Novel Phonoreceptive Mechanism of the Cochlear for Low-frequency Sound

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Nobel Laureate von Békésy experimentally discovered traveling wave vibration of the basilar membrane (BM) in the cochlear, which first reveals the motion law of the crucial structure of human phonoreceptive mechanism. However, with the further development of research, many scientists have discovered that the travelling wave vibration unable to explain many experimental observations and the low-frequency hearing of the cochlear. Because the cochlear is very small and complex, vibration data of the whole BM are not yet available from existing experiments, and low-frequency vibration data are absent from Békésy’s and other experiments. To address this question, this work technically adopts the transformation tensor mapping relation to established a theoretical analytical model of the Spiral cochlear based on the theory of physics and biology, combined with medical and modern light source imaging experimental data. In addition, a numerical model of a real human ear is also established. By performing numerous calculation, the results reproduce the known travelling wave vibration of BM. Meanwhile, an exciting finding that revealing a new standing wave vibration mode at low frequencies is obtained. More importantly, this newly discovered model intrinsically explain many experimental observations that cannot be explained by travelling wave theory, which solves a long standing various queries to travelling wave vibration among researchers. These results not only complement low-frequency vibration data that are inaccessible through experiments but also reveal a new hearing mechanism.

This paper carries out a systematic research including comparative analysis of analytical solution, numerical simulation with experimental results.

The cochlear is an important functional structure in the auditory pathway (Fig. 1), for there is a fundamental structure called basilar membrane (BM) which plays a key role for human hearing sensation [1].

The investigation of phonoreceptive mechanism of human cochlear is a major medical problem for mankind. It has received wide attention from many life scientists and medical works [2]. Up to now, scientists have not reached a consensus on the vibrating mode of the key macrostructure—basilar membrane. The achievement of auditory function in the cochlear is attributed to fluid-structure coupling motions between lymph and BM. Revealing the kinetics of BM in the lymph of cochlear is a primary and pivotal question to understanding phonoreceptive mechanism of human cochlear [3].

Regarding this crucial question, Békésy in 1960 proposed his famous traveling wave theory [4] by measuring the motions of the BM from fresh temporal bones, for which he was awarded a Nobel prize. From then on, numerous researchers have proposed mathematical and mechanical models [5-10] to describe the observed vibration behavior of the BM based on the traveling wave theory. But with the progress of research in this field, many scientists have raised doubts about the traveling wave theory since the end of last century, doubts originating from the nonviability of traveling wave theory in explaining many experimental discoveries and low-frequency sound hearing of the cochlear [11-14], as Békésy’s experimental data did not include the data of BM vibration of cochlea at low frequencies.

It is worth mentioning that it is generally believed that the low-frequency hearing ability is attributed to the apical mechanical behavior of the BM [15-16]. However, it is so difficult to obtain the coupling biological dynamic process between BM and lymph in low-frequency via vivo experiments. In particular, because the apical space is narrow and with complex structures, mechanical responses at the apex of the BM are still poorly understood since no such data have been obtained from cochlear that were reasonably free of experimenter-induced damage. The method for measuring cochlear vibrations requires the placement of artifacts on the vibrating structures and, therefore, often perforating Reissner’s membrane [17], which
destroy physiologically environment in the cochlea and affect the system motion mechanism [15]. Meanwhile, there are no experimental measurements of the BM vibration in low-frequency so far.

In view of above problems, based upon our decade spanning endeavor in the field of biomechanical investigation of human ear, this work first technically adopts the transformation tensor mapping relation to established a three-dimensional spiral cochlear fluid-structure mechanical analytical model. Meanwhile, in order to make our research more accurate and credible, a most physiologically accurate human ear numerical simulation model is established, based on the most advanced CT imaging technology in Shanghai Synchrotron Radiation Facility and then the real geometrical data of the human ear (including outer ear, middle ear and inner ear) was obtained. In addition, this model was completely in line with morphology of human ears, physiological environment and properties of biological materials. This accurate analytical model and the numerical model characterized by above remarkable features have not been reported in past works.

The presented analytical solutions and numerical simulation results predict the displacement amplitude of BM in low frequencies that cannot be measured in the experiment. A new and exciting discovery is found that there exists a new kind of wave, that is standing wave, which is notably distributed on the BM in low frequencies. This finding has not been reported so far and cannot be measured via present experimental technology. More importantly, the standing wave vibration can explain the experimental phenomena which are unexplainable by the travelling wave theory, thus giving an answer to the questions of many scientists about the travelling wave theory for many years.

The cochlear fluid is generally treated to be incompressible and inviscid [4-5,14]. As such, the Laplace equation is given by:

\[ \nabla^2 \Phi(s,n,\xi) = 0 \]  

(1) 

where \( \nabla^2 \) is the Laplace operator in the curvilinear coordinates. Since we obtain the mapping tensor \( G \) from \((s,n,\xi)\) to \((x,y,z)\), \( G^{-1} \) denotes the mapping tensor from the curvilinear coordinates \((s,n,\xi)\) to rectangular coordinates \((x,y,z)\). Based on the variation method, we deduce the Laplace operator \( \nabla^2 \) in the curvilinear coordinates. The Einstein’s summation convention has been used and the Laplacian takes the form:

\[ \nabla^2 = \frac{1}{|G|} \frac{\partial}{\partial x^i} \left( |G| G^{ij} \frac{\partial}{\partial x^j} \right), \quad (i = x,x^i = n,x^i = \xi) \]  

(2)

where \(|G|\) represents the determinant of \( G \).

The derivation process of \( G \) is shown in Supplemental Material in detail. \( (G^{-1})^j \) denote the element in Row \( j \) Column \( i \) of the mapping tensor from the curvilinear coordinates to rectangular coordinates. Substitute Eq. (2) into Eq. (1), we obtain:

\[ (1-\kappa n) \frac{\partial^2 \Phi}{\partial n^2} + (1+\kappa n) \frac{\partial^2 \Phi}{\partial x^2} \left( \frac{\partial^2 \Phi}{\partial x^2} + \left( \frac{x^2 \partial^2 \Phi}{\partial x^2} + \xi \partial^2 \Phi}{\partial x^2} \right) \right) + [1-\kappa n] \frac{\partial^2 \Phi}{\partial x^2} \left( \frac{\partial^2 \Phi}{\partial x^2} + \left( \frac{\partial^2 \Phi}{\partial x^2} + \xi \partial^2 \Phi}{\partial x^2} \right) \right) \]

(3)

where \( \Phi(s,n,\xi) \) is the fluid velocity potential function. \( \kappa \) and \( \tau \) are curvature and torsion of BM respectively (The derivation of \( \kappa \) and to \( \tau \) shown in Supplemental Material in detail). When \( \tau = 0 \), the formulation can return to that describes the cochlear cavity rotating on the same surface around the cochlear axis. Herein, the Laplace equation of fluid can be simplified as:

\[ (1-\kappa n) \frac{\partial^2 \Phi}{\partial n^2} + (1+\kappa n) \frac{\partial^2 \Phi}{\partial x^2} \left( \frac{\partial^2 \Phi}{\partial x^2} + \left( \frac{x^2 \partial^2 \Phi}{\partial x^2} + \xi \partial^2 \Phi}{\partial x^2} \right) \right) + [1-\kappa n] \frac{\partial^2 \Phi}{\partial x^2} \left( \frac{\partial^2 \Phi}{\partial x^2} + \left( \frac{\partial^2 \Phi}{\partial x^2} + \xi \partial^2 \Phi}{\partial x^2} \right) \right) = 0 \]

(4)

and gives

\[ u = \sqrt{(G^{-1})^T \frac{\partial \Phi}{\partial s}} + \sqrt{(G^{-1})^T \frac{\partial \Phi}{\partial n}} \]

\[ v = \sqrt{(G^{-1})^T \frac{\partial \Phi}{\partial s}} + \sqrt{(G^{-1})^T \frac{\partial \Phi}{\partial n}} \]

\[ w = \sqrt{(G^{-1})^T \frac{\partial \Phi}{\partial s}} + \sqrt{(G^{-1})^T \frac{\partial \Phi}{\partial n}} \]

(5)

where \( u, v, w, v \) are displacement components of fluid along \( s, n, \xi \) respectively. And dot denotes differentiation with respect to time. For Eq. (5), assuming that \( n_1, n_2 \) are unit normal vectors respectively along the upper boundary and outer boundary, and \( n_3, n_4 \) are unit normal vectors of upper boundary and lower boundary. The fixed external boundary of cochlear cavity has a zero flux, then gives:

\[ \frac{\partial \Phi}{\partial n_i} = n_i \cdot \nabla \Phi = 0 \]

(6)

In addition, at the interface of the fluid and BM, the velocity of fluid and BM remain the same, and gives:

\[ \frac{\partial \Phi}{\partial n_i} = n_i \cdot \nabla \Phi = \frac{-\partial}{\partial t} W(s,n,\pm h/2,t) \]

(7)

where \( W \) represents the BM vertical displacement that perpendicular to the central plane of the cochlear. Because there are no vertical displacement in spiral lamina that adjoins the two sides of BM, based on the
variation principle, the BM displacement should be a sine form, expressed by:

$$w_p(s,n,t)=W\sin\left[\frac{\pi(n+b_{BM}/2)}{b_{BM}}\right]e^{i\phi}$$

(8)

Furthermore, the phase $\phi$ is given by:

$$\phi=\omega t-\lambda s$$

(9)

where $\omega$ denotes frequency, $\lambda$ is wavenumber. The solution which satisfies the first two conditions of Eq. (6) is:

$$\Phi=\sum_{j=0}^{\infty}B_j\cosh m_j(\xi-H)\cos\left[j\pi\left(n+\frac{b_j}{2}\right)\right]e^{i\phi}$$

(10)

where $B_j, m_j$ can be obtained through Eq. (6). It should be noted that $B_j, m_j$ are both function of the curvature and torsion. Once the $\Phi$ is determined, the fluid pressure can be obtained by N-S equation:

$$p=-\rho\frac{\partial \Phi}{\partial t}$$

(11)

where $\rho$ is the fluid density, $p$ is the fluid pressure. The nonlinear terms can be ignored when compared with the linear term.

In order to derive the $n\cdot\nabla$ term of the boundary conditions of fluid, using the following expression:

$$\vec{n}\cdot\nabla=G^{-1}N_p\frac{\partial}{\partial u^T}$$

(12)

Herein, define $\{\vec{E}_n, \vec{E}_n, \vec{E}_\zeta\}$ as contravariant vector, that is, the unit normal vector to the index of coordinates. In the above, the $G^{-1}$ term in Eq. (12) has been determined. Thus, $N_p$ term is only needed to determine the normal directional derivative. Let $F_i(n,s)=n-n_i(s)=0$, the normal vector of the inner boundary of cochlear can be expressed as:

$$\vec{n}_i=-K_i\nabla F_i=-K_i\left(\vec{E}_n-n_i^T\vec{E}_n\right)$$

(13)

where $K_i$ is scaling factor which makes $n_i\cdot m_i=1$. Through the expression of scalar product tensor $m_i=n_iG^{-1}n_i$, it gives:

$$\vec{m}_i=-\frac{1}{\sqrt{1+n_i^T E_n-n_i^T E_n}}$$

(14)

and then gives:

$$\vec{m}_i=G^{-1}N_p\frac{\partial}{\partial u^T}=-\frac{1}{\sqrt{1+n_i^T E_n-n_i^T E_n}}\left[\frac{\partial}{\partial \zeta}+\frac{n_i}{\partial n_i^T E_n}\right]$$

(15)

Similarly, the normal directional derivative of outer boundary of cochlear can be derived as:

$$\vec{n}_i\cdot\nabla=G^{-1}N_p\frac{\partial}{\partial u^T}$$

(16)

Let $F_i(s,\zeta)=\zeta-h(s)=0$, $F_i(s,\zeta)=-\zeta=0$, the normal derivative of upper boundary and lower boundary can be expressed as:

$$\vec{n}_i=K_i\nabla F_i=K_i\left(h^T\vec{E}_n+\vec{E}_\zeta\right)$$

(17)

$$\vec{n}_i=-K_i\nabla F_i=-K_i\vec{E}_\zeta$$

(18)

where

$$K_i=\frac{1}{\sqrt{1+(\kappa+h)^2/n}}$$

According to above equation, the normal directional derivative of upper boundary can be written as:

$$\vec{n}_i\cdot\nabla=G^{-1}N_p\frac{\partial}{\partial u^T}=-\frac{1}{\sqrt{1+(\kappa+h)^2/n}}$$

(19)

The normal directional derivative of lower boundary can be written as:

$$\vec{n}_i\cdot\nabla=G^{-1}N_p\frac{\partial}{\partial u^T}=-\frac{1}{\sqrt{1+(\kappa+h)^2/n}}\left[\frac{\kappa}{\kappa}+\frac{\kappa}{\kappa}+\frac{\kappa}{\kappa}+\frac{\kappa}{\kappa}\right]$$

(20)

The BM is regarded as a isotropic thin plate and the vibration control equation can be written as:

$$h\left[1-h^2/12\right]\left[\vec{m}\frac{\partial}{\partial \zeta}+\beta\frac{\partial}{\partial t}\right]w_p^T+D\left[\vec{m}\frac{\partial}{\partial t}+2\tau^2\left[\vec{m}\frac{\partial}{\partial t}+\tau^2\vec{w}_p\right]ight.$$  

$$=\left[1-h^2/12\right]\left[\vec{m}\frac{\partial}{\partial \zeta}+\beta\frac{\partial}{\partial t}\right]\vec{m}$$

(21)

where $\sigma^{3}$ denotes the Row 3 and Column 3 element of second order Piola-Kirchoff stress tensor, m denotes the mass density of BM, $\beta$ denotes the damping of BM, and $f$ denotes the function of BM curvature and torsion. Only the BM motion in $\zeta$ axis is considered, the kinetic energy is:

$$T_p=\int_{b_{BM}}^{b_{BM}}\frac{1}{2}\int_0^{2\pi}\int_0^{\pi/2}\frac{1}{2}\rho_p h\vec{w}_p^T d\mathcal{Q}dn$$

(22)

where $\rho_p$ is the density of BM. Substitute Eq. (8) into Eq. (22), it yields

$$T_p=\frac{1}{4}\rho_p h^2\int_{b_{BM}}^{b_{BM}}\eta^2(n)dn$$

(23)

For a homogeneous, isotropic plate, the averaged potential energy is:

$$V=-\int_{b_{BM}}^{b_{BM}}\left[\frac{1}{2}\int_0^{2\pi}\int_0^{\pi/2}\int_2^{2\pi}\frac{\partial\vec{w}_u}{\partial t} \frac{\partial\vec{w}_u}{\partial t}+2\int_0^{2\pi}\int_0^{\pi/2}\int_2^{2\pi}\frac{\partial\vec{w}_u}{\partial t} \frac{\partial\vec{w}_u}{\partial n} \frac{\partial\vec{w}_u}{\partial \zeta}\right] d\mathcal{Q}dn$$

(24)

where $\nu$ is Poisson’s ratio,$D=\nu h^3/[12(1-\nu)]$, method is usually used to solve the
steady-state solutions. The basic idea behind the WKB is that when the wavelengths are sufficiently short, the properties can be taken as essentially constant over the space of a wavelength. Therefore, the previously derived results can be used in this phase-integral solution, and the total phase can be written as:

\[ \varphi = \omega t - \int_0^s \lambda(s) ds \]  

Here \( \lambda \) and \( \omega \) in Eq. (8) and Eq. (25) are functions of \( s \) to be determined. We mainly focus on the coupling motions between fluid and BM, assuming that the vibration in \( \xi \) is the most severe, the pressure on the BM then can be written as:

\[ p(s, n, 0, t) = \sum_j e^{i \eta_j(n)} e^{i \omega_t} \left| \eta_j \right|^2 e^{i \lambda s} \]  

where \( e^{i \eta_j(n)} \) is the higher order vibration modal, \( \lambda \) is the pressure amplitude on BM. Combine with Eq. (11), Eq. (25) and Eq. (26), using the orthogonality of different modes, then it gives:

\[ P = \frac{-i \rho_0 \lambda}{\lambda^{1/2} \eta^2(n) \lambda} \sum_j B_j \lambda_j \cos m_j \lambda \]  

where \( B_j = \int_{\eta^{1/2}} \eta(n) \cos \left[ \frac{j \pi (n + b_{\text{jam}}/2)}{b_{\text{jam}}} \right] dn \)  

The time-averaged kinetic energy of the fluid per unit length is expressed as:

\[ T_k = \frac{1}{2\pi} \int_0^{2\pi} \int_0^1 \frac{1}{2} \rho \left( \dot{u} + \dot{v} + \dot{w} \right) d\eta d\varphi \]  

For the conservative system, the total energy can be expressed as:

\[ L = T_k + T_p - V \]  

Substitute Eqs. (23), (24) and (29) into Eq. (30), the variation of \( W \) and \( \lambda \) yields the Euler-Lagrange equations:

\[ \frac{\partial L}{\partial W} = 0, \quad \frac{\partial L}{\partial \lambda} = 0 \]  

where the first equation of Eq. (31) gives the eikonal equation which determines the wavenumber of the wave:

\[ f(\lambda) = 0 \]  

The second equation of Eq. (31) provides the transport equation and the solution of which is the vibration amplitude of BM. It can be written as:

\[ W = C \left( \frac{\partial F}{\partial \lambda} \right)^{1/2} \]  

It is usually normalize the BM amplitude with respect to that of the stapes. With the stapes motion defined as positive outward, its amplitude is:

\[ \delta_0 = - \frac{-i}{B_{\text{jam}}} \int_0^{2\pi} \frac{1}{\lambda^{1/2} \eta^2(n) \lambda} e^{i \eta_j(n)} e^{i \omega t} \left| \eta_j \right|^2 e^{i \lambda s} \]  

Together with Eqs. (33) and (34), the relative amplitude of BM to the stapes can be obtained as follows:

\[ W_0 = \frac{\int_0^{2\pi} \int_0^1 \left( \frac{\partial F}{\partial \lambda} \right)^{1/2} e^{i \eta_j(n)} e^{i \omega t} \left| \eta_j \right|^2 e^{i \lambda s} \right| d\eta d\varphi}{\int_0^{2\pi} \int_0^1 \left( \frac{\partial F}{\partial \lambda} \right)^{1/2} e^{i \eta_j(n)} e^{i \omega t} \left| \eta_j \right|^2 e^{i \lambda s} \right| d\eta d\varphi} \]  

Meanwhile, in order to make our research more accurate and credible, we also established a highly physiologically accurate human ear numerical simulation model which reflecting the real spiral shape, biological material properties and lymph physiological environment of human ear, as shown in Fig. 1. The material properties and boundary conditions are chosen according to the previous literature [18-22]. The constructing process of the model can be seen in Supplemental Material part in detail.

Based on the analytical model and the numerical model, the vibration amplitude of BM at two frequencies 100Hz and 200Hz were calculated, as shown in Fig.2. At low frequencies (<200 Hz), the BM vibrates with equal amplitude at a regular distance along the spiral longitudinal direction, exhibiting a characteristic standing wave. The standing wave forms nodes and anti-nodes, where the amplitudes of the standing wave are maximum and minimum, respectively. As the frequency rises, the displacement of the BM increases, and the distance between adjacent anti-nodes decreases. In addition, all the points between the nodes are in phase, whereas the points on either side of a node are exactly out of phase, undergoing a phase change of \( \pi \) radians. Compared with the analytical solution, at the ends of the BM, the standing wave pattern has a variable amplitude, which may be attributed to the more accurate geometrical boundaries, material properties and lymph physiological environment of human ear numerical model. The variation of magnitudes of BM with longitudinal positions at two middle frequency 1000Hz and 2000Hz are shown in Fig. 3. With the increase of the distance from the cochlear base, there exists a transition of BM vibration from standing wave mode to traveling wave mode. The vibrating amplitude of the standing wave pattern is comparatively lower than that of the traveling wave pattern which has a notable single peak. As the frequency rises, the peak of the response curve
shifts from the apex to the base. After the peak, the curve declines sharply and finally tend to be flat and juggled at high frequencies. Moreover, the phase of the BM response decreases with distance from the cochlear base, which indicated that waves travels in the apical direction, that is, they form a forward traveling wave, which is exactly described by von Békésy in his traveling wave theory. At two high frequencies 10000Hz and 15000Hz, with the increase of the distance from the cochlear base, there exists a transition of BM vibration from traveling wave mode to standing wave mode. The vibrating amplitude of the standing wave pattern is also comparatively smaller than that of the traveling wave pattern.

Similar to the analytical solutions, at middle and high frequencies, the BM vibrates in a obvious traveling wave pattern. When the frequency increases to 1000Hz, the standing wave and travelling wave are concomitant, the standing wave vibration begins weakening. When the frequency is higher than 1000 Hz, the standing wave is slight, and the travelling wave vibration mode becomes dominant.

To verify the analytical and numerical models, we calculated the relationship between the magnitude of BM and the frequency at the position 12 mm from the oval window, which were compared with the measurements [23-24], shown in Fig. 4. The results showed good agreement with both measurements with the best frequency of 3000 Hz, especially for experimental data 2.

It is worth noting that, in previous numerical models, the cochlea was assumed to be a straight shape and the lymph was assumed to be incompressible, which is not consistent with the real morphology and biomaterial properties of the cochlea [25-26]. Thus, the previous results were not consistent with the experimental measurements. Before the best frequency, the curve is not smooth but shows little pits. After the best frequency, the curve declines sharply with increasing frequency until reaching a certain high frequency, and then appears juggled. This finding is consistent with test results that have never been reflected in previous numerical models. This result may have some connection with the standing wave vibration mode.

The frequency-peak mapping curve of BM is obtained and compared with the measurements [4, 27]. We find that the simulation curve is consistent with the test curve. In addition, we predict results at very low frequencies that cannot be obtained via
corresponding characteristic positions of single peaks of the BM vibration as depicted by traveling waves [13]. Bell discovered in his experiments that no many phases were accumulated or delayed at characteristic frequencies for vibration of the BM [28]. After experiments, Naidu and Mountain found that the test results of stiffness distribution of the BM could hardly correspond to characteristic frequencies of the membrane [29], so the vibration of BM cannot be explained by the traveling wave theory at some frequencies. Shera proposed after an experiment that otoacoustic emissions of cochlear would be explained by vibration of standing wave [30].

The standing wave vibration discovered in this paper could describe the above phenomena that unable to be explained by the traveling wave theory. We discovered that on the BM, there exhibits a standing wave which causes the BM vibrate with nodes and anti-nodes at regular distance along the longitudinal direction, appearing multiple peaks with equal amplitude (consistent with the predictions of Kleiner [12], Richard [13], and Proctor and Zandt [14]). However, the standing wave is a non-propagating wave without phase accumulation from base to the apex (coincide with Bell observations [28]). Instead, all the points between nodes are in phase, whereas the points either side of a node are exactly out of phase, undergoing a phase change of $\pi$ radians. Compared with the single-peak traveling wave vibration in medium-high frequencies, the standing wave vibration in low-frequency is a global and severe vibration occurring entirely on the BM along the longitudinal direction. Therefore, there is no definite relation between the characteristic frequency and correspondent individual position of BM (consistent with the observations of Naidu and Mountain [29]). Although the standing wave is different from the traveling wave, there is a certain relationship between them. The standing wave is a superposition of the forward traveling wave (from base to apex) and backward traveling wave (from apex to base) that is generated by the apical boundary conditions. The standing wave vibration is a new kind of vibration mode, which is accompanied by the generation of reflecting waves (verified Shera’s predictions in his experiments [30]).

As mentioned above, BM vibration data at low-frequency, which were not available through experiments, were obtained in the presented model. Meanwhile, the newly discovered vibration mode of standing waves has responded a long time puzzle of aurists and researchers, namely: why traveling wave theory could not explain many experimental observations and the behavior of the basilar membrane in low frequency vibration.

**FIG. 4** Comparison of the BM magnitude and frequency-position mapping relation (A) Displacement amplitude (B) The frequency-peak mapping curve.
The standing wave theory has explained the coupling mechanical behaviors of low-frequency sounds in cochlea. Not single response was made in certain position on the top of BM whereas longitudinal vibration within the same amplitude is discovered along the entire BM. This new vibration mode not only enlarge sensation area of BM, but also strengthened abilities of cochlea to hear low-frequency sounds. Such inherent vibration modes in low frequencies are fundamental for cochlea to sense and encode low-frequency sounds. Besides, vibration of standing waves possibly affects the active function of cochlea, and thus explain the active phonosensitive mechanism in the cochlear which is unexplainable by the traveling wave theory.

In conclusion, the standing wave theory unveiled by this paper is a new breakthrough for fully elucidating human ear hearing sensation mechanism. It promotes the deepening development of the human ear medicine, and may also provide theoretical basis for devising new clinical treatment of sensorineural deafness.

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