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Near Field Fluid Coupling Between Internal Motion of the Organ of Corti and the Basilar Membrane

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Abstract. The pressure distribution in each of the fluid chambers of the cochlea can be decomposed into a 1D, or plane wave, component and a near field component, which decays rapidly away from the excitation point. The transverse motion of the basilar membrane, BM, for example, generates both a 1D pressure field, which couples into the slow wave, and a local near field pressure, proportional to the BM acceleration, that generates an added mass on the BM due to the fluid motion. When the organ of Corti, OC, undergoes internal motion, due for example to outer hair cell activity, this motion will not itself generate any 1D pressure if the OC is incompressible and the BM is constrained not to move volumetrically, and so will not directly couple into the slow wave. This motion will, however, generate a near field pressure, proportional to the OC acceleration, which will act on the OC and thus increases its effective mass. The near field pressure due to this OC motion will also act on the BM, generating a force on the BM proportional to the acceleration of the OC, and thus create a "coupling mass" effect. By reciprocity, this coupling mass is the same as that acting on the OC due to the motion of the BM. This near field fluid coupling is initially observed in a finite element model of a slice of the cochlea. These simulations suggest a simple analytical formulation for the fluid coupling, using higher order beam modes across the width of the cochlear partition. It is well known that the added mass due to the near field pressure dominates the overall mass of the BM, and thus significantly affects the micromechanical dynamics. This work not only quantifies the added mass of the OC due its own motion in the fluid, and shows that this is important, but also demonstrates that the coupling mass effect between the BM and OC significantly affects the dynamics of simple micromechanical models.

INTRODUCTION

The distribution of pressure in the fluid chambers of the cochlea can be thought of as having two components: a 1D, or plane wave, component, which can couple along the whole length of the cochlea, and a near field component, which only couples locally. The near field component is mainly concentrated around the part of the basilar membrane, BM, that is vibrating with the largest amplitude and smallest wavelength, and is proportional to its acceleration, and thus acts as an added mass on the BM [4] whose magnitude is significantly greater than its physical mass [3]. In this paper the near field pressure is considered due to both BM motion and also internal organ of Corti, OC, motion, due to outer hair cell activation for example. If the OC is incompressible and the BM is assumed not to move during internal OC motion, this motion will not excite the plane wave in the upper fluid chamber, since it has no volumetric component, and so will not itself couple into the slow cochlear wave. In the normal mode of operation for the cochlea, there would clearly be both motion of the BM and internal motion of the OC, due to their coupling. We artificially separate these two motions here, in order to calculate the individual contributions to the near field pressure. They are later combined together in the lumped parameter model.

Figure 1A shows the instantaneous magnitude of the pressure distribution across a 3D finite element model of a section of the cochlea when only one section of the BM is excited [5]. The pressure distribution is almost uniform across the width of the BM and in phase with its acceleration. Figure 1B shows the instantaneous magnitude of the near field pressure distribution when the BM does not move, but one section of the OC is excited by opposing forces at the ends of the outer hair cells. The Hensen cells move inward as the reticular lamina and tectorial membrane are forced upward, since the OC is assumed to be incompressible. It can be seen that this internal OC acceleration generates a near field pressure distribution that is quite complicated, but has a positive component in phase with the upward motion of the tectorial membrane and a negative component in phase with the inward motion of the Hensen cells, thus generating a force on the OC that would act as if it had an added mass.

If the near field pressure due to internal OC acceleration is integrated over the width of the BM, it can also be shown to generate a finite force on the BM. It is thus clear that the near field pressure due to such OC motion, which is proportional to its acceleration, not only acts on the OC itself, creating an added mass, but also acts on the BM, creating a significant "transfer mass" effect. The magnitude of these mass loading effects can be most easily quantified

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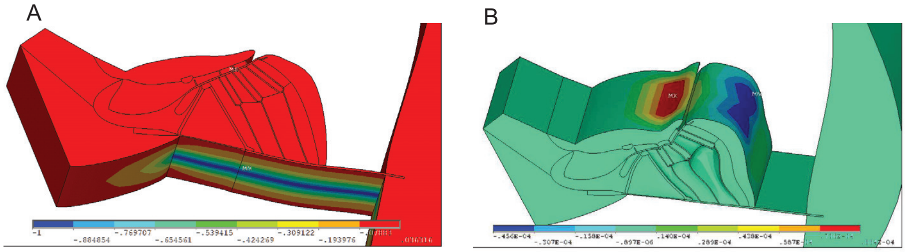

FIGURE 1. [Color version of figure available online] The near field pressure distribution in a 3D finite element model of a slice of the cochlea when the BM only is driven into motion, and there is no internal motion of the OC (A), and when the BM does not move but the OC is driven by forces at the outer hair cells (B).

using the theoretical wavenumber model, outlined in Section "Theoretical Analysis". Its effects on a lumped parameter model of the micromechanics are discussed in Section "Effect of Fluid Mass Loading on Micromechanics".

THEORETICAL ANALYSIS

A wavenumber approach is used to quantify the near field fluid coupling between the motion of the BM and the OC. It is assumed that the BM motion corresponds to the first radial mode of a beam, with a displacement proportional to $sin\left(\pi y/B\right)$, where y is the radial distance along the cochlear partition and B is the width of the BM, so that there is a half wavelength across the BM. The motion of the OC, on the other hand, is assumed to correspond to the second radial mode of a beam, with a displacement proportional to $sin\left(2\pi y/B\right)$, so that there is a whole wavelength across the BM. Clearly this modal behaviour does not describe the full 3D motion of the OC, but it does show the feature that the flow is outwards at some radial positions and inwards at others, with no overall volumetric component.

The wavenumber approach of Steele and Taber [7] can be generalized, using a similar approach to Taber and Steele [8], to calculate the near field fluid coupling from one mode of radial BM motion to another mode of the radial pressure distribution. The n-th mode of the pressure difference distribution in the wavenumber domain, $P_n\left(k\right)$, can thus be written, for a rectangular box model, in terms of the m-th mode of the velocity distribution, $V_m\left(k\right)$, as

$$P_n\left(k\right) = \varepsilon_{nm} i\omega\rho Q_{nm}\left(k\right) V_m\left(k\right), \tag{1}$$

where ω is the angular frequency, ρ is the fluid density and ε_{nm} is a normalization factor that will be explained below. The “equivalent height”, $Q_{nm}\left(k\right)$, is equal to

$$Q_{nm}(k) = \frac{A_{n0}B_{m0}}{k}\coth\left(kH\right) + \sum_{l=1}^{\infty}\frac{A_{nl}B_{ml}}{2m_l}\coth\left(m_l H\right), \tag{2}$$

where l is the order of the transverse acoustic mode, m_l is equal to $\sqrt{k^2 + l^2\pi^2/W^2}$, H and W are the physical height and width of each fluid chamber and a reasonable approximation to the infinite sum is found by taking 200 terms. A_{nl} is the coupling coefficient between the l-th transverse acoustic mode and the n-th mode of the radial pressure distribution, with mode shape $\psi_n\left(y\right)$, and B_{ml} is the coupling coefficient between the m-th model of BM motion, with mode shape $\chi_m\left(y\right)$, and the l-th transverse acoustic mode, so that

$$A_{n0} = \frac{1}{W}\int_0^W \psi_n\left(y\right)dy, \qquad B_{m0} = \frac{1}{W}\int_0^W \chi_m\left(y\right)dy, \tag{3}$$

and for l greater than zero,

$$A_{nl} = \frac{2}{W}\int_0^W \cos\left(\frac{l\pi y}{W}\right)\psi_n\left(y\right)dy, \qquad B_{ml} = \frac{2}{W}\int_0^W \cos\left(\frac{l\pi y}{W}\right)\chi_m\left(y\right)dy, \tag{4}$$

where the normalised mode shapes, for example, $\psi_n\left(y\right) = \chi_n\left(y\right) = \sqrt{2W/B}\sin\left(n\pi y/B\right)$, if B is the width of the BM [2].

In the original formulation [7], $\psi_n\left(y\right)$ is equal to $\chi_m\left(y\right)$, which is a single assumed BM mode shape, typically a half sine wave across the width of the BM. In this generalized formulation, $\psi_n\left(y\right)$ may, for example, be equal to this first

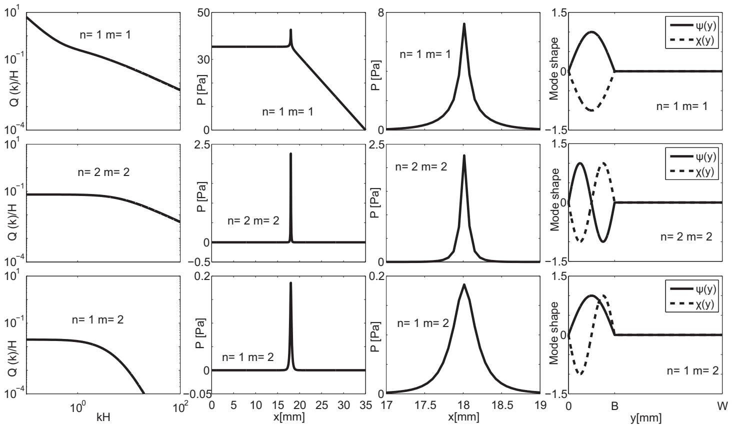

FIGURE 2. Wavenumber distributions of equivalent height (First column), spatial total pressure difference (Second column) and pressure difference due to the near field component (Third column), together with the corresponding radial mode shapes (Fourth column).

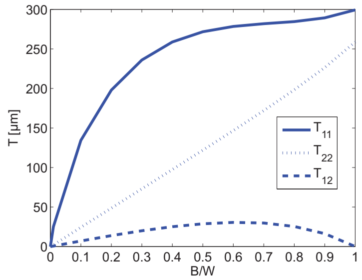

FIGURE 3. Distributions of effective thickness, T_{11} due to BM motion acting on the BM, T_{22} due to OC motion acting on the OC and T_{12} due to OC motion acting on the BM, calculated for different values of ratio of the BM width to the fluid chamber width, B/W.

pressure mode shape with $n = 1$, but $\chi_m(y)$ can now be equal to a second mode shape with $m = 2$. $Q_{12}(k)$ will then quantify the fluid coupling between the second mode of BM motion and the first mode of radial pressure distribution on the BM, which drives the first mode of the BM. The second mode of motion has no volumetric component, so cannot excite the plane wave pressure distribution in the fluid chambers and hence cannot couple into the slow wave. It does, however, represent an approximation to the excitation due to internal OC motion, in which the negative flow due to the upward tectorial membrane motion is exactly equal to the positive flow due to the resulting outward motion of the Hensen cells, in order to preserve the volume of the OC, which is assumed to be incompressible. If n and m are equal to 1, then the BM is driving both fluid chambers, so the normalization factor, ε_{11}, is equal to 2. If, however, m is equal to 2, corresponding to OC motion, this will only drive one fluid chamber, so that ε_{n2} is equal to 1, for n is both 1 and 2. Figure 2 shows the wavenumber distribution of $Q_{11}(k)$, $Q_{22}(k)$ and $Q_{12}(k)$ for $B/W = 0.3$, and the resulting pressure distribution along the cochlea, obtained by inverse Fourier transformation [2], when exciting an element of the BM in about the middle of the cochlea, $Q_{11}(k)$ corresponds to the normal excitation of the BM and its pressure response, $Q_{22}(k)$, corresponds to the modal pressure on the OC when the OC is moving, and $Q_{12}(k)$ corresponds to the pressure driving the first BM mode when the OC is moving. Also shown in Fig. 2 is an expanded view of the longitudinal distribution of the near field pressure in each case, and the corresponding radial mode shapes.

The near field pressure contributes an added mass to the moving parts, which can be calculated by integrating the near field pressure distribution along the cochlea. This is equivalent to taking the limiting case as k tends to zero in the wavenumber formulation [2], so that this mass is equal to $\varepsilon_{nm}\rho$ multiplied by an effective thickness given by

$$T_{nm} = \lim_{k\to 0} Q_{nm}^{N}(k), \tag{5}$$

where $Q_{nm}^{N}(k)$ is the near field component of $Q_{nm}(k)$. The effective thicknesses T_{11}, T_{22} and T_{12} are plotted as a function of B/W for $W = H = 1$ mm in Fig. 3, corresponding to the added mass on the BM and OC when acting alone, and the transfer mass between the OC and BM. For a typical value of $B/W = 0.3$ at the base of the cochlea, T_{11} is about 230 μm, T_{22} is about 70 μm and T_{12} is about 15 μm, so that T_{12} is about 10% of the average value of T_{11} and T_{22}.

EFFECT OF FLUID MASS LOADING ON MICROMECHANICS

Many models of cochlear mechanics used lumped parameter representations of the motion of various parts of the OC. An example of such a lumped parameter micromechanical model with two-degree-of-freedom is shown in Fig. 4. In this model m_1 represents the mass of the BM, the Deiters cells and associated elements, and m_2 represents the mass of the reticular lamina, RL, tectorial membrane, TM, and the upper part of the Hensen cells, s_1 and s_2 represent the stiffness associated with those masses and s_3 the coupling stiffness of the outer hair cells and associated elements, each of which has an associated damping term. Strictly speaking, the radial motion of the tectorial membrane, which can be resolved into an equivalent transverse motion [1], should also be included in such a micromechanical model. This gives a three-degree-of-freedom micromechanical model, as used, for example, by Ramamoorthy *et al.* [6]. It has been assumed here that this additional degree of freedom does not significantly affect the passive response of the system, however, and so has not been included in Fig. 4.

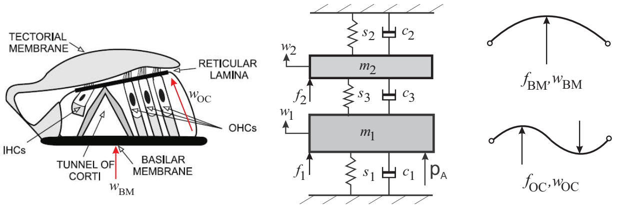

FIGURE 4. Sketch of the OC and a two-degrees-of-freedom lumped parameter model of its internal dynamics with no fluid loading, together with the motion of the BM and OC assumed in the calculation of the fluid loading.

The dynamic response of the two-degree-of-freedom lumped parameter model shown in Fig. 4, from the forces on the two masses, f_1 and f_2, to their displacement, w_1 and w_2, can be written as

$$\begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} m_1 & 0 \\ 0 & m_2 \end{bmatrix} \begin{bmatrix} \ddot{w}_1 \\ \ddot{w}_2 \end{bmatrix} + \begin{bmatrix} c_1+c_3 & -c_3 \\ -c_3 & c_2+c_3 \end{bmatrix} \begin{bmatrix} \dot{w}_1 \\ \dot{w}_2 \end{bmatrix} + \begin{bmatrix} s_1+s_3 & -s_3 \\ -s_3 & s_2+s_3 \end{bmatrix} \begin{bmatrix} w_1 \\ w_2 \end{bmatrix}. \tag{6}$$

The effect of fluid loading is to change the diagonal terms in the mass matrix to m_1' and m_2' and introduce a transfer mass m_{T}, so that the equation describing the dynamic response of the system now becomes

$$\begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} m_1' & m_{\mathrm{T}} \\ m_{\mathrm{T}} & m_2' \end{bmatrix} \begin{bmatrix} \ddot{w}_1 \\ \ddot{w}_2 \end{bmatrix} + \begin{bmatrix} c_1+c_3 & -c_3 \\ -c_3 & c_2+c_3 \end{bmatrix} \begin{bmatrix} \dot{w}_1 \\ \dot{w}_2 \end{bmatrix} + \begin{bmatrix} s_1+s_3 & -s_3 \\ -s_3 & s_2+s_3 \end{bmatrix} \begin{bmatrix} w_1 \\ w_2 \end{bmatrix}. \tag{7}$$

Since the OC motion must be calculated relative to that of the BM in the calculation of the fluid loading and if w_{BM} is equal to w_1, then w_{OC} is equal to $w_2 - w_1$, similarly f_1 due to the fluid loading is equal to $f_{\mathrm{BM}} - f_{\mathrm{OC}}$ and f_2 due to fluid loading is equal to f_{OC}. It can then be shown that m_1' is equal to $m_1 + \rho\,(T_{11} - 2T_{12} + T_{22})$, m_2' is equal to $m_2 + \rho T_{22}$ and m_{T} is equal to $\rho\,(T_{12} - T_{22})$.

The dashed curves in the left hand plots of Fig. 5 show the calculated distribution of passive BM admittance, $\dot{w}_1/f_1$, along the cochlea for this micromechanical model, using the parameters listed by Ramamoorthy *et al.* [6], but corrected for the fluid mass loading on m_1 and m_2, when driven at a frequency of 8.2 kHz. It has been shown above that the transfer mass between the BM and internal OC motion is about 10% of the average of the added fluid masses of these two components individually. The BM admittance using this model in the passive case is shown as the solid line in the left hand plot of Fig. 5. The resonant frequency, surprisingly, has slightly dropped as a result of adding this additional mass. This can be understood by considering the two modes of this micromechanical model. When the system includes the transfer mass, m_1 and m_2 at $x \approx 8$ mm move out of phase when driven at 8.2 kHz, so the motion of m_2 reduces the effective mass on m_1. In order to calculate the active response of this micromechanical model, additional, equal and opposite, forces have been introduced acting on m_1 and m_2 to represent the action of the outer hair cells. These forces are made proportional to the velocity of m_2 via a filter that includes both the dynamic response of the TM and the low pass filtering effect of the OHCs. The results are shown in the right hand plots of Fig. 5 for the original model and that including the coupling mass, which are now very different.

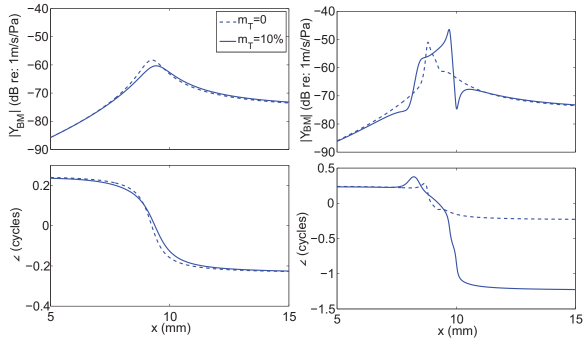

FIGURE 5. The calculated distribution of BM admittance along the cochlea when driven at 8.2 kHz using the original parameters of Ramamoorthy *et al.* [6], dashed lines, and when the transfer mass is taken into account, solid lines, for both the passive (left hand plots) and active (right hand plots) cases.

CONCLUSIONS

It has been shown that as well as significantly increasing the effective mass of the basilar membrane, the near field component of the fluid pressure also generates a force on the internal organ of Corti motion proportional to its acceleration, which significantly increases the effective mass of this micromechanical element. What is more, the near field pressure component due to internal OC motion also acts on the BM generating a “transfer mass” effect that couples those components. The magnitude of this transfer mass is about 10% of the average added mass of the BM and OC. The effect of this added mass in the dynamics of a simple two-degree-of-freedom lumped parameter model of the micromechanics has also been considered. Although the effect is small in the passive case, it makes a very significant difference in the active case. The selection of the parameters for any micromechanical model generally involves the identification of the range of the various physical parameters, which are reasonable from the morphology and mechanical characteristics of the individual elements, and then a tuning of at least some of these parameters in order to get results which agree with experimental measurements of the coupled response. Although the parameters selected for the micromechanical model used here were originally selected based on measured values [6], they were tuned without taking into account the transfer mass effect. When this transfer mass is introduced, it very significantly affects the predicted responses, but it is not possible to say which of these responses is “correct”, since no tuning has been carried out in the latter case. The importance of the present work is not only to identify the mechanism of a new coupling mechanism between the BM and OC, but also to quantify this effect so that it can be taken into account in future micromechanical models.

ACKNOWLEDGMENTS

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COMMENTS AND DISCUSSION

Joris Soons: Authors show the importance of a coupling mechanism between the (macroscopic) BM and (cellular) OHC for active models and try to quantify this coupling. I do not completely understand the theoretical analysis. First thing I do not understand is the assumption that the BM do not to move. Is this always a valid approximation?

Third page: I do understand that the second mode of motion has no volumetric component and thus cannot excite the plane wave pressure distribution in the fluid chambers and cannot couple into the slow wave. But why exactly does this state (Q12 (k)) represents the transfer mass between BM and OC?

Stephen Elliott [reply to Joris Soons]: I agree that it is rather artificial to assume independent motion of the basilar membrane and of the organ of Corti, as done initially in this paper. This is only considered in order to allow an analysis of the individual contributions of these two motions to the near field pressure. When the two degree of freedom micromechanical model is introduced later, these two motions are clearly coupled, as they would be in normal operation, and the added fluid mass due to both of the individual motions can then be accounted for. The manuscript will be revised in the final version to make this more clear. The 3D FE model had a CF of 1kHz and was driven at this frequency.

It is assumed that all the elements of the organ of Corti are essentially incompressible, so that there is no net volumetric change due to the internal organ of Corti motion on its own, and so this does not couple into the plane wave pressure distribution.

Tobias Reichenbach: I find the topic very interesting. The situation of a "silent" basilar membrane and a moving organ of Corti may be relevant near the cochlear apex where amplification by outer hair cells may not couple back to the basilar membrane (theoretical analysis in Reichenbach & Hudspeth PNAS 2010; talk on experimental results by Warren & Fridberger at this meeting).

As a question, you write that the near-field fluid coupling significantly increases the mass of the basilar membrane. However, from the two-degrees of freedom model (equations (6) and (7)), it appears that the near-field fluid coupling provides a coupling between the reticular lamina and the basilar membrane, namely in form of a mass term. Does it hence not depend on the phase of vibration between the basilar membrane and the reticular lamina whether this coupling term provides an added mass to the basilar membrane or, for example, and added damping or an added stiffness?

Stephen Elliott [reply to Tobias Reichenbach]: Thanks for the interest and references. Since the fluid is almost incompressible, its motion can only add mass to the system. The force on the reticular lamina, for example, is thus due to an added mass term times its own acceleration plus a transfer mass term times the basilar membrane acceleration. The stiffness and damping in the system thus all comes from the internal structure of the organ of Corti.

Andrew Bell: I like your approach, especially that of seeing how the basilar membrane responds to motion of the OHCs alone, without contributions from a "travelling wave". It is possible to interpret the travelling wave as more apparent than real (Bell 2012), so your modelling gives some insight into what the OHCs themselves are capable of doing. This is taking the "Flock motility" idea seriously.

A core issue in cochlear mechanics is to decide whether the motion of the OHCs causes motion of the BM, or whether BM motion stimulates the OHCs. You seem to be getting some interesting results, and I encourage you to continue this line of investigation.

It is of interest to compare your results with a model of the cochlea based on a surface acoustic wave (SAW) resonator (Bell 2014). In the SAW model the three rows of OHCs cooperatively interact to produce a whole-wavelength standing wave in the subtectorial space, very like the mode shown in your Fig. 2 (last column, middle row), except that the mode occurs between OHC1 and OHC3 and not across the whole width of the BM (0 to B). To efficiently drive such a mode into resonance, you need to have the length changes in OHC2 acting in antiphase to those in OHC1 and OHC3, and this might be due to some pressure-sensitive channel in the body of the cells or certain neural connections between the rows. This whole-wavelength mode corresponds to the way in which a xylophone bar resonates (so OHC2 is in the middle of the bar and OHC1 and OHC3 at the free ends). It would be of interest to drive your model in this fashion and see the outcome. A half-wavelength mode might also be worth examining.

I don't understand why in Fig. 4 you consider the RL to be part of the second moving mass, m-sub2. Surely if the TM moves radially (which I presume the unlabelled arrow in Fig. 4 is supposed to represent), then the stereocilia will undergo shear, not the RL relative to the OHCs to which they are intimately connected. Again, as with my question to your other presentation, I am more inclined to view the RL as an ultrathin (1-3 um) diaphragm separating endolymph from perilymph (like Reissner's membrane) rather than a stiff plate. You identify an interesting "added mass" effect, and this could be usefully compared with a finite-element modelling of Rapson (2012) who looked at the power transfer in the cochlea when the BM mass was relatively large and compared it with the power transfer when the fluid mass was larger than the BM mass. He found that the there was no energy transfer in the first case, but power transfer in the second. He concludes it is an empirical matter to find the relative masses and decide whether the travelling wave is "real" (carries energy) or "apparent" (no energy transfer), an important result which your work relates directly to. Although I understand why for simplicity you would make the entire OC incompressible, there is some virtue in considering the OHCs to have some compressibility. In that case, OHCs, surrounded by incompressible fluid, would directly sense the pressure imposed on the cochlea by inward movement of the stapes. Moreover, change in volume of an OHC would immediately give rise to an otoacoustic emission in the ear canal, solving the problem of how OAEs are generated without needing to call on reverse travelling waves. It might be interesting to give the OHCs some compressibility and see the effect in your FE model.

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Stephen Elliott [reply to Andrew Bell]: Thanks for the comments and suggestions. The arrow on the tectorial membrane is rather misleading, and will be removed, since we are not considering radial motion of the tectorial membrane here. The second moving mass corresponds the reticular lamina and the tectorial membrane together moving upwards, along with the Henson cells moving inwards, since, as you note, we are assuming that the organ of Corti is incompressible.