Cochlear Potential Difference Between Endolymph Fluid and the hair Cell's Interior: a Retold Interpretation Based on the Goldman Equation

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REVIEW

Cochlear potential difference between endolymph fluid and the hair cell's interior: a retold interpretation based on the Goldman equation

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ABSTRACT

Reported cochlear potential values of near 150 mV are often attributed to endolymph itself, although membrane potentials result from ion fluxes across the adjacent semipermeable membranes due to concentration gradients. Since any two fluids separated by a semipermeable membrane develop potential due to differences in solute concentrations, a proposed interpretation here is that positive potential emanates from the Reissner membrane due to small influx of sodium from perilymph to endolymph. Basolateral hair cell membranes leak potassium into the interstitial fluid and this negative potential inside hair cells further augments the electric gradient of cochlear potential. Taken together as a sum, these two potentials are near the reported values of cochlear potential. This is based on reported data for cochlear fluids used for the calculation of Nernst and Goldman potentials. The reported positive potential of Reissner membrane can be explained almost entirely by the traffic of Na+ that enters endolymph through this membrane. At the apical membrane of hair cells, acoustic stimulation modulates stereocillia permeability to potassium. Potassium concentration gradients on the apical membrane are low (the calculated Nernst value is <+3 mV), suggesting that the potassium current is not caused by the local potassium concentration gradient, but an electric field between the positive sodium generated potential on the Reissner membrane and negative inside hair cells. Potassium is forced by this overall electric field to enter hair cells when stereocilia are permeable due to mechanical bending.

Key words: membrane potential, ion traffic, membrane permeability, labyrinth

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INTRODUCTION

Despite many advances in our understanding of hearing (1) and cochlear anatomy (2), several questions remain open. Without exceptions, recent editions of physiology textbooks (3-5) note that hearing is lost without an adequate cochlear potential. Endolymph solute concentrations are similar to the cellular fluid, while the perilymph composition resembles cerebrospinal fluid (CSF) and plasma values.

Cochlear potential is attributed to the vascular stria that actively pumps ions between plasma and endolymph. High potassium level in endolymph is explained by potassium pumping from plasma and also by recuperation of potassium that leaked from hair cells to the interstitial space in the organ of Corti (1,3,4). It is unexpected that the extremely low sodium concentration in endolymph is not generally considered important in our textbooks for the generation of cochlear potential.

Unusually high reported values (near 150 mV between endolymph and hair cells) are often attributed to the endolymph fluid itself (‘’.. the hair cells have a negative intracellular potential of -70 mV with respect to the perilymph, but -150 millivolts with respect to the endolymph at their upper surfaces where the hairs project through the reticular lamina and into the endolymph’’, ‘’... auditory endolymph has a voltage of +80 mV relative to the perilymph...’’) (3,4), although cellular membrane potentials are generally considered to result from chemical gradients across semipermeable membranes due to membrane permeability (6,7). This means that fluid confined within an impermeable membrane has no electric potential and the endolymph potential can be measured only in comparison to another fluid behind a semipermeable membrane. Two membranes that separate three cochlear scales are often considered electrically unimportant, although at least the Reissner membrane is permeable to certain ions and water (1) and thus should generate measurable membrane potential.

Another related but almost neglected point is that membrane potential cannot be higher than the Nernst value calculated for the concentrations of the most permeable ion. Therefore, values between 120 and 150 mV cannot result from the Goldman equation using reported solute concentrations (1). Beside all that, a less explained feature of endolymph is that this fluid is normally slightly hypertonic (1), some 330 mosm/L in comparison to 280mosm/L in perilymph.

This paper aims to reconsider electrophysiological aspects of hearing by attributing electric potential values measured in cochlear fluids to permeability of Reissner membrane and hair cell membranes to certain ions. Described interpretation is based on previous papers about ion traffic in cystic fibrosis (7,8) and importance of chloride (Cl-) membrane traffic and Donnan effect of cytoplasmic proteins (9,10).

BASIC ASSUMPTIONS BEHIND THE PROPOSED INTERPRETATION

A description of the cochlear potential, presented here, is based on several assumptions.

Membrane ion traffic is governed by electric fields, concentration gradients and the ion specific membrane permeability (3-5). All cell membranes act as diffusion bottlenecks and if ions accumulate near the membrane, their electric charges alter diffusion of other ions.

If a membrane allows only one ion to diffuse along its concentration gradient, the diffusion will continue until the membrane potential reaches the Nernst value for that ion (3-5). Further ion traffic depends on the Brownian kinetic that washes away ions adjacent to the membrane surface and thus allows further diffusion through the membrane.

Cell membranes are almost always permeable to more than one ion and the actual membrane potential can be calculated by the Goldman equation. Cells permeable to potassium (K+) and chloride (Cl-) ions normally have membrane potential somewhere between the respective Nernst values for these ions (3-5).

An example: the resting potential in neurons is near the potassium Nernst potential and further traffic of K+ is opposed by a strong electric force (3-5). Traffic of ions across the membrane becomes intensive only during the action potential due to momentary altered membrane potential. During depolarization, the potential shifts from a value near the potassium Nernst value toward the sodium Nernst value. Only the weakened membrane electric field while shifting between these two Nernst potentials allows ions to follow their concentration gradients and cross the membrane (3-5, 8). Despite membrane conductance

for a certain ion, stable membrane potential near the Nernst potentials of that ion prevents further traffic of that ion across the membrane.

The apical membranes of hair cells face the endolymph, while laterobasal membranes are exposed to perilymph (3-5). Under no circumstances can membrane potential exceed beyond the overall range of Nernst values for all ions able to cross that membrane, since the actual potential is a resultant of all existing ion currents (3-5).

Based on solutes and electric potential in the cytoplasm (reported -50 to -70 mV relative to perilymph (1), it can be assumed that basolateral membranes are permeable to potassium and chloride. Therefore, leaking of potassium from hair cells into the interstitial fluid is probably the main determinant of the cytoplasmic potential in hair cells, as it happens in other cells (3-5).

Hyperosmolar fluids are expected to accumulate in compartments with active pumping of solutes, but only if traffic of ions and water with adjacent tissues is limited and thus allows accumulation of solutes. For instance, hyperosmolar kidney medulla is of reduced vascularity (slow perfusion through vasa recta) and topologically isolated in renal pyramids (11). Intense solute pumping happens on the border between medulla and cortex, so diffusing solutes remain trapped in medulla and thus undisturbed by circulation.

Elevated osmolarity of endolymph can also result from ion pumping in stria vascularis (Na/K pumps, proton pumps etc. (1) combined with specific cochlear vasculature and vascular permeability.

The proposed interpretation of the cochlear potential as a sum of two membrane potentials

The interpretation proposed here is based on the idea that any two fluids separated by a semipermeable membrane can develop electric potential due to differences in solute concentrations and membrane permeability for certain ions. Without ion traffic through a semipermeable membrane, no measurable electric potential is expected, so it cannot be assumed that endolymph is per se positive, or perilymph neutral and hair cell's interior negative.

All reported potentials in these three fluids are expected to come from ion traffic across some membrane between them. The Reissner membrane is between perylimph and endolymph, while the apical hair cell membrane with stereocilia separates endolymph from the hair cell cytoplasm. Basolateral hair cell membranes are between the cytoplasm and perilymph. This simple approach suggests that the unusually high cochlear potential should be considered as a sum of two membrane potentials. Both potentials are relative to the perilymph potential that can thus be regarded as neutral or 0 mV (1).

The basic idea of the proposed interpretation is that positive potential emanates from the endolymphatic side of the Reissner membrane, while the negative potential exists on internal sides of the laterobasal membranes of cochlear hair cells. Taken together, these two potentials are near the reported values of cochlear potential.

Since selective permeability values for sodium, potassium and chloride of these three semipermeable membranes are not reported, we can use Nernst values as a surrogate marker. If the reported fluid potential is near the Nernst value of a certain ion, traffic of that ion is the dominant cause of the reported potential.

Here presented tables and figures are based on published data (1), while Nernst potentials were calculated by the Goldman's equation calculator (12,13).

A. Interpretation of cochlear potential

Data and calculated membrane potential values are shown in Table 1 and Figure 1.

Table 1. Interpretation of normal cochlear potential*

Parameters for the Goldman equation	**Reissner membrane**	**Apical hair cell membrane**		**Basolateral hair cell membrane**
		Minimal stereocilia K^+ conductance	**Large stereocilia K^+ conductance**	
pK^+	1	1	19	100
$[K^+]_o$	5	130		5
$[K^+]_i$	130	120		120
EK^+	-87	+2.1		-84.9
pNa^+	100	100		2
$[Na^+]_o$	140	1		140
$[Na^+]_i$	1	15		15
ENa^+	+132	-72.3		+59.7
pCl^-	1	1		1
$[Cl^-]_o$	115	130		115
$[Cl^-]_i$	130	115		115
ECl^-	-3.3	+3.3		0.0
Goldman potential (mV)	**+100**	**-43.4**	**-10.0**	**-69.7**

*pX^x, relative permeability; $[X^x]o$, outside concentration (mmol/L); $[X^x]i$, inside concentration (mmol/L); EX^x, the Nernst potential (mV for the ion X^x); The expected Nernst potential values and Goldman potential calculated by the Goldman's equation calculator (17) from reported data (6)

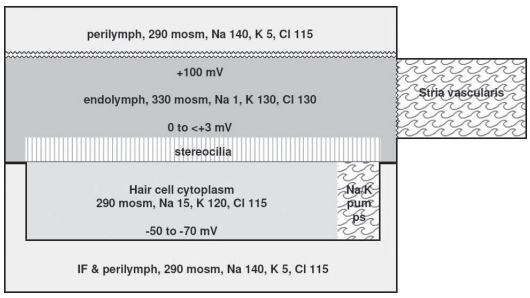

Figure 1. Model of normal cochlear potential
The expected Nernst potential values calculated by the Goldman's equation calculator (12) from reported data (1)

Here are a few remarks.

It is obvious that the reported highly positive potential of the Reissner membrane can be explained almost entirely by the traffic of Na+ that enters endolymph. Reduced traffic of potassium and of chloride ions produce negligible negative potentials that prevent reaching the sodium Nernst potential. Since the cochlear potential is near the sodium Nernst value, the sodium current is limited due to the presence of the sodium traffic opposing electrical field, so the sodium leak from perilymph to endolymph is very small. Sodium ions, after entering the endolymph, are pumped out of the cochlear endolymph by pumps in the vascular stria pumps. The result is that a highly positive electrostatic field emanates from the Reissner membrane and spreads throughout endolymph and organ of Corti.

If we look at the apical membrane of hair cells that carries stereocilia, acoustic stimulation modulates their permeability to potassium. Potassium concentration gradients on the apical membrane are low and only weak membrane potential is expected from the gradient of potassium concentrations (Nernst value is <+3 mV) (Table 1). If the apical membrane around stereocilia is impermeable to ions there would be no electric potential, but if it is permeable to sodium, a strong electric potential would be generated, positive on the endolymph side and negative on the perilymph side due to sodium leakage from hair cells to the endolymph. Here again, the leak is very small due to the opposing electric field that facilitates potassium influx through bended stereocilia. This clearly suggests that the potassium current does not depend on the local potassium concentration gradient, but on the electric potential due to sodium traffic across the Reissner and the apical membrane.

Basolateral hair cell membranes leak potassium into the interstitial fluid and this negative potential inside hair cells further augments the electric gradient of cochlear potential (near 150 mV of potential difference is expected between the fluid bellow the Reissner membrane and in the bottom part of hair cell cytoplasm). This huge potential difference is generated by adding values of two ions, positive potential due to sodium leaking across the Reissner membrane and a negative value due to potassium leaking through basolateral membranes of hair cells.

Potassium is forced by this overall electric field to enter hair cells if stereocilia are permeable due to mechanical bending, regardless of local potassium concentrations. This means that potassium current will allow hair potential to be accurately modulated according to the momentary changes in stereocilia position.

In short, acoustic stimulation makes apical membrane permeable to potassium ions, they enter due to the cochlear potential and their accumulation below the apical membrane makes the overall hair cell membrane potential less negative, thus allowing more transmitter molecules to be released. Since transmitter secretion from hair cells depends on potential fluctuations and not on the action potential generation, the proposed chain of actions does not result in a binary-coded detection of a threshold change (0- threshold value not reached, 1- threshold value exceeded). Instead, the hair cell potentials produce a real-time analog measurement of auditory stimulation by modulation of the potassium current that governs transmitter secretion.

The proposed setting for the cochlear potential has several important features:

all auditory hair cells are subjected to the similar electric field that emanates from the positively charged Reissner membrane above them resulting in a low and predictable energy metabolism of individual cells.

Modulated and uninterrupted potassium flow from endolymph to interstitial fluid through hair cells has two effects on membrane potential of hair cells: apical K+ influx makes the local membrane potential less negative and thus the overall basolateral potential becomes less negative and this change increases secretion of neurotransmitters.

The potassium current is undisturbed as long as stereocilia are permeable to potassium. Basolateral K+ efflux from hair cells to interstitial fluid restores the overall cytoplasmic negativity of hair cells. Although noise exposure can probably increase the average potassium inflow, there is no risk of K+ accumulation within hair cells since the added K+ ions can leak out through basolateral membranes. This leakage to the interstitial fluid acts as a protective potassium sink against the increased apical influx of potassium ions.

Reduced negativity of basolateral membranes also enhances leakage of potassium through them. These actions regain the membrane potential without additional ion pumping in and out of hair cells. Metabolically undemanding hair cells can thus be smaller and more densely packed, allowing better sound differentiation within limitations of cochlear dimensions.

B. Interpretation of extracochlear potentials within the membranous labyrinth

Data and calculated Nernst values are shown in Table 2 and Figure 2.

Table 2. Interpretation of the normal extracochlear potential within the membraneous labyrinth

Parameters for the Goldman equation	Reissner membrane	Apical hair cell membrane		Basolateral hair cell membrane
		Minimal stereocilia K^+ conductance	Large stereocilia K^+ conductance	
pK^+	<~1	5	100	100
$[K^+]_o$	5	15		5
$[K^+]_i$	15	120		120
EK^+	-29.3	-55.5		-84.9
pNa^+	100	1		2
$[Na^+]_o$	140	100		140
$[Na^+]_i$	100	15		15
ENa^+	+9.0	+50.7		+59.7
Goldman potential (mV)	**+9.0**	**-33.6**	**-53.8**	**-73.1**

*pXx, relative permeability; [Xx]o, outside concentration in mmol/L; [Xx]i , inside concentration in mmol/L; EXx, the Nernst potential in mV for the ion Xx. The expected Nernst potential values and Goldman potential calculated by the Goldman's equation calculator (17) from reported data that lack chloride concentrations (6).

Here are some remarks:

It was reported that although the endolymphatic sodium concentration is here much higher than in the cochlea, the extracochlear endolymph is of low positive potential near +10 mV (1).

The exact chloride concentrations for these settings were not reported (1), so Goldman is calculated only for potassium and sodium (permeability for chloride ions was set to 0).

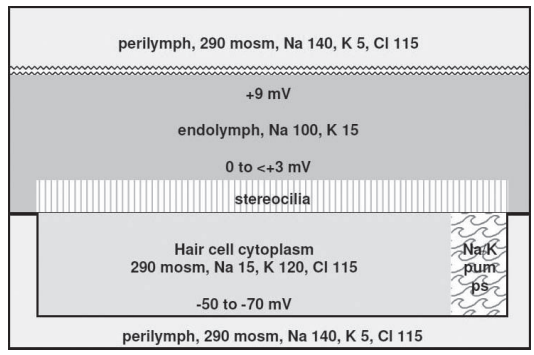

Figure 2. Model of the normal extracochlear potential
The expected Nernst potential values calculated by the Goldman's equation calculator (12) from reported data (1)

Nernst potentials of sodium and potassium for this setting on the Reissner membrane (Table 2) suggest that even here the weak leak of sodium from perilymph to endolymph maintains the reported positive potential (sodium Nernst value on the Reissner membrane is +9 mV, the reported value is +10 mV), suggesting that the sodium current is adequately opposed with an electric field, so only minimal sodium leaks from perilymph to endolymph are expected. This means that here absent stria vascularis is not required to maintain the reported concentrations of these solutes, dark cells that secrete some potassium (1) are probably sufficient, endolymph circulates through the labyrinth, so in areas remote from cochlea, fluid

Table 3. Comparison of solid electrets with the proposed interpretation of cochlear potential

Comparison of electric field features	Solid electrets	Large semipermeable membranes between fluid compartments
Stable electric field maintained without drain of energy	YES, due to permanently bound electrostatic charges	NO, membrane layered charges depend on the membrane ion permeability and thus on energy invested in ion pumping in adjacent fluid compartments
Dipole polarity of the electric field	YES, solid electrets usually have two opposed faces: one positively and one negatively charged	YES, concentration gradients force ion traffic through the membrane and generate electric potential according to the Goldman equation. One membrane side more positive in comparison to the other side
Electric fields generated by two-dimensional sources	A homogenous electric field can easily be created by placing two charged and congruent surface areas at small distance, thus resembling a charged capacitor field across the dielectric	

accumulates sodium and loose potassium ions through adjacent membranes.

Potassium concentration gradient on the apical hair cell membrane suggests that a strong electric potential must drive potassium into the hair cells through bended stereocilia against its concentration gradient. Two situations are shown in Table 1. In the case with low potassium permeability of unbended stereocilia, the calculated apical membrane potential is -33.6mV, while in the case of 20 times greater potassium permeability, the potential is more negative, -53.8mV.

If we compare Tables 2 and 1, this interpretation predicts that apical membranes of hair cells differ in their sodium conductivity. Cochlear hair cells allow more sodium than potassium to cross the apical membrane. In extracochlear hair cells sodium conductivity through the apical membrane is much lower than the potassium conductivity.

This difference results in opposite changes in the membrane potential due to stereocilia bending. In cochlear hair cells, increased potassium traffic through bended stereocilia makes membrane potential less negative, while in extracochlear hair cells, the same change of potassium traffic makes the potential more negative. It is important to note that direction of electric potential alteration is probably unimportant as long as transmitter secretion is adequately modulated by the mechanical stress of stereocilia.

POSSIBLE EXTRAPOLATIONS OF THE PRESENTED INTERPRETATION

Comparison of the cochlear potential with electrets

Several authors have put forward the idea that electrostatic fields around cell membrane are similar to electrets (14-16), since an electret is a stable dielectric material with a static electric charge, or with oriented dipole polarization. Table 3 is intended to give a broader look at similar features of the here proposed cochlear electric field and electrets.

Electrets are similar to permanent magnets in their dipole polarization easily detectable on their surface. Reissner membrane mimics two-dimensional sources of stable positive electric field emanating from the endolymph side. The main distinction is that the Reissner membrane is not a permanently polarized dielectric. Instead of that, the membrane polarization depends on ion leakage due to concentration gradients imposed by ion pumping in the vascular stria, so it requires energy to be maintained.

In short, the two-dimensional source of positive charge above the Corti organ is similar to a solid electret facing a vibrating membrane, as it can be found in any contemporary electret microphone. This analogy suggests that variable distance between the basilar and the Reissner membrane, caused by the basilar membrane vibrations, might be important in the process of cochlear sound detection and differentiation mainly due to changes in the strength of the electric field forcing potassium ions through hair cell stereocillia.

Comparison of the cochlear function with an electronic tube amplifier

The interpretation presented here in several ways resembles design and function of the amplifying electronic tube known as the triode (17). In both cases, weak signals are used to modulate current of charges that is driven due to an outside source. A triode is the simplest amplifier, so it seems plausible that we should also consider complex ion traffic of hair cells with endolymph and perilymph as an amplified mechanoelectrical analog converter that transforms sound vibration into real-time variations of electric membrane potential that modulates transmitter secretion from hair cells.

Complex cochlear transports of sodium possibly facilitate potassium accumulation in endolymph

It has been reported that hypoxia, ouabain, furosemide, amiloride and proton pump inhibitors can change the cochlear potential thus impairing hearing, so we can assume that all structures targeted by these drugs must be involved in the endolymph content maintenance (1,2). Since low sodium and high potassium in endolymph seem responsible for the cochlear potential, our hearing depends on Na/K pumps, proton pumps, sodium cotransporters etc.

Sodium ions can enter the cochlear endolymph compartment from two structures, the Reissner membrane and the terminal sulcus (1). Since the vascular stria is placed between these two structures, it seems possible that sodium leakage through these two linear structures (below and above the vascular stria) can help the local function of Na/K pumps that will pump sodium back to plasma in

exchange for potassium. Chloride ions probably enter endolymph along the electric gradient from perilymph and possibly from hair cells. It seems plausible that chloride ions are not easily carried away by plasma in stria vascularis due to the Donnan effect of plasma proteins that force out negative ions, so we should not be surprised that their concentration in the endolymph is increased, leading to the reported endolymph hyperosmolarity.

We should here keep in mind that Na/K pumps deliver 2 K+ (from plasma into the endolymph) for 3 Na+ (from the endolymph into plasma), meaning that Na/K pumps are electrogenic (trading three positive for two positive ions) and also osmogenic (pumping three well-hydrated Na+ for two less hydrated K+ ions (6, 7)). Potassium levels in plasma are low (near 5 mmol/L), so when sodium levels in endolymph are also near that concentration, or even lower, local Na/K pumps are forced to reduce their activity, primarily due to lack of sodium in endolymph. Local influx of sodium through the Reissner membrane and marginal sulcus can then help restart Na/K pumps that stopped due to the lack of sodium exposure on the endolymph side of stria vascularis. By this mechanism, lower levels of sodium and higher levels of potassium can be reached in endolymph.

The interpretation presented here suggests that a weak sodium current might exist in the apical hair cell membrane supporting the membrane potential of hair cells (negative on inside and positive on the endolymph side). Stereocilia bending allows potassium to enter and thus reduce internal negativity proportionally to the degree of bending. Therefore, this is a unique modulation of hair cell membrane potential that is quantitatively related to the auditory stimulation. This analogous modulation is quite the opposite from the action potential in which a sufficient stimulus that passes the threshold potential imposed by the diffusion of chloride ions enables the full depolarization (the "all or none" principle). If we want to put it in technical terms, neurons handle signals as a binary code (polarized vs. depolarized), while the sound exposed cochlear hair cells analogously modulate their secretion of transmitters.

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TRANSPARENCY DECLARATION

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Razlika potencijala između endolimfe i tekućine citoplazme kosatih stanica u unutarnjem uhu – reinterpretacija prema Goldmanovoj jednadžbi

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SAŽETAK

Uobičajeno je izmjerenu vrijednost razlike električnog potencijala u pužnici uha od blizu 150 mV navesti kao značajku same endolimfe, iako svi membranski potencijali nastaju iz prometa iona kroz polupropusne membrane, duž koncentracijskih gradijenata. Budući da bilo koje dvije tekućine, odvojene polupropusnom membranom, mogu razviti razliku električnih potencijala na membrani, ukoliko postoje razlike u koncentracijama iona, ovdje predloženo tumačenje je da pozitivni potencijal potiče iz Reissnerove membrane zbog malog utoka natrija iz perilimfe u endolimfu. Bazolateralne stijenke kosatih stanica propuštaju kalij u intersticijsku tekućinu, što stvara negativni potencijal unutar kosatih stanica koji dodatno povećava električni gradijent kohlearnog potencijala. Zbrojeni zajedno, ova dva membranska potencijala su u blizini izmjerenih vrijednosti kohlearnih potencijala. Model se temelji na dostupnim podacima o sastavu endolimfe i perilimfe u pužnici, koji su uporabljeni za izračun Nernstovih i Goldmanovog potencijala. Pozitivni potencijal Reissnerove membrana može biti gotovo u potpunosti objašnjen ulaskom Na+ iz perilife u endolimfu. Na gornjoj membrani kosatih stanica, akustičke stimulacije moduliraju propusnost stereocilija za kalij. Gradijenti koncentracije kalija su na gornjoj membrani niski (izračunati Nernst vrijednost <3 mV), što ukazuje da struja kalija nije uzrokovana lokalnim gradijentom koncentracija, već električni, poljem između pozitivnog potencijala na Reissnerovoj membrani i negativnim potencijalom unutar kosatih stanica. Kalij, pod snažnim električkim poljem, nastoji ući u kosate stanice i u tome uspjeva proporcionalno mehaničkom savijanju stereocilija zvučnim valovima.

Ključne riječi: membranski potencijal, kretanje iona, membranska propustljivost, labirint