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Classical and non-classical models of the cochlea

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In a “classical” model of the cochlea the response is controlled by a local parameter function, for instance, the BM impedance. In a non-classical model, the response is controlled by parameters that are distributed over space. In this note it is shown to which extent classical and non-classical models are equivalent. To each non-classical model there exists one classical model that yields the same response. However, the BM impedance of that classical model does not necessarily obey the requirements of a driving-point impedance. © 1997 Acoustical Society of America.

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INTRODUCTION

In a “classical” macromechanical model of the cochlea (Viergever, 1986) the dynamics of the cochlear partition (CP) at a certain location x is described by a *local* parameter, i.e., by a parameter that depends only on one location, x . In the case of a linear model, that parameter is usually referred to as the BM impedance, written as $Z_{BM}(x, \omega)$ (cf. Viergever, 1978). Of late, “non-classical” models are beginning to appear in which the dynamics of the CP is not determined by a local parameter. For instance, Hubbard (1993) described a model based on two interacting wave-propagating structures. In the model proposed by Steele *et al.* (1993) the response-enhancing outer hair cells (OHCs) receive their input from another location than where they deliver their “load,” i.e., the pressure or force they generate. In a more detailed form, this idea has been worked out by Geisler and Sang (1995) who achieved model responses with quite remarkable properties. These non-classical models—note that all are *linear* models—form a welcome extension of the class of models considered earlier. This note describes the connection between classical and non-classical models. The basis of the derivation lies in the hydrodynamics of the fluid, which is, for simplicity, assumed to be ideal (i.e., incompressible, inviscid and linear). It will be shown that, once the *effective BM impedance* of a non-classical model has been determined, a classical model with the same function inserted as its BM impedance will have the same response. Some implications of this property are obvious. A short concluding section is devoted to a few less obvious corollaries.

I. DERIVATION

We will consider a linear three-dimensional model of the cochlea that is described in a Cartesian coordinate system x - y - z . When the fluid is linear, all parameters and variables can be considered as functions of the radian frequency ω . In such a model the fluid pressure at the level of the BM can generally be expressed as an integral of the BM acceleration

over the length of the model. In terms of BM velocity $v_{BM}(x, \omega)$ and channel pressure $p(x, \omega)$ (both taken at the center of the BM), this property reads:

$$p(x, \omega) = 2i\omega\rho \int_0^L g(x, x') v_{BM}(x', \omega) dx' + i\omega\rho(L-x)v_{stapes}(\omega). \quad (1)$$

Here, L is the length of the model, $v_{stapes}(\omega)$ the velocity of the stapes (assumed constant over the area of the stapes), and $g(x, x')$ is the *Green's function* associated with the geometry of the fluid channels. See for the derivation in a two-dimensional model Allen (1977), Equations (3) and (12). Models with different dimensionality differ in their $g(x, x')$ functions. See, for instance, Mammano and Nobili (1993). In simple structures with a completely regular geometry, $g(x, x')$ depends only on $(x-x')$ (cf. Sondhi, 1978). *Equation (1) is valid for classical as well as non-classical models because it expresses only a property of the fluid.*

It is stressed at this point that Eq. (1) does not include any specification of the organ of Corti or any steps taken in the actual solution of the model equations. The equation represents—by way of the functional form of the function $g(x, x')$ —the type of longitudinal coupling that is purely due to the fluid, irrespective of any assumptions about the mechanics of the organ of Corti. In the case of a two-dimensional model the equation takes into account that the fluid is moving uniformly over the width of the partition. In the case of a three-dimensional model a specific pattern of movement over the width is assumed, namely, that the BM is moving as a (co)sine function over its width (cf. de Boer, 1981). Pressure and BM velocity are then taken at the center of the BM.

Consider a *non-classical* model of the cochlea, and let it be linear in all variables. Assume that BM velocity $v_{BM}(x, \omega)$ and channel pressure $p(x, \omega)$ have been solved as functions of x . The quotient of $p(x, \omega)$ and $v_{BM}(x, \omega)$ produces the *effective BM impedance* $Z_{BM}^{(eff)}(x, \omega)$. According to Eq. (1) there is only one function $p(x, \omega)$ associated with the ‘given’ $v_{BM}(x, \omega)$ function, and thus there is only *one* effective BM impedance $Z_{BM}^{(eff)}(x, \omega)$ associated with this solution. This fact solely relates to the fluid. The computed imped-

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ance, however, includes all details about the dynamics of the cochlear partition that have been used in the formulation of the model.

Consider now a *classical* model, also linear, with exactly the same geometry, insert the effective impedance $Z_{\text{BM}}^{\text{eff}}(x, \omega)$ as its BM impedance $Z_{\text{BM}}(x, \omega)$ and use the same boundary conditions at the stapes and helicotrema ends. Next, solve the equations for that model. Let the solutions for BM velocity and pressure be $w_{\text{BM}}(x, \omega)$ and $q(x, \omega)$, respectively. According to Eq. (1), the two solution functions $w_{\text{BM}}(x, \omega)$ and $q(x, \omega)$ are related in the same way as $v_{\text{BM}}(x, \omega)$ and $p(x, \omega)$. They are also related because they have the same ratio, namely, the function $Z_{\text{BM}}^{\text{eff}}(x, \omega)$. In the Appendix it is shown that there exists only one set of functions having both these properties. Therefore, $w_{\text{BM}}(x, \omega)$ is identical to $v_{\text{BM}}(x, \omega)$, and $q(x, \omega)$ is identical to $p(x, \omega)$.

In general terms, *the response of a classical model which has the effective BM impedance $Z_{\text{BM}}^{\text{eff}}(x, \omega)$ of the non-classical model as its BM impedance, is equal to the response of that non-classical model.* The two models must have the same structure and geometry, and the solutions must obey the same boundary conditions at the two ends of the models. This property is valid for long-wave, two- and three-dimensional models.

II. COROLLARIES

The first consequence of the property derived in the preceding section is that *a non-classical model always shows a response that could also have been obtained in a classical model.* In this respect there seems to be no difference between these two classes of models. The major point is, however, that a non-classical model *allows for a far greater freedom in the functional form of the effective BM impedance $Z_{\text{BM}}^{\text{eff}}(x, \omega)$.* Indeed, we have to remember that $Z_{\text{BM}}^{\text{eff}}(x, \omega)$ is a *derived* parameter: it can only be found *after* pressure and BM velocity in the nonclassical model have been solved. Therefore, the function $Z_{\text{BM}}^{\text{eff}}(x, \omega)$ depends on the character of the solution and the form of the model, and it cannot be chosen beforehand or independently (as in a classical model). An additional, not too obvious, factor involved is the following. In a classical model the BM impedance $Z_{\text{BM}}(x, \omega)$ must be a *causal* function, which means that it must correspond to a causal impulse response. The same applies to the admittance function $1/Z_{\text{BM}}(x, \omega)$. This restriction does not apply to the non-classical model because $Z_{\text{BM}}^{\text{eff}}(x, \omega)$ is derived from two functions $p(x, \omega)$ and $v_{\text{BM}}(x, \omega)$, each of which can be seen as the response of a model to excitation at the stapes, and is therefore causal. However, their quotient does not need to be causal: the denominator $v_{\text{BM}}(x, \omega)$ in $Z_{\text{BM}}^{\text{eff}}(x, \omega)$ may well have zeros in the right-half of the complex s -plane that are not offset by corresponding zeros in the numerator $p(x, \omega)$. Hence $Z_{\text{BM}}^{\text{eff}}(x, \omega)$ may well be non-causal.¹ In general, in a non-classical model, the relation of the local pressure $p_{\text{OHC}}(x, \omega)$ generated by, for instance, outer hair cells (OHCs) to the distribution of BM velocity $v_{\text{BM}}(x, \omega)$ over x may well be non-local; in that case the OHC pressure $p_{\text{OHC}}(x, \omega)$ is a functional of $v_{\text{BM}}(x, \omega)$ defined over a cer-

tain domain of x . Furthermore, the pressure $p_{\text{OHC}}(x, \omega)$ does not necessarily contribute to the channel pressure $p(x, \omega)$ at the *same* place x . For all these reasons, the impedance function $Z_{\text{BM}}^{\text{eff}}(x, \omega)$ cannot always be realized as a driving-point impedance and the resulting response cannot be obtained in a classical model with a realizable BM impedance. In this respect, the class of non-classical models is definitely wider than that of classical models (see also Geisler and Sang, 1995).

A principal point in the use of classical models has always been that longitudinal stiffness in the BM had to be neglected. In fact, it has invariably been found that very small amounts of longitudinal coupling destroyed the main character of the model response (Allen and Sondhi, 1979). At present it is possible to explore this limitation to a far greater degree of accuracy, and to study the influence of mechanical and constructural constraints based on material properties on the performance of the model. The property derived here may well be of use in this field.

In the field of cochlear nonlinearity, the equivalence between classical and non-classical models may be exploited, too. It has been shown by Kanis and de Boer (1993) that, in view of the small degree of nonlinearity that the cochlea exhibits in most stimulation conditions, non-linear effects may be treated as perturbations. That is, concepts of linear-system theory like impedance, amplitude and phase angle, can be retained and used to full advantage. It remains to be studied whether the Kanis–de Boer method is equally useful in non-classical as in classical models. If this proves to be correct, non-classical nonlinear models can be studied in the same way as nonlinear classical models via the quasi-linear approximation.

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APPENDIX

In this Appendix we prove that there is only one pair of functions $p(x)$ and $v_{\text{BM}}(x, \omega)$ that have a given impedance function $Z_{\text{BM}}^{\text{eff}}(x, \omega)$ as their quotient, *and* are related to each other as dictated by the geometry of the fluid channels and the properties of the fluid. Divide the x axis into N discrete points x_i and rewrite Eq. (1) in a more universal form as a matrix equation:

$$\mathbf{p} = \mathbf{G}\mathbf{v} - \mathbf{s}. \quad (\text{A1})$$

Here $\mathbf{p}$ and $\mathbf{v}$ are column vectors representing the pressure $p(x)$ and the BM velocity $v_{\text{BM}}(x, \omega)$, respectively, at the points x_i ($i = 1, \dots, N$) and $\mathbf{s}$ is a column vector which represents the way the stapes boundary condition expresses itself in the pressure $p(x)$; see, e.g., the term $i\omega\rho(L-x)v_{\text{stapes}}(\omega)$ in Eq. (1). The matrix $\mathbf{G}$ (size $N \times N$) represents the fluid coupling — the function $2i\omega\rho g(x, x')$ in Eq. (1). Assume that pressure and velocity are solutions of

the model equation for the non-classical model and that their ratio is $Z_{\text{BM}}^{\text{(eff)}}(x, \omega)$. Rewrite this condition as

$$\mathbf{p} = \mathbf{Z}\mathbf{v}, \quad (\text{A2})$$

where $\mathbf{Z}$ is an $N \times N$ matrix which has $Z_{\text{BM}}^{\text{(eff)}}(x_i, \omega)$ ($i=1, \dots, N$) in its main diagonal and zeros everywhere else. Substitute Eq. (A2) in Eq. (A1):

$$(\mathbf{G} - \mathbf{Z})\mathbf{v} = \mathbf{s}. \quad (\text{A3})$$

This matrix equation has to be obeyed by the solution to the non-classical model. It is, however, exactly the same matrix equation that *produces* the solution to a classical model with the same $\mathbf{Z}$. Equation (A3) has, in general, a unique solution. This, then, must be the same for the classical and the non-classical model. Therefore, there exists only one velocity vector $\mathbf{v}$ which has the property that its associated pressure vector $\mathbf{p}$ is related to it by Eq. (A1) as well as Eq. (A2) (with $\mathbf{Z}$ given). In other words, for a model with given geometry there is only one solution for which pressure and velocity have the quotient $Z_{\text{BM}}^{\text{(eff)}}(x, \omega)$.

¹In less abstract terms: assume that the model studied is a simple non-dispersive transmission line and that the input to OHCs at location x is

taken from a more basalward location $x - \Delta x$; in this case $Z_{\text{BM}}^{\text{(eff)}}(x, \omega)$ contains a component that is a pure predictor.

- Allen, J. B. (1977). "Two-dimensional cochlear fluid model: New Results," J. Acoust. Soc. Am. **61**, 110–119.
- Allen, J. B., and Sondi, M. M. (1979). "Cochlear macromechanics-time domain solutions," J. Acoust. Soc. Am. **66**, 123–132.
- de Boer, E. (1981). "Short waves in three-dimensional cochlea models: Solution for a 'block' model," Hear. Res. **4**, 53–77.
- Geisler, C. D., and Sang, C. (1995). "A cochlear model using feed-forward outer-hair-cell forces," Hear. Res. **86**, 132–146.
- Hubbard, A. E. (1993). "A traveling wave-amplifier model of the cochlea," Science **259**, 68–71.
- Kanis, L. J., and de Boer, E. (1993). "Self-suppression in a locally active nonlinear model of the cochlea: A quasi-linear approach," J. Acoust. Soc. Am. **94**, 3199–3206.
- Mammano, F., and Nobili, R. (1993). "Biophysics of the cochlea: Linear approximation," J. Acoust. Soc. Am. **93**, 3320–332.
- Sondhi, M. M. (1978). "Method for computing motion in a two-dimensional cochlear model," J. Acoust. Soc. Am. **63**, 1468–1477.
- Steele, C. R., Baker, G., Tolomeo, Jr., and Zetes, D. (1993). "Electromechanical models of the outer hair cell," in *Biophysics of Hair-Cell Sensory Systems*, edited by H. Duifhuis, J. W. Horst, P. van Dijk, and S. M. van Netten (World Scientific, Singapore), pp. 207–214.
- Viergever, M. A. (1978). "On the physical background of the point-impedance characterization of the basilar membrane in cochlear mechanics," Acustica **39**, 292–297.
- Viergever, M. A. (1986). "Cochlear macromechanics-a review," in *Peripheral Auditory Mechanisms*, edited by J. B. Allen, J. L. Hall, A. Hubbard, S. T. Neely, and A. Tubis (Springer-Verlag, Berlin), pp. 63–72.