New and Notable

Poking versus Deflection: Anisotropy in Action

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The concept that vibrations of the organ of Corti result in bending of hair cell stereocilia has been a tenet of cochlear biophysics since the mid-1960s. The reasoning underlying the concept was unassailable. Growing evidence that bending of the stereocilia bundle was required to modulate the flow of ions into the hair cells converged with ultrastructural images showing that the bundles were highly organized relative to the central axis of the cochlea (1). Integration of the structural and functional concepts resulted in a cartoon that showed an upward movement of the basilar membrane deflecting the stereocilia away from the central axis of the cochlea, resulting in an increased flow of ions into the hair cells. The cartoon possessed strong explanatory and teaching value and the essential validity of the concept was recently confirmed (2). Good cartoons provide a comfort, and the influence of this cartoon may explain why there has been no systematic study as to why stereocilia bend, instead of poking further into the overlying tectorial membrane. The question of ''why'' was neglected until Gueta and colleagues (3), in this issue, realized it was, in fact, a problem. Once the question is asked, the science follows; and the study described in this issue bears a resemblance to the apocryphal story of Newton asking why the apple falls.

The tectorial membrane is an extracellular matrix, containing at least three types of collagen and the noncollagenous glycoproteins: α-tectorin, β-tectorin, and otogelin. The organization of these proteins within the tectorial membrane is anisotropic in that they project radially away from the central axis of the cochlea. Within the body of the tectorial membrane, a laminated striated sheet matrix is formed from 7- to 9-nm diameter filaments. The lower fibrous layer near the hair cells consists of collagen organized in bundles of straight 20-nm diameter filaments. The marginal band at the lateral edge of the tectorial membrane and the cover-net bundles on the top of the tectorial membrane contain anastomosing networks of thick collagen fibrils. The development of the tectorial membrane occurs in concert with the development of the organ of Corti and differentiation of hair cells during embryogenesis. The tectorial membrane matrix is secreted by supporting cells and some of the supporting cells resorb, leaving it attached medially only to the spiral limbus and stretching across the surface of the organ of Corti. Once the cochlea has fully developed, the tectorial membrane is thought to remain relatively inert with minimal protein turnover. Hair cell stereocilia movement is coordinated by the tectorial membrane because the tips of outer-hair cell stereociliary bundles are embedded in its lower surface. Microscopic inspection of freshly dissected tectorial membrane reveals how beautiful the arrangement is. The array of stereociliary pits is aligned at right angles to the radially oriented collagen fibrils. Gueta et al. (3) show theoretically and experimentally how the anisotropic material properties of the tectorial membrane prevents the bundle from penetrating but instead bends the bundle as it is mechanically guided by the fibrillar structure.

The organ of Corti is a biophysical delight. It converts the mechanical vibrations of sound into electrical signals that are transmitted to the brain. It performs a spectral analysis of the acoustic environment over a range of frequencies the upper limit of which exceeds 100 kHz for some mammals. The basic structure of the organ was described in the mid-19th century. Helmholtz was inspired by these early anatomical descriptions, and his own experiments suggest the inner ear was mechanically tuned. In the mid-20th century, Von Békésy measured the systematic variations in basilar membrane mechanics that renders a given location along the basilar membrane sensitive to a specific frequency. It is important that the outer-hair cell stereociliary bundles are deflected because the outer-hair cells generate a membrane-based electromechanical force (4) that counteracts the viscous damping imposed by the inner ear fluid environment. Bending of the bundle produces a sensory receptor potential across the cell membrane which is converted directly into mechanical energy. The feedback of energy into the system greatly refines its tuning and sensitivity and underlies our ability to discriminate tones and understand speech.

Among the many forms of deafness are some that have been traced to mutations of the proteins that are found in the tectorial membrane (5). In addition to alterations in its morphology, one must now ask if some of the hearing loss is due to alterations in material properties of the tectorial membrane. The findings described by Gueta et al. (3) suggest that variations in elastic moduli may alter hearing function by changing the magnitude of the receptor potentials in the outer hair cells.

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Submitted January 22, 2008, and accepted for publication January 23, 2008.

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Editor: Thomas Schmidt.

0006-3495/08/06/4157/02 $2.00

doi: 10.1529/biophysj.108.129049

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