



Published in final edited form as:

Curr Opin Otolaryngol Head Neck Surg. 2011 October ; 19(5): 382–387. doi:10.1097/MOO.0b013e32834a5bc9.

Auditory Mechanics of the Tectorial Membrane and the Cochlear Spiral

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Abstract

Purpose of review—This review is timely and relevant since new experimental and theoretical findings suggest that cochlear mechanics from the nanoscale to the macroscale are affected by mechanical properties of the tectorial membrane and the spiral shape.

Recent findings—Main tectorial membrane themes covered are i) composition and morphology, ii) nanoscale mechanical interactions with the outer hair cell bundle, iii) macroscale longitudinal coupling, iv) fluid interaction with inner hair cell bundles, v) macroscale dynamics and waves. Main cochlear spiral themes are macroscale low-frequency energy focusing and microscale organ of Corti shear gain.

Implications—Findings from new experimental and theoretical models reveal exquisite sensitivity of cochlear mechanical performance to tectorial membrane structural organization, mechanics, and its positioning with respect to hair bundles. The cochlear spiral geometry is a major determinant of low frequency hearing. Suggestions are made for future research directions.

Keywords

Tectorial membrane; cochlear spiral; cochlear mechanics

Introduction

The mammalian cochlea has two very distinct features that are not present in lower vertebrates. During evolution, the mammalian cochlea spiraled into a snail-like shape, and the tectorial membrane (TM) developed anisotropy through embedded collagen fibers that slant along the spiral. This brief review discusses the implications of these two evolutionary developments on the mechanics of hearing as reported in recent literature. To establish the context a few older references should be mentioned. In 1953 von Békésy probed the TM with a needle and remarked that it had both elastic and viscous properties [1]; the TM could be easily separated between its fibers; and the spiral curvature limited the base-apex deformation of the TM. In 1968, Hallowell Davis pointed out that the TM was undervalued, and predicted that it would be the next ‘structure of the year’ [2]. Even so, at that moment, and during the following decades, models of cochlear mechanics gave little relevance to the

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TM. Only two models treated the TM as a basic structure overlying the sensory hair bundles that somehow aided in bending them via a radial shearing mechanism [3,4]. As we show here, the most recent TM research has finally transformed Davis's prediction to reality. TM research has centered on its composition and morphology, its mechanical interaction with outer hair cell (OHC) bundles at the nanoscale, its fluid interaction with inner hair cell (IHC) bundles, TM longitudinal coupling at the macroscale, and TM dynamics and waves. Research on spiral curvature has impacted primarily low frequency mechanics, and is beginning to influence studies in development and evolution. Together, the present review and the one previously published in this journal [5] suggest that the classical picture of a single transverse traveling wave, instigated at the stapes, and peaking at a frequency-dependent place on the cochlear partition to locally stimulate outer and inner hair cells needs modification and extension. This mechanical process is certainly influenced by both the TM and the spiral shape.

Composition and morphology of the Tectorial Membrane

The TM is composed of collagen types II, V, IX and XI and three non-collagenous glycoproteins: α -tectorin (encoded by TECTA gene), β -tectorin (TECTB) and otogelin (OTOG) [5]. During the last decade, generation of mice with mutations on the genes encoding these proteins has expanded our knowledge on how the TM operates. In the last year, studies aimed at further characterizing TM composition have focused on identifying the proteins involved in the attachment crown, i.e the physical interaction between the TM and OHCs. In adult animals, stereocilin forms a ring around the tip of each stereocilium in the tallest row of stereocilia [6]. Stereocilin is also detected forming a similar pattern on the undersurface of the TM, surrounding the imprints produced by the tallest row of stereocilia. Although these results indicate that stereocilin links the attachment crown of the stereocilium to the TM, additional proteins may be involved. A likely candidate is carcinoembryonic antigen-related cell adhesion molecule 16 (Ceacam16), a secreted protein that interacts with α -tectorin and is detected at the tips of the OHC hair bundles (HB) in adult mice [7]. Interestingly, Ceacam16 may also have a role in TM maintenance. To support this hypothesis, Ceacam16 has been detected in the main body of the TM. Furthermore, in humans, a mutation in CEACAM16 is one of the few that involves the TM and results in progressive hearing loss [8].

The most prominent feature of the TM are the thick collagen bundles that run radially. These bundles are composed of 20nm diameter collagen filaments imbedded in a tectorin-based striated-sheet matrix [5]. Several morphological features of the TM vary along the length of the cochlea. Both the width and thickness of the TM increase from base to apex [9]. Also, there is a gradient in the thickness of the radial collagen bundles, which are thicker and more densely packed in the base [10**]. Finally, there is a slow variation in the slanting of the collagen bundles with respect to the radial direction, from 15° in the base to 25° in the apex [11]. Corresponding to this gradient, collagen bundles seem to be aligned with the orientation of maximal sensitivity of HBs all along the length of the cochlea. Nevertheless, it is unknown whether the mechanical interaction of the TM with the HBs contributes to the alignment of the two structures during development. In this connection, TMs obtained from transgenic mice defective of proteins involved in the attachment crowns, as well as those with shortened HBs (Shaker2) may provide insight into the question.

Interaction of the TM with OHCs – Role of mechanical anisotropy

Aligned collagen bundles confer mechanical anisotropy to the TM. A material with such mechanical properties opposes deformation with a resistance that depends on the direction of force applied onto it, and surface deformations extend differently along different

directions. These features are key to understanding the mechanical interaction between TM and HBs at the nanoscale. The TM is more compliant to forces applied in the surface rather than perpendicular to it [12*]. Thus, it has been hypothesized that the relative motion between TM and HBs translates into stereocilia deflection, rather than TM indentation. This effect would maximize opening of mechano-electrical transduction (MET) channels, disregarding the direction of relative motion between the TM and the organ of Corti. TM deformations extend further in the direction parallel to the collagen fibers (radial) than perpendicular to them (longitudinal) [10**]. As a result, there is strong coupling of the 3 OHCs most sensitive to the same frequency. Conversely, OHCs sensitive to different frequencies, i.e those laying in the same cell row along the longitudinal direction, remain uncoupled [10**]. A recent model estimating the contribution of TM coupling on HB spontaneous oscillations [13*] can be used to predict that a system of three cooperative resonant HBs will increase by three-fold a putative HB-based cochlear amplifier. This hypothesis is further supported by data obtained from two transgenic mice with reduced OHC coupling: *Col11a2*^{-/-} mice, which lack collagen XI and have lower density of TM collagen bundles and smaller radial mechanical coupling [14]; and *Tecta*^{C1509G/+}, in which the TM contacts only one row of OHCs [15]. Accordingly, these mice have up to 50 dB auditory threshold elevations as measured by ABR or DPOAE [14,15].

An exquisite balance between TM radial stiffness and HB rotational stiffness along the length of the cochlea guarantees that HBs operate at an optimal point on their current-displacement function. Cochlear microphonics is a useful tool to characterize the aforementioned phenomenon *in vivo*, because recordings on animals whose HBs are optimally tuned have symmetric receptor potentials with no phase lags. One revealing example are mice lacking β -tectorin (*Tectb*^{-/-}), which display symmetric potentials [16] and retain unaltered TM radial stiffness (authors' unpublished data), even though coupling in other directions is severely decreased [17*, authors' unpublished data]. Similarly, the observed symmetric potentials [18] can be used to predict that the Y1870C missense mutation in *TECTA* doesn't affect TM radial stiffness, although mechanical measures at the nanoscale are still lacking. Interestingly, mice lacking stereocilin have no TM imprints, but they preserve symmetric potentials at P14, an age when auditory function is still not impaired [6,19**]. This surprising result shows that an actual protein linkage is not required for proper mechanical interaction between TM and HBs, suggesting that contact of the two structures is enough to guarantee optimal performance of the HBs.

Interaction of the TM with IHCs

The HBs of the IHCs are freestanding, and they are excited by fluid flow generated by shearing movement between the TM and the reticular lamina (RL) [20,21]. Recent experiments indicate that other types of relative motion between TM and RL may also exist, such as a mode with the RL pivoting over the tunnel of Corti, resembling the movement of a teeter-totter [22]. Such a mode would create additional fluid flow via a pumping effect, contributing to HB deflection [23,24]. Elevated neural thresholds are observed in mice with an enlarged subreticular space [18]. To explain this observation, it is generally accepted that the magnitude of fluid flow and thus HB deflection depend strongly on the TM-RL distance [25]. Nevertheless, a recent model points out that the close presence of the TM prevents the different rows of stereocilia from splaying when oscillating in fluid, thus contributing to HB coherence and synchrony of MET channel openings [26*]. According to this model, elevated neural thresholds in *Tecta*^{Y1870C/+} mice can be explained by the lack of HB coherence, which results in some MET channels being always in a closed state. This model also predicts that the temporal pattern of IHC depolarization during one cycle will be affected when the subreticular space is enlarged [26*], whereas a model hypothesizing only reduced fluid flow predicts smaller magnitude of depolarization with unaltered temporal

patterns [25]. Thus, detailed analysis of cochlear microphonics measurements on Tecta^{Y1870C/+} mice can help elucidate the validity of each model and further our understanding of the mechanisms involved in IHC excitation.

TM coupling at the macroscale, dynamics and travelling waves

Measurements performed at the macroscale (hundreds of microns) have shown that the TM is a structure with significant longitudinal coupling [27,28]. The implications of TM longitudinal coupling on hearing were brought to light by Tectb^{-/-} mice. TMs obtained from the base of the cochlea have a 2-fold reduction in the longitudinal coupling both at the nanoscale (author's unpublished data) and the macroscale [17*]. Accordingly, the sharpness of tuning of basilar membrane and neural recordings ($Q_{10\text{dB}}$) is increased by a factor of 2–3 at mid to high frequencies [16]. Interestingly, increased tuning arised at the expense of sensitivity, which was reduced by 10dB SPL. These findings challenged previous ideas stating that sensitivity and frequency selectivity increase together, and showed instead that sensitivity and selectivity are two opposing features that need to be balanced through proper longitudinal coupling [29]. Longitudinal coupling allows a large number of OHCs to work in synchrony, thus promoting sensitivity. Nevertheless, as the number of coupled OHCs grows larger, so does the extent of frequencies excited by a given stimulus, thus reducing frequency selectivity [29]. In parallel with experimental results, new models are emerging which include the effect of TM longitudinal coupling on cochlear mechanics and are able to better replicate the magnitude of basilar membrane tuning measured *in vivo* [30*].

Together with sensitivity and frequency selectivity, the third cornerstone of proper hearing is time discrimination. Viscoelasticity of the TM plays a crucial role in the duration of impulse responses, with oscillations that continue for a longer time when viscoelasticity is reduced or not included [30*]. *In vitro* measurements show that the TM is indeed a viscoelastic material and that the ratio of elastic to viscous components ranges from ~3 for low and mid-range probing frequencies [31] to ~1 at high probing frequencies [32]. Interestingly, mutations in tectorins or collagen XI do not alter the elastic to viscous ratio, even though global values of impedance are in some cases largely decreased [14,28].

The TM has been shown to support travelling waves *in vitro*, which decay with a space constant of ~200 μm [27]. This discovery has prompted models in which the extent of longitudinal coupling along the cochlea, and thus frequency selectivity, arise from the length of the region where TM and basilar membrane (BM) waves interact [17*]. In particular, effective amplification due to HB shearing is predicted only in the regions where the velocities of BM and TM waves are matched [17*,33]. As an example, the reduced wave velocity and wave decay constant measured in Tectb^{-/-} mice would lead to fewer OHCs performing amplification simultaneously, thus explaining not only the increased frequency selectivity but also the decreased sensitivity observed [17*]. It should be noted that the aforementioned predictions are based on interactions between a BM pressure-driven wave and a TM radial wave [29]. Nevertheless, recent findings suggest the existence of other modes of BM vibration, with resonances at ~0.3 octaves below the characteristic frequency of the BM for a particular location [34]. In this connection, new models including multiple modes of TM and BM vibration may provide further understating on the interaction between TM and BM, and its role on proper hearing.

Mechanics of the spiral geometry

The purpose of the coiled shape of the cochlea, unique to the mammalian cochleae, has been the focus of research and speculation for over half a century. The spiral shape is not required for hearing, as monotreme mammals have cochleae shaped like a slightly bent tube and physical models of the cochlea have shown that the place frequency map remains the same

in straight and toroidal cochlear models [1]. This supports earlier suggestions that the purpose of the coiled shape is to pack a long organ into a small space in the skull, as well as to provide an efficient organization of the nerve and blood supply to an organ that is protected inside a central shaft.

Other observations, however, suggest a functional role for the coiled geometry. The radial movement of the HB near the maximal amplitude of the traveling wave indicates an effect of fluid motion in a curved channel [1]. Also, a morphometric analysis of the cochleae of different mammals showed a strong correlation between the number of spiral turns times BM length and the low frequency limit of hearing [35]. The effect of spiral geometry on the mechanics of the cochlea has been the focus of theoretical studies over many years [36–41]. More recently such studies have suggested an important effect of cochlear coiling on low frequency hearing [42–44**].

The spiral shape, which evolved together with the lengthening of mammalian cochleae, allows a wider range of audible frequencies. However, the spiral shape achieves more than that. Like a whispering gallery, which is known for propagating even slight whispers along its concave walls, the spiral cochlea not only propagates, but also focuses acoustic wave energy along its concave outer wall. The focusing of wave energy is inversely proportional to the radius of curvature of the cochlea [44**] and becomes greatest towards the apex of the cochlea, where low frequency sounds are analyzed. This focusing results in an increased vibration of the BM towards the outer wall of the cochlear duct, which creates an effective dynamic tilt of the reticular lamina (RL) over and above its geometric tilt. Both geometric and dynamic tilts increase as the radius of the spiral decreases. The effect is greatest at the apex, where the radius of curvature is smallest and low frequencies are analyzed [43]. The RL dynamic tilt, in turn, affects the shear gain (radial displacement of RL per unit of BM displacement). Shear gain amplitude increases as the cochlear radius decreases towards the apex, while shear gain phase becomes such that an upward deflection of the BM bends the OHC HB in the excitatory direction [42]. For physiological values of the human ear responding to a 200 Hz sound, the predicted RL radial motion was 20% of the BM motion [43], comparable to measurements at the apex of the guinea pig [45].

The tilted radial distribution of fluid pressure acting on the BM was confirmed by an independent analysis [46], which calculated different pressure modes by assuming an ideal fluid as done in a previous model [47]. While the simplest mode of their analysis agrees well with previous predictions [43], higher modes show a more complex behavior, such as a small shift of the maximum fluid pressure tilt from the apex towards the base of the cochlea.

All of the above results point to a potentially functional role of the spiral geometry on the mechanics of hearing. While genes that affect coiling have been suggested, no experiments so far have been able to control the cochlear coil while keeping the auditory functionality of the cochlea. Theoretical predictions were thus put to the test indirectly, by comparing the hearing limits and the geometrical characteristics for different land and marine mammals. Theory suggests that the ratio of the radii of curvature $R_{\text{base}}/R_{\text{apex}}$ of the spiral at the basal turn to that at the apex determines the degree of wave energy focusing at the apex. Indeed, this geometrical parameter of mammalian cochleae is linearly correlated with the logarithm of the low frequency limit of hearing for all mammals tested [44**].

Conclusions

Two often neglected but unique features of the mammalian cochlea, the anisotropic tectorial membrane and the cochlear spiral geometry, conspire to increase sensitivity and selectivity in mammalian hearing.

Key Points

- Strong tectorial membrane radial coupling to outer hair cell bundles improves hearing sensitivity.
- Weak tectorial membrane longitudinal coupling to outer hair cell bundles improves frequency selectivity.
- Proper spacing between the tectorial membrane and the reticular lamina is necessary for optimal mechanotransduction.
- Cochlear curvature gradient determines the low frequency hearing limit across mammalian species.

Acknowledgments

This work was supported by the intramural program project DC00033-15 in the National Institute on Deafness and other Communication Disorders. DM thanks the Technical University of Crete for their support.

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