Hearing Research xxx (2017) 1–11

Contents lists available at ScienceDirect

Hearing Research

journal homepage: www.elsevier.com/locate/heares

Review Article

An elemental approach to modelling the mechanics of the cochlea

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ARTICLE INFO

Article history:
Received 16 July 2017
Received in revised form
10 October 2017
Accepted 30 October 2017
Available online xxx

Keywords:
Cochlea
Basilar membrane motion
Micromechanics
Fluid coupling
Elemental model

ABSTRACT

The motion along the basilar membrane in the cochlea is due to the interaction between the micromechanical behaviour of the organ of Corti and the fluid movement in the scalae. By dividing the length of the cochlea into a finite number of elements and assuming a given radial distribution of the basilar membrane motion for each element, a set of equations can be separately derived for the micromechanics and for the fluid coupling. These equations can then be combined, using matrix methods, to give the fully coupled response. This elemental approach reduces to the classical transmission line model if the micromechanics are assumed to be locally-reacting and the fluid coupling is assumed to be entirely one-dimensional, but is also valid without these assumptions. The elemental model is most easily formulated in the frequency domain, assuming quasi-linear behaviour, but a time domain formulation, using state space method, can readily incorporate local nonlinearities in the micromechanics. Examples of programs are included for the elemental model of a human cochlea that can be readily modified for other species.

Contents

Abbreviations: BM, basilar membrane; CF, characteristic frequency; OHC, outer hair cell; SM, scala media; SV, scala vestibuli; ST, scala tympani; 1D, one-dimensional; 3D, three-dimensional; Dof, degree of freedom

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https://doi.org/10.1016/j.heares.2017.10.013

1. Introduction: modelling the mechanics of the cochlea

It is important to develop mathematical models of the mechanics of the cochlea in order to test our understanding of the physical processes involved in hearing. These models can have various levels of abstraction, depending on what features of the cochlear mechanics they are attempting to describe. Wave models, for example, are good at describing the global behaviour of the motion along the cochlea without getting too involved in the detailed physical processes that give rise to the wave motion. The most widely used wave model uses the WKB method (de Boer and Viergever, 1982; Steele and Taber, 1979a,b; Wang et al., 2016), in which the response along the cochlea can be predicted from an assumed distribution of complex wavenumbers. There are, however, several assumptions inherent in using the WKB method. Although it can account for both forward and backward travelling waves in the cochlea, its main assumption is that there is only one type of wave propagating. This is generally called the "slow wave", to distinguish it from the so-called "fast wave" that travels at the compressional speed of sound in the cochlear fluids. The fast wave is not thought to play an important role in normal hearing, since the pressure is the same in the two fluid chambers and so there is no pressure difference acting on the basilar membrane, BM, which is then not driven into motion. There are, however, several other kinds of wave that might play a significant role in determining the mechanical response of the cochlea, including those due to higher-order fluid modes (Watts, 2000; Elliott et al., 2013) and those due to mechanical coupling along various parts of the organ of Corti or the fluid within it (Zwislocki and Kletsky, 1979; Ghaffari et al., 2007; Ramamoorthy et al., 2007; Lamb and Chadwick, 2011; Meaud and Grosh, 2010). The way that these and other modes couple into the slow wave is still a matter of some debate.

An alternative approach to modelling the mechanics of the cochlea is to divide the length of the cochlea into a finite number of elements and describe the individual physical processes involved in cochlear mechanics. These equations can be coupled together in a numerical model that makes no explicit assumptions about the type of wave propagation. The earliest example of this approach is the "transmission line" model (Shera and Zweig, 1991; Zweig, 1991; Zwislocki, 1950), in which the inertance of the fluid in the cochlear chambers is represented as a series inductance and the response of the BM is represented as a shunt impedance. At the other extreme, the detailed behaviour of the fluid in the chambers and the motion of the organ of Corti could be represented by a finite element model, where both the fluid in the chambers and the different parts of the organ of Corti are meshed into many small elements and the coupled set of equations of motion are, typically, solved using commercial software such as ANSYS (Ni et al., 2016). It is important to note that such finite element methods simultaneously solve for both the pressure in the fluid and the motion of the organ of Corti. This can significantly increase the computational time compared to solving for the fluid pressure and the organ of Corti motion individually, since the computational time typically rises in approximate proportion to the square of the total number of degree-of-freedom in a finite element model. It also means that both the fluid coupling and the organ of Corti motion must be analysed numerically, even if there may be a simple analytic formulation in one case or the other.

An elemental approach to the formulation of cochlear mechanics can be viewed as a generalisation of the transmission line model, in that the fluid motion and the organ of Corti dynamics are analysed separately and then coupled together. In the elemental model, however, the organ of Corti dynamics are not restricted to being locally-reacting and the fluid flow is not restricted to being proportional to the pressure difference between adjacent elements. The elemental model reduces to a transmission line model if these restrictions are imposed, but can also account for the more general case.

This paper first introduces the elemental model, for the case of a locally-reacting basilar membrane and 1D fluid coupling in a uniform box model. If the BM response is linear, the coupled solution can be solved efficiently in the frequency domain and this formulation is considered first. A time domain formulation is considered at the end of this paper which leads to a state space implementation of the elemental model that can be used to simulate the nonlinear response of the cochlea but is also important in assessing the stability of linear models. It is shown how the fluid coupling part of the formulation can be adapted to model non-uniform distributions of fluid chamber area and the near field component of the pressure that is present when the fluid coupling is analysed in 3D. More general forms of the BM response are also then considered, where both longitudinal mechanical coupling along the BM and non-symmetrical feedforward behaviour along the organ of Corti can be accounted for.

The theoretical formulation behind the fluid coupling within the cochlea and its passive micromechanics are reasonably well understood. The intention of the present review paper is to demonstrate how these individual responses may be integrated into a numerical formulation that can be readily used to predict the coupled response of the cochlea under different conditions. Although there have been a number of micromechanical models proposed for the active cochlea, there is still considerable debate about the form of such a model and how it should couple into the fluid. Since this is still unclear, and also for reasons of brevity, the elemental model will be developed and illustrated here only using passive micromechanical models, on the understanding that active models can be incorporated with a more general form of BM admittance.

2. Formulation of the elemental model in the frequency domain

In this section, we assume a linear micromechanical response, and an excitation of the cochlea at a single frequency, so that the amplitude and phase of all the dynamic variables can be considered complex and proportional to $e^{i\omega t}$. The essence of the elemental model is that the length of the cochlea is divided into a finite number of sections and that the interaction between the fluid in the chambers and the mechanical response of the BM is described in terms of the transverse modes of the element in each section. The general form of the assumed model is illustrated in Fig. 1, which also shows the coordinate system that will be used below. The cochlea is shown uncoiled since the coiling is not thought to play an important role in its dynamics (Steele and Zais, 1985). The origin of the coordinates system is on the basilar membrane at the base of the cochlea and it consists of a longitudinal variable, x, a radial variable, y, and a transverse variable, z. The aim of the elemental model is to reduce the complicated interaction that occurs between

Please cite this article in press as: Elliott, S.J., Ni, G., An elemental approach to modelling the mechanics of the cochlea, Hearing Research (2017), https://doi.org/10.1016/j.heares.2017.10.013