



THE TWO FUNCTIONS OF THE RETICULAR LAMINA

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The cell body of the outer hair cells connects the reticular lamina and the basilar membrane through supporting cells. According to the predominant view of cochlear mechanics, the outer hair cells enhance wave propagation in the scala media by dynamically expanding and contracting their body, thus providing an active driving force to the basilar membrane. In order to maximize the efficiency of such mechanism, the reticular lamina should behave like a rigid anchor; in this way the force associated with the length change of the outer hair cells body is efficiently transmitted to the basilar membrane. On the other hand, the motion of the reticular lamina provides a direct drive to the inner-hair cells through a fluid-cilia coupling mechanism. Therefore a free-to-move reticular lamina would be highly responsive to the activity of outer hair cells, thus locally enhancing the sensitivity of inner hair cells. Within this view, the reticular lamina should trade-off between the two conflicting requirements of 1) providing a firm attachment to the outer hair cells and 2) being sensitive to outer hair cells motility. A different thesis, partially supported by recent recordings of the intact organ of Corti, is that a longitudinal coupling of motion in the scala media (similar as in feed-forward cochlear models) allows for a simultaneous enhancement of basilar membrane and stereocilia vibrations without imposing contradicting requirements for the functioning of the reticular lamina. In this study, we discuss the recent experimental and theoretical findings under this perspective.

1. Introduction

Although most literature about cochlear mechanics focuses on the vibrations of the basilar membrane (BM), the relationship between BM vibration and hearing sensations is still far from established. In fact, the stereocilia of the inner hair cells (IHC), which are the mechanical receptors of the auditory system, are relatively distant from the BM and are positioned in proximity to structures of which the vibratory patterns have yet to be established.

Figure 1 shows a simplified cross-section of the organ Corti to guide the reader through the following discussion. In the classical view, the IHC's stereocilia are deflected by the radial shear motion of reticular lamina (RL) and tectorial membrane (TM). In particular, because the IHC stereocilia are not embedded in the TM, their deflection is caused by viscous drag with the fluid in the subreticular space, turning them into sensors of fluid velocity. The modern view is that the fluid-flow in the IHC surroundings is determined by the different elements in the organ of Corti [1, 2, 3, 4].

For a long time the discussion about the IHC mechanical excitation was about whether IHC tuning reflects that of the BM or whether the organ of Corti acts as a "second filter" enhancing the frequency

selectivity of IHCs. Second filter theories have been highly disregarded for the last two decades, as *in vivo* recordings from sensitive preparation in the guinea-pig and the chinchilla base [5, 6] showed similar BM and neural tuning. However recently, second filter theories have been revived under a new perspective by studies showing a different tuning of the structure in proximity of the IHC than that of the BM (e.g. [7, 8]).

Based on recordings from chinchilla and guinea-pig [5, 6], as well comparison of psychophysical and BM tuning in humans [9] we can reasonably exclude that the differences between IHC and BM tuning are substantial. Nonetheless, the greater awareness that the structures near the stereocilia retain different vibration patterns than the BM requires to think that the objective of the active processes is to enhance vibrations near the IHC stereocilia, not that of the BM. Therefore, the functional role of the BM needs to be questioned because often cochlear mechanics theories tend to treat the vibrations of the BM as cochlear mechanics itself rather than a means to excite IHCs.

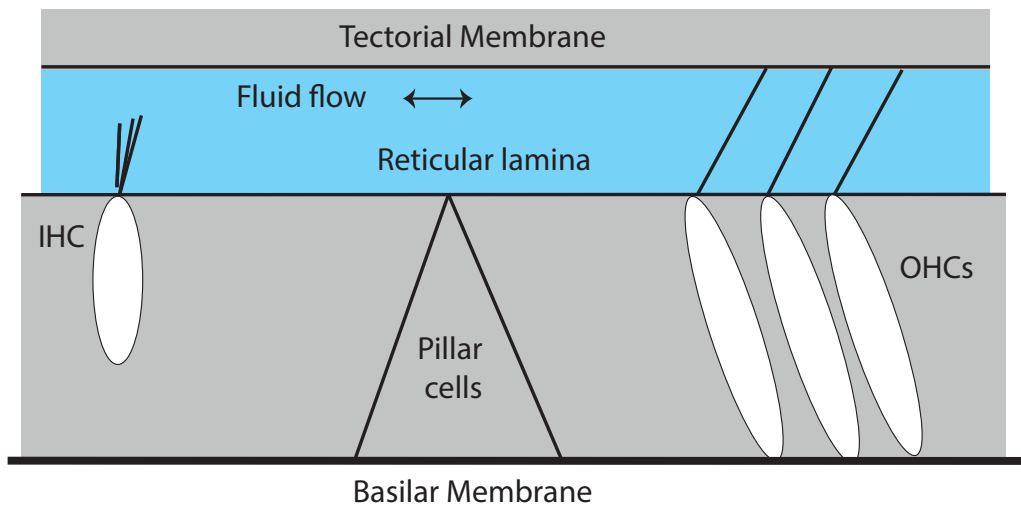


Figure 1: Simplified cross section of the organ of Corti.

2. Reticular lamina transverse motion can drive the inner hair cells

Within the modern view of organ of Corti mechanics, the action of outer hair cells (OHCs) significantly contribute to determine IHC responses, since they are active elements that can provide a strong drive to IHC at low sound pressure levels [1]. This idea has been recently discussed by [4], who identified four distinct drives contributing in deflecting the IHC stereocilia bundles. These drives operate via compression and expansion of the gap between reticular lamina and tectorial membrane, which causes the fluid to flow in and out of the subtectorial space, along with the classical radial shear coupling between tectorial membrane and stereocilia bundles. In particular it has been postulated that the OHC somatic motility pulls the RL up and down [4], creating a significant fluid-flow in the subtectorial space which plays a major role in driving the IHC from low to moderate SPLs.

From this idea, it is natural to question whether the primary function the OHC somatic motility is to amplify BM vibrations, or to improve the sensitivity of sensory cells. If OHCs function is only to improve the IHC sensitivity, then the optimal transmission of energy from the OHCs to the IHC's stereocilia happens if the BM acts a rigid support for the OHCs and the RL is free to pivot on the top of pillar cells.

3. Cochlear amplifier and OHC somatic motility

One of the main characteristic of the active process of cochlear mechanics is the enhancement of BM longitudinal waves. The so-called cochlear amplifier does not only increase the amplitude of the BM waves, but has a dramatical effect in shaping the frequency selectivity of the hearing organ. The predominant view is that the cochlear amplifier is the result of the combined action of somatic motility of OHCs and active motion of OHCs's stereocilia-bundles [10].

The active process can be modelled mathematically through an additional force proportional to BM velocity (negative damping), compensated by a delayed stiffness [11]. Since such mathematical formulation can be explained through a delayed force proportional to the BM displacement, a local action of OHCs somatic motility is in principle a good candidate to provide such explanation. Contrary to what discussed in section 2, for the OHCs motility to exert a significant amount of force to the BM, the RL needs to provide a fairly rigid attachment to the OHCs.

4. Longitudinal coupling through reticular lamina

The fact that the OHCs are not perpendicular to the BM, lead to the development of the so-called feed-forward models of cochlear macro-mechanics [12, 13]. In these models the action of OHCs is to enhance the frequency selectivity of the BM by providing an active force term which propagates from one cochlear partition to a more basal one.

In vivo recordings from the guinea-pig organ of Corti show that the phase and amplitude of RL response seem to reflect the combination of BM motion in the same longitudinal location with the one from 100 to 200 μm on a more basal location [8]. Such coupling distance, although similar to the one determined empirically in feedforward models of cochlear mechanics [12], cannot be accounted for by the OHCs orientation, as they can provide longitudinal coupling over much smaller distances (e.g. [13]). Plausible physical mechanisms providing such long-distance coupling are additional waves in the TM [14, 15], or electrical coupling of OHCs [16].

According to the recordings from [7, 8] showing a phase lead of about 90° of RL and BM in the same partition, this longitudinal coupling can provide an additional force to displace the BM which is approximatively in phase with BM velocity, to act as a negative damping.

If these results are further confirmed experimentally, then the combined action of longitudinal BM waves and RL through the active OHCs and passive supporting cells, can indeed explain the frequency selectivity of the BM. This explanation does not require the RL to act as a rigid support for OHCs, because large RL vibrations would be beneficial for amplifying both BM waves and driving the IHC.

5. Conclusions

The recent theoretical and experimental advances in cochlear mechanics indicate that the local action of OHC somatic motility to explain the frequency selectivity and sensitivity of the hearing organ imposes two conflicting requirements to the RL. First, because the motion of the RL provides a connection from OHCs to IHC stereocilia through the fluid in the subreticular space, the RL has to be free to follow the OHCs motion in order to increase maximally the IHC sensitivity. Second, the cochlear amplification through a local action of OHC somatic motility requires that the RL provides a rigid anchor to the OHCs in order to increase maximally the sensitivity of the BM. These two requirements are in conflict, requiring the RL and BM to trade-off between the two.

Another hypothesis is that the mechanical basis for the cochlear amplifier consists of an active coupling between cochlear partitions, as postulated by "feed-forward" models of cochlear mechanics (e.g. [12]). Such a feed-forward realization of the cochlear amplifier does not impose conflicting requirements for the functioning of the RL. Additionally, it would not only serve to enhance wave propagation in the scala media, but also to increase the sensitivity of the IHCs.

To conclude, recent experimental studies in the guinea-pig [7, 8] and mouse [17] show opposite results about the phase relationship between BM and RL vibration. Therefore at this time it is not possible to establish what is the precise mechanism behind the cochlear amplifier. In particular the guinea-pig studies that show higher peak frequency and phase lead of RL over BM [7, 8] are compatible with a feed-forward basis for the cochlear amplifier. The mouse study showing in-phase motion of RL and BM at the characteristic frequency [17] is of more difficult interpretation. In any case both sets of studies point out that the cochlear active process amplify RL vibrations more than those of the BM, an aspect that need to be addressed by future cochlear mechanics models.

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