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UNIVERSITY OF SOUTHAMPTON

INSTITUTE OF SOUND AND VIBRATION RESEARCH

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CONTENTS

1. INTRODUCTION

The micromechanical behaviour of the cochlea is an important part of any physiologically-plausible model of hearing. Figure 1 shows the main components of the organ of Corti, at one position at the edge of the basilar membrane. The tunnel of Corti is widely believed to pivot about the bottom left hand corner so that this part of the basilar membrane (BM) rotates as a more or less rigid body about this point. Similarly, the tectorial membrane (TM) is believed to rotate about the point of attachment on the left hand side of Figure 1, but may also undergo other forms of motion. The TM is separated from the organ of Corti by the cilia, also called the stereocilia, of the outer hair cells (OHC).

In this report, various lumped-parameter models of the structures shown in Figure 1 will be considered. Initially, the TM will be assumed only to rotate with the same angular motion as the BM, so that the mechanical system has only one degree of freedom. The relationship is derived, after Allen (1980), between the transverse motion of the BM and the shearing motion experienced by the OHC cilia due to the geometry of the structure.

The TM is then also allowed to move radially, and the equations of motion of this two degree of freedom mechanical system are derived directly, rather than employing the electrical analogy used by Allen (1980). This allows the assumptions and approximations in the model to be clearly expressed, and also provides the motivation to convert this physically-based two degree of freedom system into an equivalent two degree of freedom system that only involves single-axis motion, and is thus easier to visualise.

The active force generated by the OHC body is then incorporated into the model, as in the model of Neely and Kim (1986), although it is difficult to physically justify what structure this force on the BM reacts off. An alternative active model is then discussed, in which the force is assumed to act across a very stiff organ of Corti, resulting in an active displacement, as in the model of Neely (1993).

We next allow the OHC cilia to have a finite transverse stiffness, so that the BM and TM can have independent transverse displacements. It is shown that this leads to a three degree of freedom model, into which an active force due to the OHC cilia can be readily incorporated.

2.   One degree of freedom models

If the transverse stiffness of the OHC cilia is high enough that both the basilar membrane (BM) and the tectorial membrane (TM) always move parallel to each other and neither have any radial motion, their geometry can be represented as in Figure 2. The BM and TM are modelled as rigid structures, of length l, rotating about two pivots that are a distance h apart. They are assumed to undergo a transverse motion of w at their ends. If the cilia of an outer hair cell at the end of the rotating BM is assumed to be firmly attached to the rotating end of the TM, then as these structures rotate, the cilia will experience a shearing displacement of Δ.

This geometry was analysed by Allen (1980), who pointed out that the two right hand triangles in Figure 2 are similar and so, if θ is the angle of rotation, then

$$\sin\theta = w/l \quad \text{and} \quad \sin\theta = \Delta/h. \tag{2.1, 2.2}$$

Thus the "shear gain", g, which is a real number defined to be the ratio of the shear displacement of the cilia to the transverse displacement of the BM is equal to

$$\Delta/w = g = h/l. \tag{2.3}$$

If the masses of the BM and TM are assumed to be concentrated at their ends and to be equal to M_T and M_B, and the transverse stiffness of the BM is assumed to be K_B, then the transverse response to an external force f_{BM}, is governed by the complex-frequency domain expression

$$f_{BM} = (K_B + s^2 M_B + s^2 M_T)w, \tag{2.4}$$

where s is equal to $j\omega$ for a stable system, and K_B may be complex to include damping.

The BM mechanical impedance, Z_{BM}, for the one degree of freedom model is thus equal to

$$Z_{BM} = \frac{f_{BM}}{v_{BM}} = \frac{K_B}{s} + s(M_B + M_T), \qquad (2.5)$$

where $v_{BM} = sw$.

3.   Two degree of freedom model

A very influential model of the cochlea micromechanics, which has two degrees of freedom, is described by Allen (1980). Although the physical insight in this paper is remarkable, some of the assumptions and implications of the model are not immediately clear and so are worth spelling out.

The model again assumes that the transverse stiffness of the cilia is sufficiently large that the BM and TM move with the same transverse motion. This is the first degree of freedom. The TM is, in addition, now allowed to move radially, which is the second degree of freedom. Figure 3 shows the lumped element representation of this model, in which M_B, M_T and K_B again refer to the masses of the BM and TM, and the transverse stiffness of the BM. Figure 3 also shows the radial stiffness of the TM as K_T and the radial stiffness opposing the shear motion between the BM and TM, due to the cilia, as K_C. The roller connection shown in Figure 3 between the BM and TM is supposed to reflect the fact that their separation is kept constant by a rigid connection, but that they can slide past each other.

Since the BM and TM have the same transverse motion, as in the one degree of freedom model shown in Figure 2, the shear displacement of the BM, Δ_{BM}, due to the change in geometry caused by its transverse motion, w_{BM}, is again given by

$$\Delta_{BM} = g w_{BM} ,\qquad\qquad\qquad (3.1)$$

where g is the shear gain, given by the ratio of the height between the pivots, h, and the length of the rotating structure, l, so that

$$g = h/l.\qquad\qquad\qquad (3.2)$$

Assuming, for the time being, that there is no additional shear motion of the TM, so that Δ_{TM} is zero, that K_B is zero, and that a static force f_{BM} is used to move the BM by a transverse displacement w_{BM}, then the shear displacement experienced by K_C is Δ_{BM}.

This shear displacement creates a radial force of f_{CR} on K_C and the energy stored in this spring, which is $f_{CR} \Delta_{BM}$, must be equal to the work done by the BM, which is $f_{BM} w_{BM}$, where the static force f_{BM} in this case is equal to the opposing transverse force due to the stretching of K_C, which is denoted f_{CT}. Using eqution (3.1) this transverse force must thus be related to the radial force by

$$f_{CT} = g f_{CR}, \tag{3.3}$$

where g is again given by equation (3.2).

The transverse motion of the BM and TM to an external force f_{BM} is thus governed by the equation

$$f_{BM} = K_B w_{BM} + s^2 (M_B + M_T) w_{BM} + f_{CT}, \tag{3.4}$$

and the radial motion of the TM due to the radial cilia force f_{CR} is governed by the equation

$$f_{CR} = K_T \Delta_{TM} + s^2 M_T \Delta_{TM}, \tag{3.5}$$

where Δ_{TM} is the radial displacement of the TM.

Note that M_T governs the inertia of the TM in both the transverse and radial directions. The radial force between the BM and TM is determined by their relative radial motion and the cilia stiffness, K_C, so that

$$f_{CR} = K_C (\Delta_{BM} - \Delta_{TM}). \tag{3.6}$$

Setting equation (3.6) equal to equation (3.5) allows the radial displacement of the TM to be expressed in terms of that of the BM as

$$\Delta_{TM} = \frac{K_C}{K_T + K_C + s^2 M_T} \Delta_{BM}. \tag{3.7}$$

The total shear displacement experienced by the cilia Δ_C is thus equal to

$$\Delta_C = \Delta_{BM} - \Delta_{TM} = \frac{K_T + s^2 M_T}{K_T + K_C + s^2 M_T} \Delta_{BM},\tag{3.8}$$

and so, using equation (3.1), the complex "shear transfer function", T_{shear}, relating the shear displacement of the cilia to the transverse displacement of the BM for this two degree of freedom model is

$$\frac{\Delta_C}{w_{BM}} = T_{shear} = g \frac{K_T + s^2 M_T}{K_T + K_C + s^2 M_T},\tag{3.9}$$

as derived by Allen (1980).

This shear transfer function is referred to as the "transduction filter" by Allen (1980), and has also been described as the "second filter". It provides additional dynamics in the response between the transverse BM motion and the shearing motion between the BM and TM. This shearing motion is often assumed to generate the neural excitation of the inner hair cells via the fluid motion in the sub-tectorial space. Note that the shear transfer function has a zero at the frequency $\sqrt{K_T / M_T}$ and a pole at the higher frequency of $\sqrt{(K_T + K_C)/M_T}$.

Also, using equations (3.3) and (3.6), the equation governing the transverse motion of the BM, equation (3.4), can be written as

$$f_{BM} = K_B w_{BM} + s^2 (M_B + M_T) w_{BM} + g K_C \Delta_C,\tag{3.10}$$

where Δ_C is given as a function of w_{BM} by equation (3.9). Thus, the overall mechanical impedance of the two degree of freedom model is, in agreement with Allen (1980), equal to

$$Z_{BM} = \frac{K_B}{s} + s(M_B + M_T) + \frac{g^2 K_C (K_T + s^2 M_T)}{s(K_T + K_C + s^2 M_T)},\tag{3.11}$$

where Z_{BM} is again defined to be $f_{BM} / s w_{BM}$.

Note that the zero in Z_{BM}, equation (3.11), does not correspond to the zero in T_{shear}, equation (3.9), but that Z_{BM} has a pole at the same frequency as T_{shear}, at

$\sqrt{(K_T + K_C)/M_T}$. In practice, it is often the mobility of the BM that is measured, which is equal to Z_{BM}^{-1}, and so the zero in this measured response, due to the TM acting as a tuned mass damper, would be at the frequency of the pole in Z_{BM}.

4. Transformation to single axis motion

The relationship between the radial and transverse motion of the BM in equation (3.1) can be used to transform the rather complicated lumped element model of Figure 3 into one which has entirely transverse motion, as in Figure 4(a).

We first define an "equivalent transverse motion" due to the shear displacement of the TM, w_{TM}^E, by analogy with equation (3.1), to be

$$w_{TM}^E = \Delta_{TM} / g. \tag{4.1}$$

Now using equation (3.3) for the transverse force acting on the TM, the equation of motion of the TM, equation (3.5), can be transformed into

$$f_{CT} = g^2 K_T w_{TM}^E + s^2 g^2 M_T w_{TM}^E, \tag{4.2}$$

which can be written as

$$f_{CT} = K_T^E w_{TM}^E + s^2 M_T^E w_{TM}^E, \tag{4.3}$$

where K_T^E is equal to $g^2 K_T$ and M_T^E is equal to $g^2 M_T$.

Similarly, the equation describing the radial stiffness of the cilia, equation (3.6) can be transformed into transverse motion to give

$$f_{CT} = g^2 K_C (w_{BM} - w_{TM}^E), \tag{4.4}$$

or

$$f_{CT} = K_C^E (w_{BM} - w_{TM}^E), \tag{4.5}$$

where $K_C^E = g^2 K_C$.

The equation for the transverse motion of the BM remains, as in equation (3.4), as

$$f_{BM} = K_B w_{BM} + s^2 (M_B + M_T) w_{BM} + f_{CT} \tag{4.6}$$

so that these three equations now define the dynamics of the equivalent two degree of freedom system shown in Figure 4(a), which only vibrates in the transverse direction. Note that the shear gain and BM impedance, equations (3.9) and (3.11), are unaffected by this change of viewpoint.

Alternatively, the multi-axis motion in Figure 3 can be transformed into an equivalent system which vibrates only radially, as assumed by Neely and Kim (1986). For this transformation, we need to define an "equivalent radial motion" for the BM as

$$\Delta_{BM}^{E} = g \, w_{BM}, \tag{4.7}$$

which is actually equal to the true radial BM motion, as defined in equation (3.1), and a corresponding equivalent radial force to be

$$f_{BM}^{E} = f_{BM} / g. \tag{4.8}$$

The equation of motion for the transverse motion of the BM and TM, equation (3.4), can then be written, using equation (3.3), as

$$f_{BM}^{E} = K_{B}\Delta_{BM}^{E} / g^{2} + s^{2}(M_{B} + M_{T})\Delta_{BM}^{E} / g^{2} + f_{CR} \tag{4.9}$$

or

$$f_{BM}^{E} = K_{B}^{E}\Delta_{BM}^{E} + s^{2}(M_{B} + M_{T})^{E} \Delta_{BM}^{E} + f_{CR} \tag{4.10}$$

where K_{B}^{E} is equal to K_{B} / g^{2} and $(M_{B} + M_{T})^{E}$ is equal to $(M_{B} + M_{T}) / g^{2}$.

The equation for the radial motion of the TM and the cilia, equations (3.5) and (3.6), remain the same in this model and equation (4.10) combined with these two equations describe a two degree of freedom system vibrating entirely in the radial direction, as shown in Figure 4(b).

It is this equivalent block diagram that is used by Neely and Kim (1986), although, rather confusingly, their Figure 3 shows the two degree of freedom system apparently moving in the transverse direction.

5. Active two degree of freedom models

In this section we consider the effect on the two degree of freedom micromechanical model of having an active force introduced by the body of the outer hair cells, as considered by Neely and Kim (1986). Note that we are not accounting for any force generated by the cilia of the outer hair cells, which in this model would act between the BM and TM, whose relative transverse positions are fixed in Figure 3, so that this force would generate no additional motion.

In Figure 5(a), the active force is assumed to react across the transverse BM stiffness. Physically this transverse stiffness is due to the BM bending stiffness, and so it is not obvious from Figure 1 how this force, which is described as being generated "within the OHC" by Neely and Kim (1986), can react off the inertial ground shown in Figure 5(a). Nevertheless, this assumption does lead to the model used by Neely and Kim.

The equation of motion of the BM, equation (3.4) is now modified to be of the form

$$f_{BM} = K_B w_{BM} + s^2 (M_B + M_T) w_{BM} + f_{CT} - f_A. \tag{5.1}$$

Since the cilia stiffness and the independent TM motion are assumed to be entirely radial, however, the active transverse force, f_A, has no effect on the equations of motion for these parts of the model, and equations (3.5) and (3.6) remain the same for this active model. Thus, the shear transfer function, defined by equation (3.9), is unaffected by the active force in this model.

Similarly, the BM impedance defined by equation (3.11), which is here written as Z_{pass}, can be used to express the equation of motion of the BM as

$$f_{BM} = Z_{pass} s w_{BM} - f_A. \tag{5.2}$$

In the active model of Neely and Kim (1986), the active force is assumed to be proportional to the shear displacement of the cilia, Δ_C, via a gain γ and a frequency-dependent OHC response, which has the dimensions of a stiffness and is written as K_{OHC}. Using the expression for the shear transfer function in equation (3.9), the active force can thus be written as

$$f_A = -\gamma K_{OHC} T_{shear} w_{BM} .$$ (5.3)

This active force can be written as

$$f_A = -\gamma Z_{act} s w_{BM} ,$$ (5.4)

where Z_{act} is equal to $K_{OHC} T_{shear} / s$, so that, referring back to equation (5.2), the overall impedance of the BM can now be expressed as

$$Z_{BM} = Z_{pass} + \gamma Z_{act}$$ (5.5)

This result is equivalent to equation (12) in Neely and Kim (1986) only if their Z_1 is defined as $K_B/s + (M_B + M_T)s$. Although Z_1 is defined ambiguously below equation (9) in Neely and Kim (1986), with an undefined mass, this has generally been taken as a typographical error and it has been assumed to be M_B. Note, however, that the definition of the mass in Z_1 does not affect the active part of the BM impedance in this model and so the model can be made to have the correct physical interpretation by a minor redefinition of the mass in Z_1.

Since the equations describing the cilia and TM motion are unaffected by the active force, the transformation of the shear motion of these elements into their "equivalent" transverse form, described in Section 4, is not affected by the introduction of this force. Also, the transformed model with only equivalent radial motion, in Figure 4(b), is only modified by the equivalent active force f_A^E, equal to f_A/g, acting on the BM, as shown in Figure 5(b), in which the radial motion is now indicated as acting vertically so that this figure can be compared more readily to Figure 3 in Neely and Kim (1986).

It is still difficult with this model to visualise where the active force, generated in the OHC body by somatic motility, would react off. Another, more physically plausible, model of somatic motility would involve the organ of Corti in Figure 1 flexing internally as the OHCs expand and contract. This would, in general, require the inclusion of an additional mass and stiffness in our lumped-parameter model, and thus lead to a three degree of freedom system.

If, however, we assume that the internal stiffness of the organ of Corti, K_{OHC}, which the active OHC forces act across, is significantly larger than all the other stiffnesses in our model, then the active force f_A will generate an active displacement of

$$w_A = f_A/K_{OHC} , \tag{5.6}$$

which is substantially independent of the dynamics of the BM and TM, as in the model of Neely (1993), for example.

Figure 6(a) shows this active displacement incorporated into the two degree of freedom model of Figure 3, where the active displacement acts between the BM and OHC cilia. This model assumes that the BM mass is still associated mostly with the structure under the OHCs in Figure 1, and that the mass of the reticular lamina, which is now flexing independently of the motion of the BM, is negligible. These assumptions allow a two degree of freedom model to be retained, since the introduction of the active displacement does not introduce any additional resonances into the system.

The equation of motion for the BM, equation (3.4), is now modified to be

$$f_{BM} = K_B w_{BM} + s^2 M_B w_{BM} + s^2 M_T(w_{BM} + w_A) + f_{CT}. \tag{5.7}$$

The analysis in Section 3 relating the relative shear motion experienced by the cilia, Δ_C, to the transverse displacement of the BM must now be modified so that Δ_C is related to the transverse displacement of the reticular lamina, w_{RL}, so that

$$\Delta_C = T_{shear} w_{RL}, \tag{5.8}$$

where w_{RL} is the sum of the transverse BM displacement and the active transverse displacement, so that

$$\Delta_C = T_{shear}(w_{BM} + w_A). \tag{5.9}$$

We now assume that the active displacement, w_A, is proportional to the shear displacement of the cilia, Δ_C, via the frequency-dependent response T_{OHC} and the gain γ, so that

$$w_A = \gamma \, T_{OHC} \, \Delta_C. \tag{5.10}$$

Using equation (5.9) for Δ_C, then equation (5.10) becomes

$$w_A = \gamma T_{OHC} T_{shear}(w_{BM} + w_A),$$

so that

$$w_A = \left[\frac{\gamma T_{OHC} T_{shear}}{1-\gamma T_{OHC} T_{shear}}\right] w_{BM}. \tag{5.11}$$

Also, f_{CT} may be written from Section 3 as

$$f_{CT} = g K_C \Delta_C, \tag{5.12}$$

and using (5.9) again,

$$f_{CT} = g K_C T_{shear}(w_{BM} + w_A). \tag{5.13}$$

The equation of motion for the BM, equation (5.7), can thus be written as

$$f_{BM} = (K_B + s^2(M_B + M_T))w_{BM} + s^2 M_T w_A + g K_C T_{shear}(w_{BM} + w_A), \tag{5.14}$$

so that using equation (5.11) for w_A, f_{BM} can be written as a function only of w_{BM},

$$f_{BM} = \left[K_B + s^2(M_B + M_T) + g K_C T_{shear} + \frac{\gamma T_{OHC} T_{shear}}{1 - \gamma T_{OHC} T_{shear}}(s^2 M_T + g K_C T_{shear})\right] w_{BM}.$$

$$\tag{5.15}$$

Thus, the overall BM impedance in this case becomes

$$Z_{BM} = Z_{pass} + \frac{\gamma T_{OHC} T_{shear}}{1 - \gamma T_{OHC} T_{shear}} Z_{add} \tag{5.16}$$

where Z_{pass} is the same as for the previous model, equation (3.11), and now Z_{add} is equal to $(sM_T + g K_C T_{shear} / s)$ which becomes active when multiplied by the factor

$\gamma T_{OHC} T_{shear} / (1 - \gamma T_{OHC} T_{shear})$.

Instead of the active part of the BM impedance being directly proportional to the feedback gain γ in the Neely and Kim (1986) model, the active part is now only directly proportional to γ for low gains, and becomes infinite as the model tends to instability as γ approaches $(T_{OHC}T_{shear})^{-1}$.

It should be noted that in the original derivation of Neely (1993), the transverse inertial force due to the mass of the TM, $s^2 M_T(w_{BM} + w_A)$ in equation (5.7), appears to have been ignored. If this term is set to zero in equation (5.7), the modified expression for the BM impedance becomes

$$Z_{BM}^N = \frac{K_B}{s} + sM_B + \frac{gK_C T_{shear}}{s(1-\gamma T_{OHC}T_{shear})}.$$ (5.17)

In the notation of Neely (1993), we can define $Z_b = \frac{K_B}{s} + sM_B$,

$$Z_t = \frac{K_T}{s} + sM_T, \qquad Z_o = \frac{K_C}{s}, \quad g = g_o \text{ and } H_c = -\gamma T_{OHC}$$

so that

$$T_{shear} = \frac{g_o Z_t}{Z_t + Z_o},$$ (5.18)

and equation (5.17) can be written as

$$Z_{BM}^N = Z_b + \frac{g_o^2 Z_o Z_t}{Z_t + Z_o + g_o H_c Z_t},$$ (5.19)

in agreement with the reciprocal of the Neely (1993) expression for the admittance of the cochlear partition, in his equations (18) and (19).

The equivalent transverse system for this two degree of freedom system is shown in Figure 6(b) and can be deduced from equation (5.7) and the equivalent system interpretation of f_{CT} in equations (4.3) and (4.5) except that now w_{RL} must be used instead of w_{BM} in (4.5). The most important additional element comes from the term $s^2 M_T(w_{BM} + w_A)$ in equation (5.7), since this is the transverse inertial force due to a mass of M_T positioned *above* the RL and so appears in addition to the element M_T^E, which is due to the radial inertia of M_T in the new equivalent mechanical system.

A slightly modified form of this two degree of freedom system, as shown in Figure 7(a), is also worth mentioning, which is consistent with the recent measurements of the relative motions of the TM, RL and BM (Gummer *et al.*, 1996; Hemmert *et al.*, 2000; Nowotny and Gummer, 2006). In this model the reticular lamina (RL) is represented as a rigid beam of negligible mass that is pivoted about the top of the tunnel of Corti. For small rotations the relationship between the cilia shear displacement and the transverse RL displacement, given by equation (5.9) is unaffected by this rotation, provided the shear displacement is defined to be above the point of application of the active displacement, where the distance between the RL and TM is kept constant by the rolling junction. This point is assumed to be at one of the OHC positions. Although the TM and/or RL would have to be allowed to bend a little if the action of all three OHCs were to be taken into account this way, such a modification would not affect the underlying dynamics. The significant difference now comes at the inner hair cell (IHC) positions, on the left of the RL pivot, which now moves out of phase with the motion at the OHCs, as observed by Nowotny and Gummer (2006). This modification does not, however, affect the motion of the BM, RL and TM at the OHC positions, which is required to deduce the BM impedance above. The relationship between the fluid motion in the sub-tectorial gap and the cilia motion of the IHC is significantly affected by the rocking of the RL, however.

The active feedback loop driving the displacement w_A can also be re-interpreted in the equivalent uni-directional system shown in Figure 7(b). This displacement is assumed to be proportional to the OHC shear cilia displacement, Δ_C, in equation (5.10). Note that equivalent transverse force acting on the RL, equation (5.12), can be written as

$$f_{CT} = \frac{K_C^E}{g} \Delta_C \tag{5.20}$$

so that the shear OHC cilia displacement is equal to

$$\Delta_{\mathrm{C}} = \frac{g}{K_{\mathrm{C}}^{\mathrm{E}}} f_{\mathrm{CT}}. \tag{5.21}$$

Combining this equation with (5.10) gives a new expression for the active displacement as

$$w_{\mathrm{A}} = \gamma H f_{\mathrm{CT}}, \tag{5.22}$$

where $H = g T_{\mathrm{OHC}} / K_{\mathrm{C}}^{\mathrm{E}}$. The active displacement can thus be thought of as being generated by the equivalent transverse force acting on the TM through $K_{\mathrm{C}}^{\mathrm{E}}$, as shown in Figure 7(b).

6. Three degree of freedom model

A more complete model of the dynamics would allow independent transverse motion of the TM, as well as shear motion. This would be possible if the OHC cilia were allowed to have a finite transverse stiffness, K_{CT}, as shown in Figure 8(a). The finite transverse stiffness of the TM, K_{TT}, could then also be accounted for, in addition to its shear stiffness, K_{TR}, as shown in Figure 8(a). Although the transverse and shear motion of the BM are still proportional to one another, since the tunnel of Corti is assumed rigid, and so this motion only constitutes a single degree of freedom, the transverse and shear motion of the TM are two additional degrees of freedom in this model, which thus constitutes a three degree of freedom system overall.

With no active force present, the equation of transverse motion for the BM is now

$$f_{BM} = K_B w_{BM} + s^2 M_B w_{BM} + f_{CT1} + f_{CT2}, \tag{6.1}$$

where f_{CT1} is again given by equation (3.3) and f_{CT2} is the transverse force generated by the transverse stiffness of the cilia, K_{CT}, so that

$$f_{CT2} = K_{CT}(w_{BM} - w_{TM}). \tag{6.2}$$

The transverse motion of the TM is now governed by the additional equation

$$f_{CT2} = K_{TT} w_{TM} + s^2 M_T w_{TM}, \tag{6.3}$$

where K_{TT} is the transverse stiffness of the TM.

The shear force acting on the TM, equation (3.6), and its equation of shear motion, equation (3.5), are not influenced by this additional degree of freedom. The transformation of the shear TM motion, Δ_{TM}, into "equivalent" transverse TM motion, w_{TM}^E, is thus unaffected by the physical transverse displacement of the TM, w_{TM}, and the two displacements w_{TM} and w_{TM}^E are independent. The equivalent single-axis model for the three degree of freedom model variables, in the transverse direction, is thus shown in Figure 8(b), where K_C^E is now $g^2 K_{CR}$ and K_T^E is now $g^2 K_{TR}$, and M_T^E is again $g^2 M_T$.

It is now possible to model the active force generated by the OHC cilia, via the "bundle motility", instead of that generated by the "somatic motility" of the OHC body. This active force acts between the BM and TM, across the stiffness K_{CT} in Figures 8(a) and 8(b).

Considering now the active force, f_A, in the equivalent single-axis model of Figure 8(b), the equation of motion for the BM can be written as

$$f_{BM} = K_B w_{BM} + s^2 M_B w_{BM} + f_{CT1} + f_{CT2} + f_A. \qquad (6.4)$$

f_{CT1} is the transverse force on the BM due to the shear motion of the TM and is thus equal to

$$f_{CT1} = K_C^E (w_{BM} - w_{TM}^E), \qquad (6.5)$$

and

$$f_{CT1} = (K_T^E + s^2 M_T^E) w_{TM}^E, \qquad (6.6)$$

so that

$$f_{CT1} = K_C^E \left[\frac{K_T^E + s^2 M_T^E}{K_C^E + K_T^E + s^2 M_T^E} \right] w_{BM}. \qquad (6.7)$$

f_{CT2} is the transverse force on the BM due to the transverse motion of the TM and is equal to

$$f_{CT2} = K_{CT} (w_{BM} - w_{TM}), \qquad (6.8)$$

and

$$f_{CT2} = (K_{TT} + s^2 M_T) w_{TM} + f_A, \qquad (6.9)$$

so that

$$f_{CT2} = K_{CT} \left[\frac{K_{TT} + s^2 M_T}{K_{TT} + K_{CT} + s^2 M_T} \right] w_{BM} + \frac{K_{CT}}{K_{TT} + K_{CT} + s^2 M_T} f_A. \qquad (6.10)$$

Thus the BM equation of motion (6.4), becomes

$$f_{BM} = Z_{pass}^{three} \, s w_{BM} + T_{three} f_A , \tag{6.11}$$

where

$$Z_{pass}^{three} = \frac{K_B}{s} + s M_B + \frac{K_C^E}{s}\left[\frac{K_T^E + s^2 M_T^E}{K_C^E + K_T^E + s^2 M_T^E}\right] + \frac{K_{CT}}{s}\left[\frac{K_{TT} + s^2 M_T}{K_{TT} + K_{CT} + s^2 M_T}\right], \tag{6.12}$$

and

$$T_{three} = \frac{K_{TT} + 2K_{CT} + s^2 M_T}{K_{TT} + K_{CT} + s^2 M_T}. \tag{6.13}$$

We now assume that the active force is proportional to the shear cilia displacement,

$$f_A = \gamma \, K_{cilia} \Delta_C , \tag{6.14}$$

where K_{cilia} is now the frequency-dependent cilia response, with the same dimensions as a stiffness, and γ is a gain. The shear displacement of the cilia, Δ_C, is still related to w_{BM} via the shear transfer function, T_{shear}, since the transverse active force again does not affect the radial TM motion, so that

$$f_A = \gamma \, K_{cilia} T_{shear} \, w_{BM} . \tag{6.15}$$

Substituting this expression for f_A into equation (6.11), the overall BM impedance can again be written as the linear sum of an active and passive impedance

$$Z_{BM} = Z_{pass}^{three} + \gamma \, Z_{act}^{three} \tag{6.16}$$

where Z_{pass}^{three} is given by equation (6.12) and

$$Z_{act}^{three} = K_{cilia} T_{shear} T_{three} / s. \tag{6.17}$$

In this section the cilia force is assumed to act in a transverse direction and thus not influence the radial motion of the TM. Similarly, the active force or active displacement generated by the OHC body in the previous section was purely

transverse. In all of these cases the active components do not affect the linear relationship between the shear displacement of the cilia and the transverse BM motion, given by equation (3.9). Thus the additional transverse force on the BM is linearly proportional to transverse BM motion in all cases, so that the overall impedance is the sum of a passive component and an active component proportional to the active gain γ. Although the interpretation of the passive and active impedances varies depending on the model being used, this useful structure of Z_{BM} is retained.

Unfortunately, seven parameters: five stiffnesses and two masses, are required to specify the behaviour of this three degree of freedom model. (Note that M_T^E is equal to $g^2 M_T$ and thus does not need to be independently estimated.) These parameters could, in principle, be deduced from dynamic measurements made on the BM and TM, although some assumptions would still need to be made about how they varied along the length of the cochlea.

Depending upon the natural frequencies of the two TM degrees of freedom in Figure 8, and that of the BM, it may be possible to approximate the effect of one of these by an additional BM mass or stiffness. This would result in another two degree of freedom model, but one that could be derived in a physiologically plausible way from the behaviour of the cochlea with bundle motility.

7. Summary and Conclusions

This report has considered various lumped-parameter models for cochlear micro-mechanics. The shear gain, between transverse basilar membrane displacement and the shear displacement of the outer hair cell cilia, is first derived using the one-dimensional model of Allen (1980). The underlying assumptions of Allen's two-dimensional model are then examined, which includes independent shear motion as well as transverse motion of the tectorial membrane. The equations of motion describing this two-dimensional model can be re-formulated to give equivalent mechanical systems that vibrate only in the transverse or only in the radial directions.

It is the latter interpretation of Allen's (1980) two-dimensional model that is used by Neely and Kim (1986) in their widely-used active micro-mechanical model. The governing equations for this model are used to derive the overall mechanical impedance of the basilar membrane, but the plausibility is questioned of having an active force on the basilar membrane, without it apparently having any physical structure to react off. An alternative active two degree of freedom model, in which the outer hair cell body produces a specified displacement, as suggested by Neely (1993), is then examined. The equivalent mechanical system vibrating only in the transverse direction is derived for this model. It is seen that the transverse inertia of the tectorial membrane appears to have been missed from the models of both Neely and Kim (1986) and Neely (1993). Whereas in the former case this inertia only affects the interpretation of the mass of one element, an additional mass has to be introduced into Neely's 1993 model to account for this inertia, which will significantly affect its dynamics.

Finally, it is noted that independent transverse motion of the tectorial membrane and basilar membrane, as required if the outer hair cell cilia are assumed to generate the active force, requires a three degree of freedom model.

8. References

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Acknowledgement

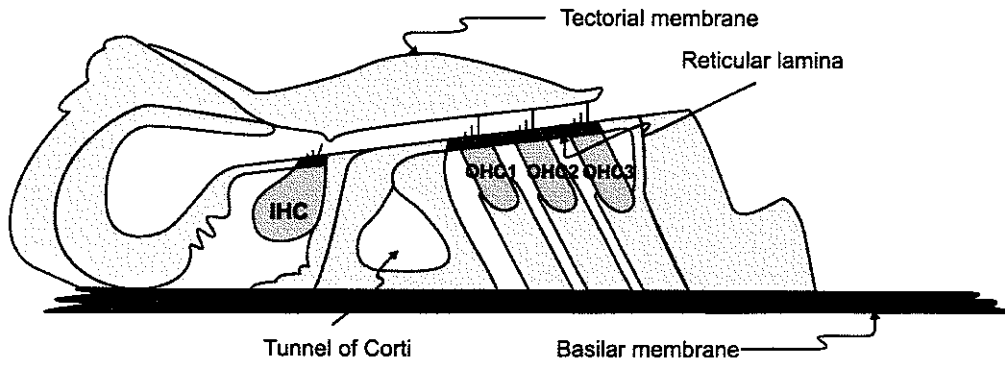The authors would like to thank Paolo Gardonio and Ruud van Doorn for their insight and helpful comments.

Figure 1. The main physiological parts of the organ of Corti, including one end of the basilar membrane (BM) and the tectorial membrane (TM), which are separated by the cilia of the outer hair cells (OHC).
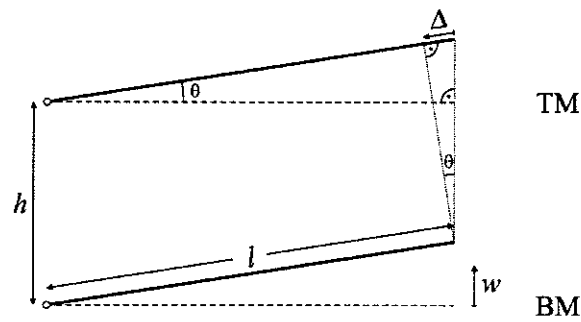

Figure 2. One degree of freedom micromechanical model, in which the BM and TM are assumed to always move parallel to one another with no radial motion, and for which the ratio of the shear displacement to the transverse displacement, the shear gain $g = \Delta / w$, is equal to h / l.
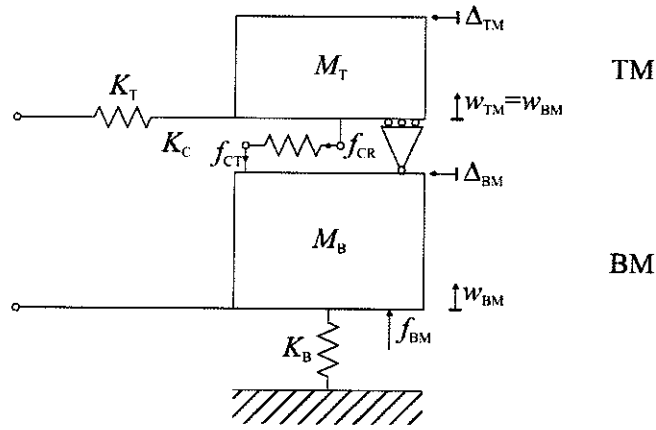
Figure 3. Two degree of freedom micromechanical model, after Allen (1980). The BM and TM are assumed to have the same transverse displacement, w_{BM}, but in addition the TM is allowed to have a radial displacement Δ_{TM}, which combines with the radial displacement of the BM due to the transverse motion, Δ_{BM}, to give the total shear displacement experienced by the cilia.
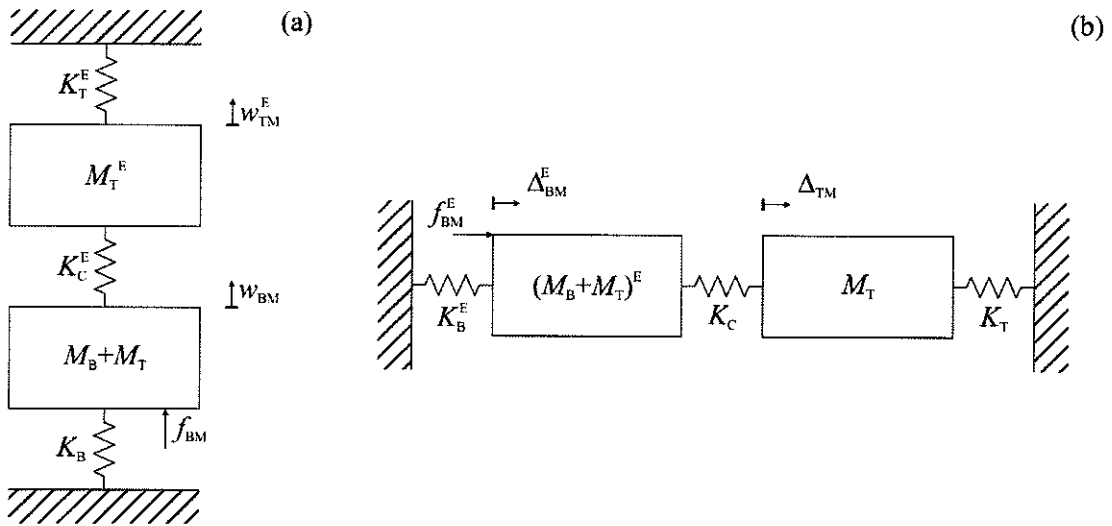

Figure 4. Two degree of freedom micromechanical model of Figure 3 transformed so all the motion is in the transverse direction (a), or so that all the motion is in the radial direction (b).
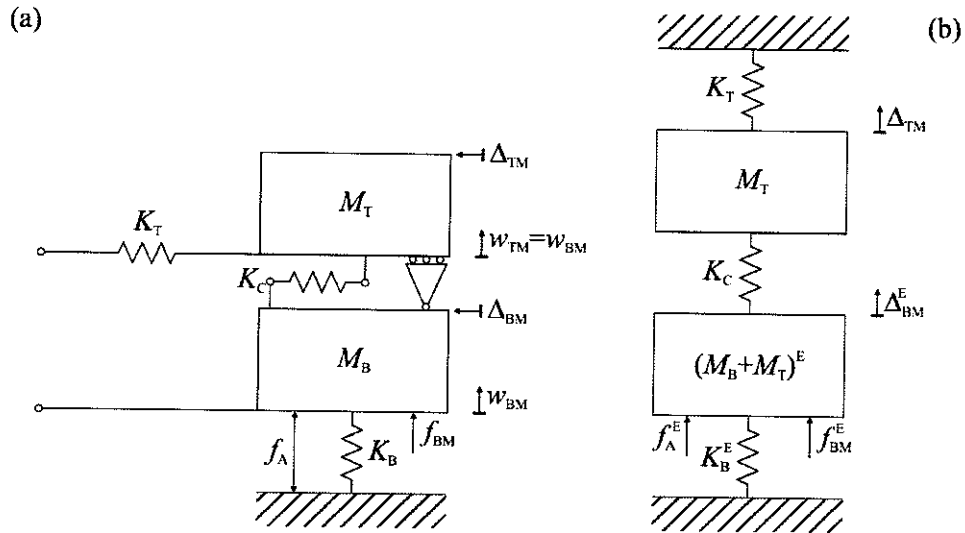
Figure 5. Two degree of freedom micromechanical model including an active force, f_A, acting on the BM: (a) in physical form, as Figure 3 and (b) so that the motion is all transformed into equivalent radial motion, as in Figure 4(b), after Neely and Kim (1986).
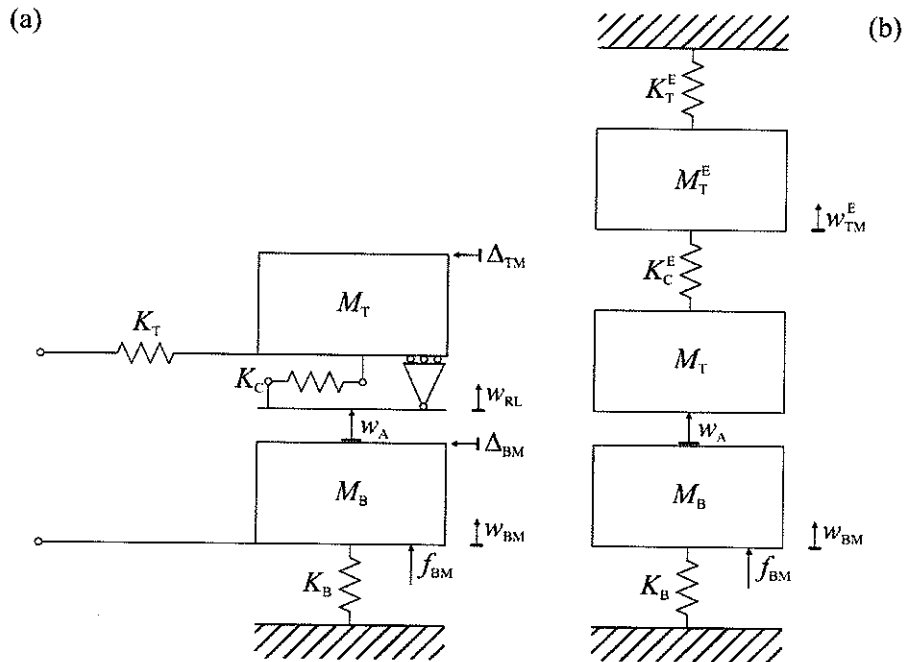

Figure 6. Two degree of freedom micromechanical model including an active displacement, w_A, generated within the organ of Corti and acting between the BM and OHC cilia in physical form (a) and when all the motion is transformed into equivalent transverse motion (b).
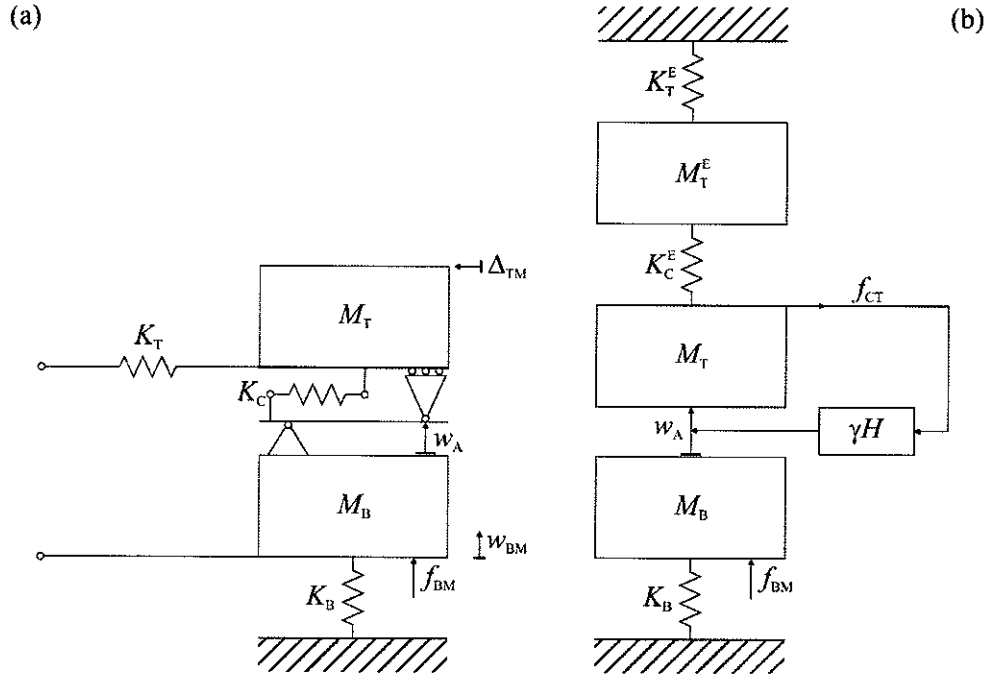
Figure 7. Modified form of the two degree of freedom model with active displacement which accounts for the rotation of the reticular lamina about the tunnel of Corti (a), and the system in which all motion is transformed into equivalent transverse motion and the feedback loop is explicitly shown from cilia force, proportional to cilia shear displacement, to the active displacement (b).
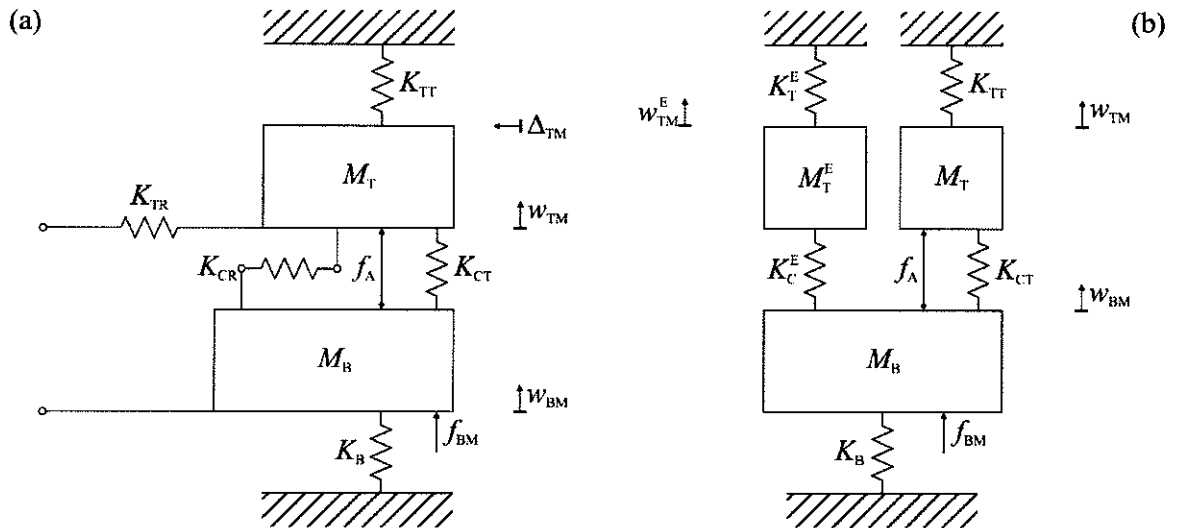

Figure 8. A three degree of freedom model allowing independent transverse motion of both the BM and TM (a) and an equivalent transformed system in which all the motions are vertical (b). The active force generated by the OHC cilia can now be modelled as acting between the BM and TM.