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THE APPLICATION OF SHELL MODEL TO BIOLOGICAL MEMBRANES

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Introduction. Cells are the basic unit of life. Our bodies are composed of many cells that are specialized for different functions; for example nerve cells for the neural system, sensory cells for senses such as vision and hearing, and muscle cells for force production. One of the most basic constituents of the cell is the plasma membrane, which separates the interior of the cell from its outside environment. It is composed of a lipid bilayer, into which proteins and other molecules are embedded. The membrane is a viscoelastic or fluid-like structure that allows the membrane to move and change the shape of the cell. The cytoskeleton, which maintains cell shape and organizes its movement, is usually found just beneath the plasma membrane. Actin filaments are one of the components of the cytoskeleton [1].

Cell movement / migration / motility plays a key role in our bodies. Cell movements have an important role in the function of outer hair cells (OHCs) in the inner ear. In the following section, we explain OHC motility based on the conformational change of the motor protein prestin. In addition, we discuss modeling and analysis of their deformation and movements.

OHC motility. OHCs are one of the two types of sensory cells found in the inner ear and they show voltage-dependent length changes, which underlie the am-

plification mechanism of the cochlea that is essential to normal mammalian hearing. Figure 1 shows a schematic of an OHC and its lateral wall. OHCs are approximately cylindrical with a radius of ~5 μm and a length of ~60 μm. The lateral membrane of OHCs consists of a unique three-layered structure; outermost plasma membrane, innermost fluid-like subsurface cisternae, and elastic cytoskeleton, which is called the cortical lattice and is located between the plasma membrane and the subsurface cisternae. The cortical lattice consists of circumferential actin filaments and axial spectrin, whereas the plasma membrane has a high density of prestin, which is believed to underlie the voltage-dependent changes in the length of OHCs [2]. Even though the electrical properties of OHCs have been examined and are believed to reflect the state of prestin, their mechanical properties, that is, macroscopic OHC length change and force produced by microscopic conformational changes of prestin, remain unclear. Therefore, it is important to analyze the passive elastic deformation of OHCs and their prestin-based motility.

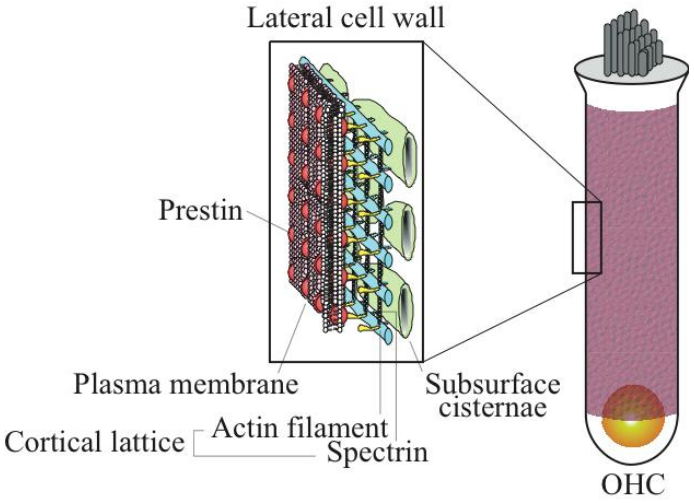

Figure 1 – Schematic of an OHC and its lateral wall. The OHC shows motility based on the conformational change of the motor proteins prestin in the plasma membrane. Its mechanism is quite specific to OHCs

Passive shell model of OHCs. To evaluate the elastic properties of the OHC lateral wall, firstly, the cell was modeled as an orthotropic elastic shell. Assuming that the deformation of the OHC is axisymmetric, the equilibrium equations are given by:

$$K_x\left(\frac{\partial u}{\partial x}+\frac{\nu_\theta}{r}w\right)=\frac{Pr}{2}-\frac{F_x}{2\pi r} \tag{1}$$

and

$$D_x\frac{\partial^4 w}{\partial x^4}+\frac{K_\theta\left(1-\nu_x\nu_\theta\right)}{r^2}w=\left(1-\frac{\nu_\theta}{2}\right)P \tag{2}$$

where u and w are axial and circumferential displacements, respectively, and P and F_x are the internal pressure and axial force applied to the cell, respectively. K_x, K_θ

and D_x in eqs. (1) and (2) are represented using Young's modulus E, Poisson's ration ν and the thickness of the lateral wall h, and are given by $K_x = \frac{E_x h}{1-\nu_x \nu_\theta}$, $K_\theta = \frac{E_\theta h}{1-\nu_x \nu_\theta}$, and $D_x = \frac{E_x h^3}{12(1-\nu_x \nu_\theta)}$, where x and θ correspond to the axial and circumferential direction, respectively. Due to the orthotropism of the lateral cell wall, the relationship between Young's modulus and Poisson's ratio of the lateral wall is:

$$E_\theta / E_x = \nu_\theta / \nu_x = \text{ratio} \tag{3}$$

By comparing the experimental results of cell inflation [3] and axial stretch [4] with the numerical results obtained from eqs. (1), (2) and (3), the elastic properties of the OHC lateral wall were obtained.

Active shell model of OHCs. Next, the function of prestin was taken into consideration in the model, and the active shell model of OHCs was constructed. Assuming that the motor elements are in the lateral wall and that they have two states, i. e., extended state and compact state, the total strain of the cell is given by:

$$\frac{\partial u'}{\partial x} = \frac{\partial u}{\partial x} + nM_{x0}P_e \tag{4}$$

and

$$w'/r = w/r + nM_{\theta 0}P_e \tag{5}$$

The first term of the right-hand side in eqs. (4) and (5) is the strain of the elastic elements of the lateral wall, whereas the second term shows the strain due to the deformation of the motor elements. n is the density of the motor elements and M_{x0} and $M_{\theta 0}$ are the axial and circumferential area changes of the unit motor, respectively [5]. P_e represents the fraction of the motor in the extended state and is given by:

$$1/P_e = 1 + \exp\left(-\left(E_0 + qV + M_{x0}N_x + M_{\theta 0}N_\theta\right)\right). \tag{6}$$

Substituting eqs. (4), (5) and (6) into eqs. (1) and (2), we observe active OHC motility. Finally, on the bases of this model, the effect of the elastic properties of the lateral cell wall on its motile response was discussed.

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