Institute of Phonetic Sciences,
University of Amsterdam,
Proceedings 18 (1994), 77-85

PROPERTIES OF THE RADIATION PRESSURE IN THE COCHLEA

J. S. C. van Dijk

Abstract

In modern hearing theory much attention is paid to the possible influence of outer hair cell, activity on the motion of the basilar membrane. In order to include those effects in models of the cochlea, an extension of the usual equations of motions is necessary. Therefore, we reconsidered the derivation of the equations of motion from a quite general point of view and showed that it is possible to incorporate additional forces in the equations. A straightforward analysis of properties of the equations shows that an uncritical application of natural parameters can lead to results without sense. Two examples of the numerical implementation of the model confirm the validity of the way in which extensions can be properly made.

1 Introduction

In most models of the cochlea the motion of the basilair membrane results from equations in which forces at the membrane are caused by a prescribed motion at the stapes. Until now, these models fail to describe important observations adequately if realistic values of the damping parameter are used. For instance, it is impossible to model the observed sharpness of tuning curves without using unnatural values for the damping. Moreover, without the introduction of additional forces it is impossible to model or to explain cochlear emissions of any kind (de Boer, 1993). So, there is a need for the extension of cochlear model equations with which observed results can be explained and understood.

At present it is believed that in a healthy cochlea outer hair cell activity contributes substantially to the motion of the basilar membrane (Ruggero, 1992). Forces in consequence of this activity (Brundin and Russel, 1993) may comprise non-linear terms which are responsible for the generation of combination tones as well as forces which are responsible for emissions.

In this research note we derive model equations which open the possibility to introduce new forces of any significance. The derivation is quite general and includes all good properties of model equations which are used by several investigators in this field. For an overview we refer to de Boer (1980, 1984, 1991). As an application the generation of a cubic difference tone will be shown.

2 General dynamics

Let us start with a particular cochlea in which all membranous structures are absent. Then the fluid in the cavity has to obey the well-known equations of Euler. In vector notation these equations can be written as

$$\frac{d\vec{v}}{dt} = -\frac{1}{\rho}\nabla p + \vec{F} \ . \tag{1}$$

The vector $\vec{v}$ is the velocity of a unit of mass of the fluid. The density of the fluid is ρ and p is the pressure. The sum of external forces - per unit of mass - is denoted by $\vec{F}$. This equation expresses the equilibrium between the inertial resistance of a unit of mass of the fluid, the pressure and external forces.

Next we assume that in addition to the fluid in a certain region of the inner ear cavity a membrane is present. The stiffness component of the membrane is not negligible. In order to find the equation of motion for this membranous medium, it is sufficient to add a term to the Euler equation (1) which expresses the restoring force in consequence of the presence of stiffness. If the stiffness per unit of volume is given by κ_m and the density of the medium is ρ_m, the restoring force per unit of mass reads

$$-\omega_0^2 \vec{u}_m \ .$$

Here $\vec{u}_m$ is the deflection of a unit of mass of the membranous medium. ω_0^2 is defined according to $\omega_0^2 = \kappa_m / \rho_m$. Then, the modified Euler equations for this medium are

$$\frac{d\vec{v}_m}{dt} = -\frac{1}{\rho_m}\nabla p_m - \omega_0^2 \vec{u}_m + \vec{F}_m \ . \tag{2}$$

In this equation subscripts m are used to distinguish between membrane quantities and the counterparts of the surrounding fluid. At the boundary between fluid and membrane the normal component of (1) reads

$$\frac{dv_n}{dt} = -\frac{1}{\rho}\frac{\partial p}{\partial n} + F_n \ . \tag{3}$$

The equivalent equation for the membranous medium is

$$\frac{dv_n}{dt} = -\frac{1}{\rho_m}\frac{\partial p_m}{\partial n} - \omega_o^2 u_{mn} + F_{mn} \ . \tag{4}$$

In both equations subscripts n refer to the normal components of the corresponding vector quantities.

3 The basilar membrane as a discontinuity

If the fluid and the membranous medium are in motion, we shall assume that at the boundary between fluid and membrane normal components of the velocity of both media are the same. Thus $v_n = v_{mn}$. Moreover, we assume that normal components of the additional forces at this boundary for both media are the same. In consequence of this, it holds that $F_n = F_{mn}$. These assumptions make it possible to compare (3) and (4) with each other at the boundary. After subtraction of (4) from (3), the difference between the equations can be written as

$$\frac{1}{\rho}\frac{\partial p}{\partial n} - \frac{1}{\rho_m}\frac{\partial p_m}{\partial n} = \omega_0^2 u_{mn} \quad . \tag{5}$$

Next we consider the membrane as a thin strip with thickness Δn. In that case the density ρ_m can be written as

$$\rho_m = \frac{m}{\Delta n} \quad , \tag{6}$$

where m is the mass per unit of area of the membrane. Insertion of this term in (5) yields

$$\frac{1}{\rho}\frac{\partial p}{\partial n} - \frac{1}{m}\frac{\partial p_m}{\partial n}\Delta n = \omega_0^2 u_{mn} \quad . \tag{7}$$

In the second term of the left member of (7), the expression $(\partial p_m / \partial n)\Delta n$ is the difference between the pressure at the upper- and lower-side of the membrane. We shall assume that this difference equals two times the fluid pressure at the upper side of the membrane. In consequence of this, we introduce the following simplification

$$\frac{\partial p_m}{\partial n}\Delta n = 2p \quad , \tag{8}$$

with which (7) is reduced to

$$\frac{1}{\rho}\frac{\partial p}{\partial n} - \frac{2}{m}p = \omega_0^2 u_{mn} \quad . \tag{9}$$

Equation (9) holds true at the boundary between fluid and membrane. The equation has the shape of an inhomogenous radiation condition. Its meaning is restricted to the presence of stiffness in the membranous region. However, in oscillating problems the importance of stiffness depends on the frequency of oscillations. This can be elucidated at the hand of equation (4). In absence of external forces, the linear counterpart of (4) reads

$$\frac{\partial^2 u_{mn}}{\partial t^2} = -\omega_0^2 u_{mn} - \frac{1}{\rho_m}\frac{\partial p_m}{\partial n} \quad .$$

Let us assume that we are dealing with complex oscillations proportional to $\exp(\pm i\omega t)$. As follows from the preceding equation, the complex amplitudes of deflection and pressure - which are denoted by $\bar{u}_{mn}$ and $\bar{p}_m$ respectively - satisfy the expression

$$-\rho_m\left(1-\frac{\omega_0^2}{\omega^2}\right)\omega^2\bar{u}_{mn} = -\frac{\partial\bar{p}_m}{\partial m} \tag{10}$$

If $\omega < \omega_0$, the stiffness term dominates and it is not difficult to conceive the membranous region as a discontinuity in a fluid-like environment. However, if $\omega > \omega_0$ the expression (10) can be considered as an Euler equation in which the inertial resistance is determined by an effective density

$$\rho_m\left(1-\frac{\omega_0^2}{\omega^2}\right) . \tag{11}$$

If ω increases sufficiently, the density (11) can be approximated by ρ_m. In that case there is no reason to introduce a discontinuity, because the dynamic properties of both media are approximately the same. In consequence of this, any pressure difference in that region must vanish. This determines the natural zero boundary condition.

Along the basilar membrane the stiffness ω_0^2 varies as a decreasing function of the distance to the stapes. Thus, at a fixed value of the frequency ω, both situations will appear. Then it will appear that the validity of the discontinuous approach is questionable. Within this work we shall accept the idea of the basilar membrane as a discontinuity in a fluid-like environment. In consequence of the preceding remarks, we shall assume that the pressure (difference) at the end of the membrane always vanishes.

4 Model equations

In models of the cochlea, the length parameter along the basilar membrane is often denoted by x. The normal direction to this abscissa is the positive y-axis. In terms of abscissa and ordinate the equation for the membrane is

$$\frac{d^2u}{dt^2} = -\omega_0^2(x)u - pm + F , \tag{12}$$

where

$$pm(x,t) = \frac{2}{m}p(x,0,t) \;;\; u(x,t) = u_{mn}(x,0,t) \text{ and } F(x,t) = F_{mn}(x,0,t) .$$

The ordinate $y = 0$ refers to the boundary between fluid and membrane. At this boundary the radiation condition can be written as

$$\frac{1}{\rho}\frac{\partial p}{\partial y} - pm = \omega_0^2 u \tag{13}$$

Equation (13) can be made suitable for numerical implementation. Let us apply the so called 'shallow water' approximation in cochlear mechanics (Van Dijk, 1990). This reduces $\partial p / \partial y$ to hp_{xx} in which h is the mean height of the cochlear scalae. After scaling of both the abscissa and ordinate to the length l of the membrane, it ultimately appears that the radiation pressure follows from the model

$$\begin{aligned} &pm_{xx} - a^2 pm = a^2 \omega_0^2(x) u \ , \quad 0 < x < 1 \\ &pm = 0 \qquad\qquad \text{at } x = 0 \\ &pm = 0 \qquad\qquad \text{at } x = 1 \ , \end{aligned} \tag{14}$$

in which the constant a is defined by

$$a = l\sqrt{\frac{2\rho}{mh}} \ .$$

pm is defined in (12). An alternative for the boundary condition at $x = 0$ is $pm_x = 0$. However, it will appear that the next results scarcely depend on boundary conditions. Therefore we shall confine ourselves to $pm = 0$. For the sake of completeness we shall always assume that zero initial conditions are supplementary to both equation (12) and problem (14). The solution of problem (14) can be written explicitly as (Van Dijk, 1992)

$$pm(x,t) = -a^2 \int_0^1 G(x,\xi,a)\omega_0^2(\xi)u(\xi,t)d\xi \ , \tag{15}$$

in which $G(x,\xi,a)$ reads

$$G(x,\xi,a) = \begin{cases} \dfrac{\sinh ax \sinh a(1-\xi)}{a \sinh a} & 0 \le x < \xi < 1 \\[2ex] \dfrac{\sinh a\xi \sinh a(1-x)}{a \sinh a} & 0 < \xi < x \le 1 \ . \end{cases} \tag{16}$$

From (12) and (15) follows that the motion of the membrane obeys the equation

$$\ddot{u}(x,t) = -\omega_0^2(x)u(x,t) + a^2 \int_0^1 G(x,\xi,a)\omega_0^2(\xi)u(\xi,t)d\xi + F(x,t) \ , \tag{17}$$

$0 < x < 1, t \ge 0$.

The behaviour of the radiation pressure $pm(x,t)$ highly depends on properties of the function of Green. In essence, this function expresses the spatial extent of the radiation in terms of an influence function, which describes all effects from a unit of pressure with density 1 placed at the point $x = \xi$. In (16), the constant a determines the sharpness of the function of Green and therefore the spatial extent of the radiation. Typical values of model parameters are $m = 0.05\ g/cm^2$; $h = 0.1\ cm$ and $l = 3.5\ cm$ (de Boer, 1980). Thus $a \approx 70$, which is a very large parameter value. Then as follows from (16), in almost the whole region $0 < x < 1$ - excepted near the endpoints of the interval - the Green's function can be approximated by

$$G(x,\xi,a) = \frac{1}{2a} e^{a|x-\xi|} , \tag{18}$$

which is the function of Green for the radiation pressure in absence of boundary conditions. In consequence of this, we conclude that from a qualitatively point of view in almost the whole cochlea properties of the radiation are uniform. It is easy to verify that

$$a^2 \int_0^1 G(x,\xi,a)d\xi = \frac{\sinh a - \sinh ax - \sinh a(1-x)}{\sinh a} .$$

From this expression follows that with exception of the endpoints of the interval [0,1]

$$\lim_{a\to\infty} a^2 \int_0^1 G(x,\xi,a)d\xi = 1 .$$

This means that in the limiting case the Green's function resembles a delta function for points belonging to (0,1). Thus we have

$$\lim_{a\to\infty} a^2 G(x,\xi,a) = \delta(x-\xi) . \tag{19}$$

In consequence of (19), a sufficiently large value of a results in the approximation

$$a^2 \int_0^1 G(x,\xi,a)\omega_0^2(\xi)u(\xi,t)d\xi \approx \omega_0^2(x)u(x,t) .$$

In that case the integral equation (17) is reduced to

$$u(x,t) = -F(x,t) ;$$

and the model fails to describe adequately basilar membrane behaviour.

5 Results and applications

After discretization of the length in n equal steps, the membrane can be considered as a system of n successive oscillators. The deflection of the *i-th* oscillator is denoted by u_i; $i = 1, 2, \ldots, n$. In consequence of this, the discrete counterpart of (17) can be written as the system (Van Dijk, 1992)

$$\ddot{\mathbf{U}} = \mathbf{AU} + \mathbf{F} \ ,$$

in which the components of the column vector $\mathbf{U}$ are the deflections of successive oscillators. $\mathbf{A}$ is a constant $n \times n$ matrix. The column vector $\mathbf{F} = \mathbf{F}(t)$ represents the sum of the external forces of the system. In absence of the radiation pressure pm, the eigenvalues of $\mathbf{A}$ are the squared resonance frequencies of successive oscillators. The presence of pm slightly lowers the eigenvalues. Therefore, the hydrodynamical environment of membrane oscillators tends to diminish the resonance frequencies.

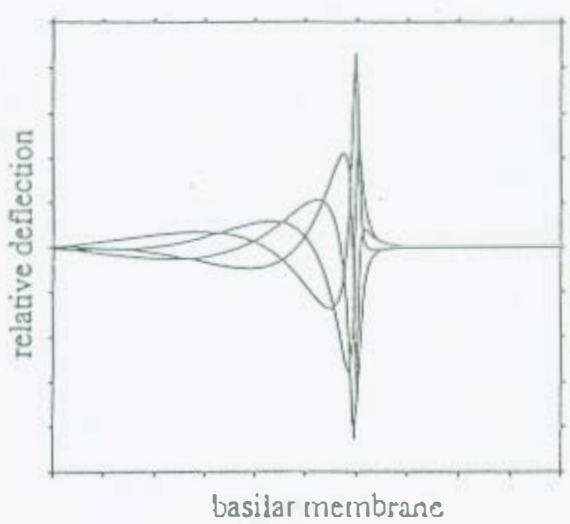
A damping force can be considered as an external force which makes part of $F = F(x,t)$ in (12). Then it is sufficient to replace in (12) the stiffness term $\omega_0^2 u$ by $\omega_0^2 u + \varepsilon\omega_0 u$, in which ε is a small positive parameter. Note that as a result of the present way of modelling, there will never be a damping term in the radiation pressure (15). In models with damping it is useful to write the discrete counterpart of (17) as a first order system

$$\dot{\mathbf{Y}} = -\mathbf{BY} + \mathbf{G} \ .$$

Here $\mathbf{Y}$ consists of $2n$ components which are the deflection and velocity of successive oscillators. $\mathbf{B}$ is a $2n \times 2n$ matrix. $\mathbf{G} = \mathbf{G}(t)$ is the vector, which denotes the sum of external forces. In this case the eigenvalues of $\mathbf{B}$ are complex. It can be proven that if the real parts of the eigenvalues are positive, the system is stable. It appears that if the damping ε is negative for at least one oscillator, the real part of at least one pair of (complex conjugate) eigenvalues is negative. In consequence of this, the system is stable only if $\varepsilon \geq 0$.

In (17), the function $F = F(x,t)$ can be defined so that the whole system equals a transmission line with an input at $x = 0$. It is well-known that the solutions of those models with a sinusoidal input are travelling waves along the membrane.

Figure 1. Four successive stages of a travelling wave in a model in which the place dependent part of the external force varies in an almost exponential way along the membrane.



However, if $F = F(x,t)$ models a propulsion which extends over (a part of) the basilar membrane, the travelling wave has been conserved. This means that the concept of travelling waves does not only depend on propulsion at the stapes, but mainly on intrinsic properties of the radiation pressure. Figure 1 is the solution of a model in which the driving force extends over almost the whole membrane.

The external force $F = F(x,t)$ may comprise terms which are proportional to the third of the deflection of membrane oscillators. The presence of this kind of terms does not disturb the stability of the system. Besides, this kind of terms generate combination tones. If outer hair cells are responsible for forces of this kind, these forces form a natural part of the external force F. The next figure is an example of the motion of the membrane in which - as a result of a small third order term - two primary frequencies f_1 and f_2 generate a cubic difference tone with frequency $f_c = 2f_2 - f_1$ $(f_2 > f_1)$. The spectral contents of the point which resonates at this frequency is given in the next figure.

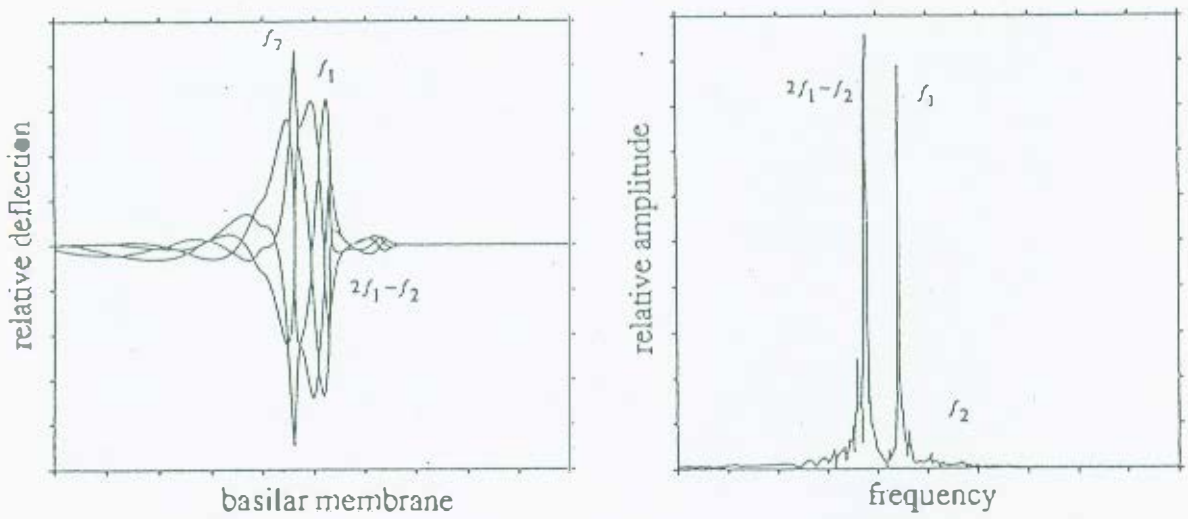


Figure 2 a. Successive stages of the wave motion in the case of two primary tones which generate combination tones. The region of resonance of the cubic difference tone is clearly visible. b. Spectrum from the motion of the oscillator at the place which is tuned at the frequency of the cubic difference tone in the case of two tone stimuli.

6 Discussion

In this work we investigated possibilities to enlarge the way in which mechanical processes in the cochlea can be modelled. The opportunity for this question results from the present opinion in hearing theory that the motility of the outer hair cells of the organ of Corti strongly influences the motion of the basilair membrane. Within this brief span, we did not pay attention to the precise shape of forces as a result of hair cell activity. We only showed, by starting from the first and foremost beginning, that additional forces in model equations can be incorporated in a natural way. As a side-line effect, an important restriction to the applicability of natural parameters in models has been found. Running away with those parameters can lead to degeneration of the whole model. The two examples from the preceding section show that from a qualitatively point of view, the model works.

References

Boer, E. de (1980). "*Auditory Physics. Physical principles in hearing theory, I*". Phys. Rep. 62, 87-174.

Boer, E. de (1984). "*Auditory Physics. Physical principles in hearing theory, II*". Phys. Rep. 105, 141-226.

Boer, E. de (1991). "*Auditory Physics. Physical principles in hearing theory, III*". Phys. Rep. 203, 127-229.

Boer, E. de (1993). "Some like it active" In: H. Duifhuis, J. W. Horst, P. van Dijk, S. M. van Netten (Eds.). *Biophysics of hair cell sensory systems*, 3-22. World Scientific.

Brundin, L, Russel, I (1993). "Sound-induced movements and frequency tuning in outer hair cells isolated from the guinea pig cochlea" In: H. Duifhuis, J. W. Horst, P. van Dijk, S. M. van Netten (Eds.). *Biophysics of hair cell sensory systems*, 182-191. World Scientific.

Dijk, J. S. C. van (1990). "On dipoles and the radiating membrane". In: P. Dallos, C. D. Geissler, J. W. Matthews, M. A. Ruggero and C. R. Steele (Eds.). *The mechanics and biophysics of hearing*. Lecture notes in biomathematics. 87, 340-347. Springer Verlag.

Dijk, J. S. C. van (1992). "Spectral decomposition in modelsof hearing", *Proc. Inst. Phon. Sci.* (Amsterdam) 16, 35-52.

Ruggero, M. A. (1992). "Responses to sound of the basilar membrane of the mammalian cochlea". *Current Opinions in Neurobiology* 2, 449-465.