Cochlear Mechanics

Distributed Impedance Model of Tectorial Membrane Traveling Waves

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Introduction

The mammalian cochlea is a remarkable sensor that can detect motions smaller than the diameter of a hydrogen atom and can perform high-quality spectral analysis to discriminate as many as 30 frequencies in the interval of a single semitone (Kossl and Russell, 1995; Dallos, 1996). These extraordinary properties of the hearing organ depend on traveling waves of motion that propagate along the basilar membrane (BM) (von Bekesy, 1960) and ultimately stimulate the sensory receptors. The strategic location of the TM relative to the hair bundles suggests that the TM plays a key role in stimulating hair cells. Mouse models with genetically modified structural components of the TM have been shown to exhibit severe loss of cochlear sensitivity and altered frequency tuning (McGuirt et al, 1999; Legan et al, 2000; Simmler et al, 2000; Legan et al, 2005; Russell et al, 2007), thereby providing further evidence that the TM is required for normal cochlear function. However, the mechanical processes by which traveling wave motion along the BM leads to hair cell stimulation remain unclear (Guinan et al, 2005), largely because the important mechanical properties of the TM have proved difficult to measure. Consequently, the mechanical function of the TM has been variously described as a rigid pivot, a resonant structure, and a free-floating mass (Davis, 1958; Allen, 1980; Zwislocki, 1980; Mammano and Nobili, 1993) in “classical” cochlear models, which assume that adjacent longitudinal sections of the cochlear are uncoupled except for energy propagation through the fluid (de Boer, 1997).

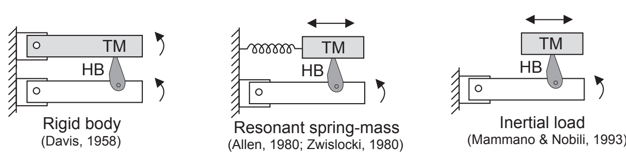

Figure 1. Classical models of the tectorial membrane. These models represent a single radial cross-section through the organ of Corti. Adjacent sections are coupled only via forces of fluid origin. In early models (left), the TM and BM were modeled as rigid structures connected with hair bundles (HB) that move as levers. Later models (center) introduced the idea that deformations of the TM could lead to resonance, and thereby enhance sensitivity and frequency selectivity. Some models (right) suggest that the TM primarily presents an inertial load that tends to convert translations of the BM to rotations of hair bundles.

Recent measurements have shown that the TM is viscoelastic (Abnet and Freeman, 2000) and can couple motion over significant longitudinal cochlear distances (Abnet and Freeman, 2000; Russell et al, 2007), suggesting that the TM also may support waves. Furthermore, we have shown that longitudinally propagating traveling waves are intrinsic to the material properties of the mammalian TM (Ghaffari et al, 2007). The longitudinal extent of wave motion suggests that TM waves can stimulate hair cells from multiple regions of the cochlea and interact with the BM traveling wave to affect cochlear function. Here we develop a quantitative model to interpret those measurements and to motivate addition experimental observations.

The Tectorial Membrane Supports Traveling Waves

To characterize the traveling wave motion of the tectorial membrane, we isolate the tectorial membrane from a mouse and mount it in a wave chamber as shown below (further details can be found in RLE Progress Report 150).

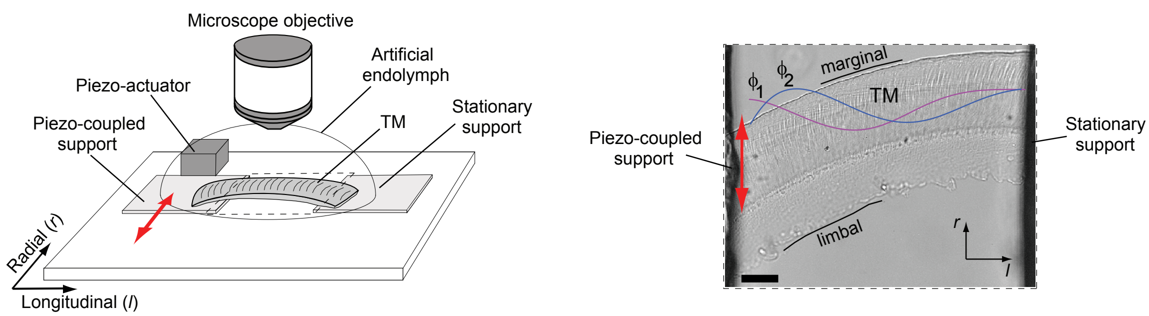

Figure 2. Left: Schematic illustration of TM wave chamber. An isolated TM is suspended between two glass coverslips that act as supports and is immersed in a drop of artificial endolymph. Motions of the left coverslip are induced by a piezoelectric crystal, and the resulting motions of the TM are observed with an optical microscope. Right: Representative TM image. Images are acquired at 16 phases of the imposed sinusoidal excitation. Motions are analyzed using computer microvision algorithms. Displacements are shown at two phases of excitation (ϕ1 and ϕ2) as a function of distance along the TM (blue and purple lines, with displacement magnitude exaggerated for clarity).

Radial forces applied at one end of the isolated tectorial membrane launch waves of motion that propagate longitudinally toward the other. The speed with which these wave propagate is similar to the speed of the basilar membrane (BM) traveling wave (von Bekesy, 1960), which suggests that interactions of the TM and BM wave play an important role in cochlear amplification.

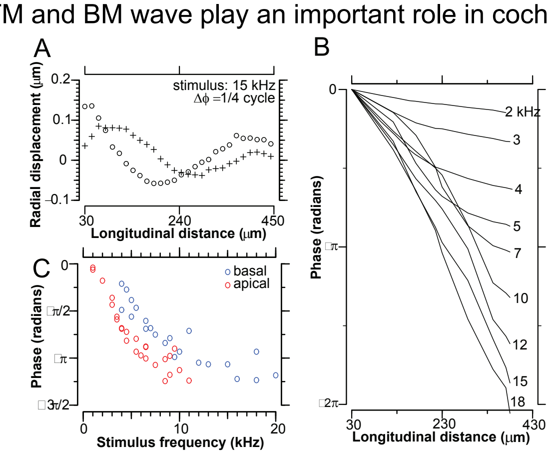

Figure 3: Measurements of TM wave motion. (A) Magnitude of TM displacement as a function of distance from the vibrating support at two phases of the sinusoidal excitation, separated by ¼ cycle. (B) Phase of TM displacement versus frequency for two segments of TM, one from the base and one from the apex. (C) Phase of TM motion vs. frequency at a location 250 μm from the vibrating support. At a given frequency, TM segments from the apex of the cochlea show more phase lag than basal segments.

These waves are potentially important because they provide insight into the material properties of the TM and because the waves themselves may play a role in cochlear function. To investigate these ideas, we have developed a computational model of TM wave propagation.

Model Formulation

The TM was modeled as a one dimensional structure with distributed impedance. The TM was divided into longitudinal sections each with a length *l*. Each section had a mass *Mm* determined from the geometry of the TM, assuming the TM had a density equal to that of water. This mass also includes a frequency-dependent contribution from the layer of fluid surrounding the TM.

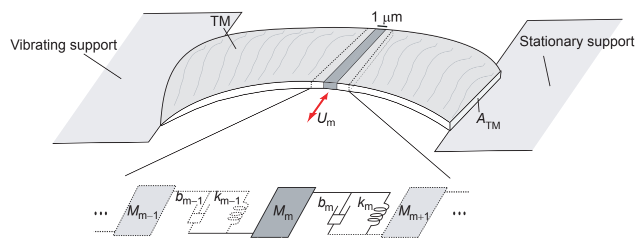

Figure 4: Model of TM wave motion. Longitudinal segments of the isolated TM are represented as discrete masses that are interconnected with springs that represent TM stiffness and dashpots that represent viscous loss in the TM.

Each mass was coupled to its neighbors through an elastic spring *km* and a viscous damper *bm*. These values were determined from the geometry of the TM, the length *l* of each section, and the material properties *G′* and η of the TM, which represent the shear and loss moduli respectively. In the general case, these values and the geometry of the TM are a function of longitudinal position. The boundary conditions of the experiment were incorporated by applying a known displacement to the leftmost mass M_0, and by imposing a displacement of zero to the rightmost mass M_N. The model was fit to measurements of TM wave propagation by allowing the parameters *G′* and η to vary. For each TM, the model was fit to measurements of TM motion at 25-30 longitudinal positions for 16 stimulus phases at each of 3-8 frequencies. Model parameters were found that best fit these measurements in a least-squares sense. The model was fit to measurements from four basal and three apical TM segments.

Comparison to Measurements

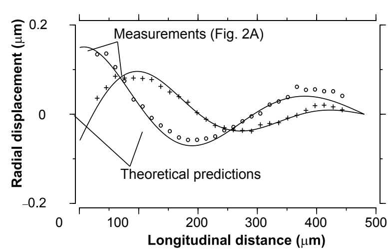

Figure 5. Comparison of measurements (symbols) and model (lines). This plot shows the best fit of the model to measurements of TM displacement vs. distance from the vibrating support in response to a 15 kHz sinusoidal displacement imposed at the left edge. Measurements and model fits at two phases separated by 90 degrees are shown. The best-fit values of *G′* for basal and apical TM segments were 47±12 and 17±5 kPa, respectively. These values are comparable to the 7-50 kPa estimated from direct measurements of TM shear impedance (Gu et al, 2008). Best-fit values for η were 0.19±0.07 and 0.15±0.04 Pa·s for basal and apical segments, respectively.

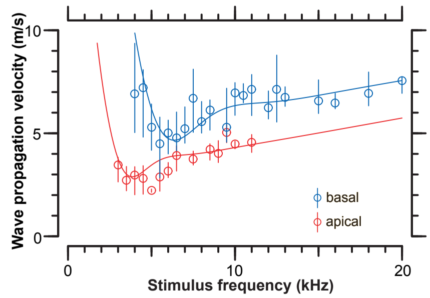

Figure 6. Comparison of measurements (symbols) and model (lines). The plot shows the effect of the boundary conditions on wave velocity. At low frequencies, the wavelength exceeds the dimensions of the TM segment, causing the velocity to increase asymptotically toward infinity. Such increases are seen in the measurements as well as the model. At intermediate frequencies, wave reflections off of the stationary support cause local minima in velocity. These local minima can also be seen in the measurements. The frequencies at which these features are observed depend on the distance between supports as well as TM material properties.

Effect of Cochlear Loads

In vivo, the TM is coupled to hair bundles, attached to the spiral lamina, and bounded below by a narrow subtectorial fluid space. To characterize effects of these attachments, we incorporated representations of each in our model.

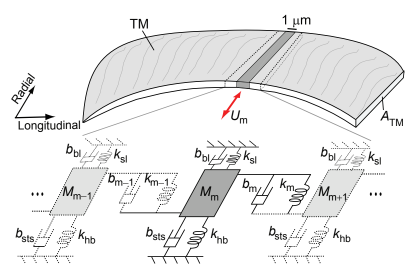

Figure 7. Incorporating effects of cochlear loads in the distributed impedance model of TM traveling waves.

We incorporated OHC hair bundles as a stiffness *khb* to ground, using a stiffness of 3.5 mN/m per bundle. The limbal attachment was modeled as an elastic solid 100 μm wide and 10 μm thick, using a Young's modulus equal to 3*G'*. The subtectorial space was modeled as a fluid undergoing Couette flow, which introduced damping *bsts* to ground along with a mass term to represent the moving fluid.

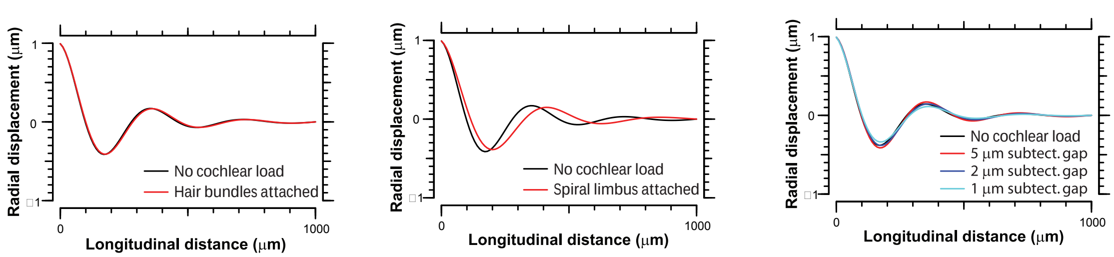

Figure 8. Effects of cochlear loads on TM traveling waves.

The plots above show the effect of these loads on wave propagation for a basal TM segment. Only the limbal attachment had a significant effect on the wave; this effect was primarily to increase the wavelength.

Summary

Radial displacements applied to one end of an isolated tectorial membrane (TM) launch traveling waves on the tissue. We have developed a transmission-line model of the TM that accounts for these waves. In the model, the TM is divided into a series of masses connected by springs and dashpots. The mass of each section was determined by assuming that the TM has the density of water. The values for the springs and dashpots were determined from a least-squares fit to measured wave motion. The resulting shear moduli were 17±5 and 47±12 kPa for apical and basal TM segments respectively. The shear viscosities were 0.15±0.04 and 0.19±0.07 Pa-s for apical and basal segments, respectively. The hair bundles and limbal attachment were each modeled as springs between the TM and stationary ground. Incorporating these springs into the model caused a modest increase in space constants at low frequencies, with little change at high frequencies. Adding subtectorial damping reduced the extent of wave propagation at low frequencies for gap sizes on the order of 1 µm. However, these gap sizes occur only in the basal high-frequency region of the cochlea. Therefore subtectorial damping did not significantly affect TM wave propagation near the best frequency at any location. These effects were small because the mass, stiffness, and viscosity of the TM are comparable to those of the entire cochlear partition. Thus even in the presence of subtectorial damping and loaded by hair bundles and the limbal attachment, a traveling wave on the TM can propagate in vivo. This simple model can be coupled to models of the BM traveling wave to investigate how the interaction of two traveling waves affects cochlear tuning.

Implications of TM Wave for Cochlear Models

The model presented here explains how the observed wave motion arises from known material properties of the TM. This model differs from TM representations in "classical" cochlear models in that energy can propagate longitudinally along the TM as well as through the fluid. Because the TM makes up a large fraction of the mass of the organ of Corti, the energy transmitted in this way may be comparable to that carried in the BM wave.

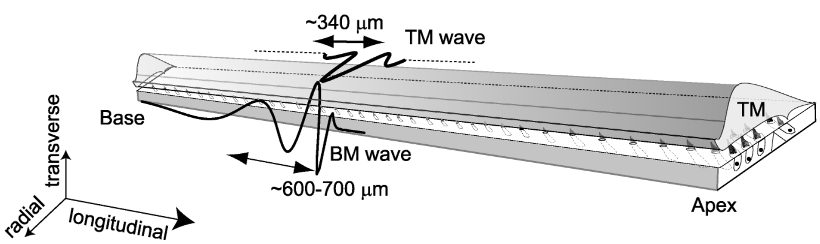

Figure 9. Schematic drawing illustrating the concept that the cochlea supports two traveling waves. TM wave (Top) and BM wave (bottom) both propagate longitudinally with comparable wavelengths and velocities near the BF place. The observed TM waves are longitudinally propagating waves of radial motion; the BM waves are longitudinally propagating waves of transverse motion. These two waves can be coupled through the OHCs and cochlear fluids.

The wave model bears some resemblance to the classical resonant TM model. At a given longitudinal position, the TM looks like a mass coupled to springs and dashpots. Thus point measurements of TM motion, such as those presented by Gummer et al., might appear resonant. However, there are two important differences between these models. First, in the wave model the

TM can propagate as well as store energy. This energy propagation may contribute significantly to the width of the tuning curve tip, as suggested by Russell et al. Second, losses in the wave model are primarily internal to the TM, rather than in the subtectorial fluid. Overall, the wave model suggests that the TM may contribute significantly to energy propagation within the cochlea.

Publications

Journal Articles, Published

Desai, Salil P., D. M. Freeman, and J. Voldman, “Plastic Masters – Rigid Templates for Soft Lithography,” Lab on a Chip, 2009.

Journal Articles, in Review

Ghaffari, Roozbeh, A. J. Aranyosi, G. P. Richardson, and D. M. Freeman, “Tectorial Membrane Traveling Waves Underlie Abnormal Hearing in *Tectb* Mutant Mice.”

Journal Articles, in Preparation

Ghaffari, Roozbeh and D. M. Freeman, “Role of Charge in Tectorial Membrane Mechanics.”

Theses

Farrahi, Shirin, “In-Vivo Measurement of Sound-Induced Motions in the Gerbil Cochlea,” June 2009.