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An analysis of mechanical interaction between the outer hair cell and two adjacent cochlear membranes

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Introduction

Discovery of outer hair cells motility gave a rise to a certain reconsideration of basic principles of cochlear mechanics. The active models became recognized as received fact. Contrary to widely accepted beliefs, vibrations of complex cross section of cochlear partition is examined here in terms of mechanics of multi-degree-of-freedom systems.

1. Statement of the eigenvalue problem.

Consider a cross section of a coupled system made up of two thin elastic plates linked with a raw of springs (Fig. 1).

Fig. 1. A model of cochlear complex cross section. TM – tectorial membrane; BM – basilar membrane; OHC – outer hair cell.

For simplicity and brevity of derivations, the energy dissipation is neglected here without loss of generality; the fluid media is provisionally removed for the same sake. A possibility to describe the tectorial membrane with a flat thin anisotropic plate is examined in Novoselova, [1].

The free vibrations of both membranes obey the plate equations:

$$D_t \frac{\partial^4 U_t}{\partial y^4} + \mu_t \frac{\partial^2 U_t}{\partial t^2} = 0, \quad D_b \frac{\partial^4 U_b}{\partial y^4} + \mu_b \frac{\partial^2 U_b}{\partial t^2} = 0, \tag{1.1}$$

where D_t and D_b are the bending stiffnesses of tectorial and basilar membranes respectively, μ_t and μ_b are the surface mass densities, $U_t(y,t)$ and $U_b(y,t)$ are the normal displacements of the membranes.

The boundary conditions for the basilar membrane are the traditional hinged edges:

$$U_b(y_0) = U_b(y_0 + b) = 0, \quad \frac{\partial^2 U_b(y_0)}{\partial y^2} = \frac{\partial^2 U_b(y_0 + b)}{\partial y^2} = 0. \tag{1.2}$$

Consider the boundaries of the tectorial membrane. Its left edge is supported onto the immovable limbus, so:

$$U_t(0) = \frac{\partial^2 U_t(0)}{\partial y^2} = 0. \tag{1.3}$$

The marginal edge of tectorial membrane experience a load from the spring resoring force $F(t)$, so the shear force Q_t is equal to this load:

$$Q_t(\eta) = D_t \frac{\partial^3 U_t(\eta, t)}{\partial y^3} = \frac{F(t)}{\Delta x}. \tag{1.4}$$

Here Δx is the distance between two neighboring OHCs in longitudinal direction.

The forth boundary condition for the tectorial membrane concerns the bending moment M_t, that is a product of the force by its arm:

$$M_t(\eta) = Q_t(\eta) \cdot \eta. \tag{1.5}$$

The force $F(t)$ that compresses and elongates OHC is proportional to variation of distance between the membranes:

$$F(t) = S(U_t - U_b)\Big|_{y=\eta} + m\frac{\partial^2(U_t - U_b)}{\partial t^2}\Bigg|_{y=\eta} \tag{1.6}$$

Here m denotes the mass of OHC and S is the restoring spring constant.

The force F also affects the basilar membrane, causing a break of shear force under the line of OHCs:

$$Q_b(\eta + 0) - Q_b(\eta - 0) = -\frac{F}{\Delta x}. \tag{1.7}$$

2. Solution.

The Fourier method is a good approach for solving of system (1.1)–(1.7). Suppose displacements U_t and U_b be the products of functions dependent only on any one of variables:

$$U_i(y,t) = W_i(y) \cdot T(t), \qquad i = t, b \tag{2.1}$$

Substituting of (2.1) into Eqs. (1.1) provides the equations with left part dependent only on y, while the right-hand part depends only on t. So, both are constant relatively these variables:

$$\frac{D_i}{\mu_i} \cdot \frac{W_i''''(y)}{W_i(y)} = -\frac{T''(t)}{T(t)} = \text{const} \tag{2.2}$$

Let ω_0^2 stand for this constant:

$$\omega_0^2 \equiv -\frac{T''(t)}{T(t)} \tag{2.3}$$

Then $T = \exp(i\omega_0 t)$, and this expression indicates the physical meaning of ω_0: it is an eigenfrequency of the complex cross section.

Let k_i be a wave number of each membrane:

$$k_i^4 \equiv \frac{W_i''''(y)}{W_i(y)}, \quad \text{then} \quad \omega_0^2 = k_i^4\frac{D_i}{\mu_i}, \quad i = t, b \tag{2.4}$$

The classical solution to the first of Eq. (2.4) has a form:

$$W_i = a_{1i}\sin k_i y + a_{2i}\cos k_i y + a_{3i}\sinh k_i y + a_{4i}\cosh k_i y \tag{2.5}$$

From the conditions (1.3) and (1.5), it follows:

$$W_t(y) = a_{1t}\left(\sin k_t y + \frac{\sin\lambda_t - \lambda_t\cos\lambda_t}{\sinh\lambda_t - \lambda_t\cosh\lambda_t}\sinh k_t y\right), \tag{2.6}$$

$$\lambda_t = k_t\eta. \tag{2.7}$$

W_t is the general form of eigenfunction of the tectorial membrane vibrations; the wavenumber k_t has to be determined from Eqs. (1.4) and (1.6).

Now return to the basilar membrane. The concentrated force F applied along the line of OHCs causes a break in the third derivative of $W_b(y)$. Let us define the part of cross section to the left from the line as W_l, and the part to the right as W_r. Application of conditions (1.2) to Eq. (2.5) yields:

$$\begin{aligned} W_l &= a_{1l}\sin k_b(y-y_0) + a_{3l}\sinh k_b(y-y_0) \\ W_r &= a_{1r}\sin k_b(y_0+b-y) + a_{3r}\sinh k_b(y_0+b-y) \end{aligned} \tag{2.8}$$

Displacement $W_b(y)$ and two its derivatives are continuous through over the cross section. Continuity in $y=\eta$ provides three equations allowing to eliminate a_{3l}, a_{1r} and a_{3r}. For the sake of simplicity and without loss of generality we assume the approximate relationships:

$$\eta = b, \qquad y_0 = \eta/2. \tag{2.9}$$

Then:

$$a_{1r} = a_{1l}, \quad a_{3r} = a_{3l}, \quad a_{3l} = -a_{1l}\frac{\cos\lambda_b}{\cosh\lambda_b}, \quad \lambda_b = \frac{k_b b}{2}. \tag{2.10}$$

The solution for basilar membrane vibrations is then described with expression:

$$W_b = a_{1b}\begin{cases} \sin k_b(y-y_0) - \frac{\cos\lambda_b}{\cosh\lambda_b}\sinh k_b(y-y_0) & \text{if } \; y_0 \le y \le \eta \\ \sin k_b(y_0+b-y) - \frac{\cos\lambda_b}{\cosh\lambda_b}\sinh k_b(y_0+b-y) & \text{if } \; \eta \le y \le y_0+b \end{cases} \tag{2.11}$$

Now consider the shear forces Q_t and Q_b; let the explicit factor T(t) be omitted:

$$\begin{aligned} Q_t = D_t W_t''' &= \frac{S-m\omega_0^2}{\Delta x}(W_t - W_b)\big|_{y=\eta} \\ Q_b(\eta+0) - Q_b(\eta-0) = \pm D_b(W_r''' - W_l''') &= \frac{S-m\omega_0^2}{\Delta x}(W_b - W_t)\big|_{y=\eta} \end{aligned} \tag{2.12}$$

The double sign $\pm$ indicates a possibility of synphase and counterphase vibrations of two membranes; formally, it arises from equal probabilities to write $W_r''' - W_l'''$ or $W_l''' - W_r'''$.

Substituting of (2.6) and (2.11) into (2.12) yields the system:

$$\begin{aligned} &a_{1t}\{Q_t(\eta) - qw_t(\eta)\} + a_{1b}qw_b(\eta) = 0 \\ &a_{1t}qw_t(\eta) + a_{1b}\{\pm\Delta Q_b(\eta) - qw_b(\eta)\} = 0, \end{aligned} \tag{2.13}$$

where

$$\Delta Q_b(\eta) = 4D_b k_b^3\cos\lambda_b, \quad q = \frac{m}{\Delta x}(\omega_c^2 - \omega_0^2), \quad w_i = W_i/a_{1i}, \; i = t, b. \tag{2.14}$$

Here $\omega_c^2 = S/m$ is the eigenfrequency of isolated outer hair cell.

System (2.13) has an untrivial solution if its determinant is zero. Following relationships then hold:

$$\omega_0^2 = \omega_c^2 \pm \frac{\Delta x}{m}\,\frac{Q_t\Delta Q_b}{w_bQ_t \pm w_t\Delta Q_b}, \quad a_{1t} = a_{1b}\frac{qw_b \mp \Delta Q_b}{qw_t} \tag{2.15}$$

The first is a nonlinear equation for the eigenfrequency of the complex cross section. The double sign indicates effect of splitting eigenfrequency which is specific to multi-degree-of-freedom systems. Substitution of (2.14) into (2.15) yields:

$$\omega_+^2 = \omega_c^2 + \frac{\Delta x}{m}\frac{1}{r_b^+ + r_t^+}, \quad \omega_-^2 = \omega_c^2 - \frac{\Delta x}{m}\frac{1}{r_b^- - r_t^-} \tag{2.16}$$

where

$$r_b = \frac{\tan\lambda_b - \tanh\lambda_b}{4D_b k_b^3}, \quad r_t = \frac{2-\lambda_t(\mathrm{cotan}\,\lambda_t + \mathrm{cotanh}\,\lambda_t)}{D_t k_t^3(\mathrm{cotan}\,\lambda_t - \mathrm{cotanh}\,\lambda_t)}. \tag{2.17}$$

We may conclude that the higher of eigenfrequencies (2.16) is associated with a counterphase movement between the marginal edge of tectorial membrane and the basilar membrane, because resistance of linkage is higher in this case. Due to that λ_t and λ_b are the arguments of periodic functions and related to $\omega_\pm$ through Eqs. (2.4), (2.7) and (2.10), we have two infinite sets of eigenfrequencies and two infinite sets of each membrane eigenfunctions. Usually, the eigenfrequencies of the linked system are named 'normal frequencies'.

Consider some special cases. Suppose $\omega_\pm = \omega_c$. The second term of Eq. (2.16) equals to zero, if either r_b, or r_t are infinite. This occurs, if either $\tan\lambda_b = \infty$, or $\mathrm{cotan}\,\lambda_b = \mathrm{cotan}\,\lambda_t$, otherwise, if either $\lambda_b = \pm(\pi/2+n\pi), n = 0,1,2\ldots$, or $\lambda_t = \pm(5\pi/4+n\pi)$. But these eigenvalues are also the eigenvalues of free vibrations of the uncoupled membranes. Hence, if the partial eigenfrequency of the isolated outer hair cell equals to any of partial eigenfrequencies of any of uncoupled membranes, it is also the normal frequency of the cross section. It is the only case, when the synphase and counterphase vibrations have one and the same frequency.

3. Forced vibrations.

To study the forced vibrations in cochlea, the cochlear hydrodynamics and longitudinal coordinate should be taken into account. Such expansion exceeds the scope of the present paper. However, some essential information on the specific features of resonance in the coupled system under examination can be obtained from the considered matters.

Let the complex cross section be subject to a periodic force $P_0 e^{i\omega t}$ applied, for example, from below. The vibrations of two coupled membranes then obey the equations:

$$D_b\frac{\partial^4 U_b}{\partial y^4} - \mu_b\omega^2 U_b = P_0 e^{i\omega t}, \quad D_t\frac{\partial^4 U_t}{\partial y^4} - \mu_t\omega^2 U_t = 0. \tag{3.1}$$

It can be verified, that the eigenfunctions W_{bm} and W_{tm} are not orthogonal to each other at least in the conventional sense. So, the traditional method of expansion into the eigenfunctional series is not applicable here in general form. However, in close vicinities of $\lambda_{bn} = \pm(\pi/2 + n\pi)$, $n = 0,1,2\ldots$, the eigenfunctions (2.11) are very close to sines. In these narrow regions, the approximate equality is justified:

$$U_b(y,t) \approx \sum_{n=0}^{\infty} c_{bn}\sin k_{bn}(y-y_0)\exp(i\omega t), \qquad k_{bn} = \pm(2n+1)\pi/b. \tag{3.2}$$

Substituting of (3.2) into (3.1) and decomposing constant P_0 into the sine series yields:

$$c_{bn} \approx \frac{2P_0(1-(-1)^n)}{n\pi\mu_b(\omega_{0n}^2 - \omega^2)}$$

Application of Eq. (2.16) results:

$$c_{bn} \approx \frac{2P_0(1-(-1)^n)}{n\pi\mu_b(\omega_c^2 \pm \frac{\Delta x/m}{r_{bn}-r_{tn}} - \omega^2)} \tag{3.3}$$

To determine the tectorial membrane displacement, we represent it as a sum of tectorial membrane eigenfunctions with indeterminate coefficients, and equate the shear forces of two membranes. This yields:

$$U_t(y,t) = \frac{D_b}{D_t}\sum_{n=0}^{\infty} c_{bn}\left(\frac{k_{bn}}{k_{tn}}\right)^3 \frac{w_{tn}(y)}{w_{tn}(\eta)}\exp(i\omega t) \tag{3.4}$$

Conclusions.

Consider the last factor of denominator of (3.3). It is seen that a resonance of complex cross section is the most pronounced, if any of partial eigenfrequencies of uncoupled basilar membrane and the eigenfrequency of isolated outer hair cell both coincide with the applied frequency.

Similarly, if the force is applied from above to the tectorial membrane, its displacement may be decomposed into the series of orthogonal eigenfunctions of uncoupled tectorial membrane in the points $\lambda_{tn} = \pm(5\pi/4 + n\pi)$, $n = 0, 1, 2\ldots$ Hence, the second probable resonance appear, if the partial eigenfrequency of the outer hair cell coincides with any of partial eigenfrequencies of the tectorial membrane.

Through the slow motility, the outer hair cell is capable to vary its partial eigenfrequency, either moving it closer to that of a membrane, or drifting apart. By this way the shape, sharpness and shift of the tuning curve can be modified. Such experimental data are in focus of attention.

Of particular interest is the leading eigenfunction of the tectorial membrane in the vicinity of its resonance. The eigenfunction has a node near the marginal edge, hence the marginal part of the tectorial membrane moves in the opposite direction to the middle portion. At resonance of a cross section, when the middle part of tectorial membrane moves downwards, it pushes out of sulcus some fluid, which streams through the opened subtectorial gap. In counterphase, the exit from the gap is closed by dropped marginal edge. Away of the resonance, the distance between the marginal edge and basilar membrane remains almost constant. Such mechanics of subtectorial streaming is strikingly similar to that supposed by Steele in 1973 [2]. If so, the resonance of tectorial membrane seems to be more important for excitation of inner hair cells then that of the basilar membrane, if the leading partial eigenfrequencies of two membranes do not coincide.

Mechanics of multi-degree-of-freedom systems can serve as a key that puts a great deal of experimental findings into a mutually associated series, as it is demonstrated in [1].

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