be subject to depolarization and contraction at the same time, e.g., 100 000/s? A limited local depolarization and contraction is possible.

The submolecular theory provides a critical take on the method for examining the maximum frequency of contractions of external auditory cells caused by electricity. The study consisted in teasing isolated

external auditory cells with electricity. Cell contractions are determined by the activity of ion channels that are restricted in time.

The new theory of hearing named the submolecular theory of hearing was first presented in the year 2000 to the National Consultant for Otolaryngology Prof. Grzegorz Janczewski. He penned a positive review. I have published the revised and supplemented submolecular theory of hearing in HSOA Journal of Otolaryngology, Head and Neck Surgery 2022,8,069.

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