Localization of non-linearities in the cochlea

M. A. VIERGEVER and J. J. KALKER

Dept. of Mathematics, Univ. of Technology Delft, Delft, The Netherlands

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SUMMARY

An attempt is made to locate the non-linear sources inside the cochlea. The possible sources can be divided in several classes: of no significance are the perilymph, the endolymph and the impedances of Reissner's membrane and the basilar membrane; of little significance is the motion of the mentioned membranes in their own plane; of uncertain significance are the oval window impedance and the spiral coiling of the cochlea, while the mechanism of tectorial membrane, haircells and organ of Corti is likely to be an important source of non-linearity. Moreover the widely used membrane equation is improved in the course of the work.

1. Introduction*

Although in many cases the cochlea may be regarded as a linear system, a number of non-linear phenomena have been observed. Whereas older theories suggested that the non-linearities could be located in the middle ear or in the nervous system, it is now recognised, owing to experiments of notably Goldstein [6] and Rhode [9], that their source lies inside the cochlea.

Several authors, e.g. Hubbard and Geisler [7], try to explain these phenomena by introducing a non-linearity and computing its effects, but they do not justify their choice, so that the results, though in good agreement with the observations, remain questionable. We have investigated non-linearities that do have a physical background. The first is the quadratic velocity term in the equation of motion of the perilymph, which will be considered in the Sections 2 and 3. Secondly we have examined the partition. It is shown in Section 4 that it is impossible to draw conclusions as to its non-linear conduct under the hypothesis that the partition behaves as a single membrane, although experiments of Von Békésy [1, 2] seem to justify this assumption, since according to them all parts of the scala media are in phase. We have dropped the supposition of membranelike action. Reissner's membrane, the endolymph and the basilar membrane are considered separately, whilst moreover endolymph velocity components parallel to the basilar membrane are taken into account. In this way we find an alternative for the equation of motion of the partition. From this equation we can deduce the weight that mass, resistance and stiffness carry in relation to the non-linearities, as well as the influence of the mentioned velocity components.

2. Sources within the perilymph; the non-viscous case

The continuity equation for a compressible fluid can be written as

$$\frac{\partial \rho}{\partial t} + \nabla \cdot (\rho v) = 0 , \tag{2.1}$$

where v is the velocity in and ρ the density of the fluid; t is the time variable.

Many workers (see e.g. [4, 14]) have shown that the compressibility of the perilymph is negligible for small frequencies, while its influence remains small for high frequencies ($\approx 10^4$ Hz). An other reason for ignoring the compressibility is that the occurrence of the non-linearities was found to be frequency-independent. Therefore, one often considers the fluid as incompressible;

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* For a description of the cochlea we refer to [2, 8, 14].

then (2.1) simplifies to

$$\nabla \cdot v = 0 .$$ (2.2)

Denote the fluid pressure by p. Then the equation of motion reads

$$\rho \frac{\partial v}{\partial t} + \rho (v \cdot \nabla) v + \nabla p = 0 .$$ (2.3)

Here, the viscosity of the fluid has been disregarded; in Section 3 we will treat the viscous case.

In [13] the order of magnitude of the left hand terms in (2.3) is investigated. With an input transmembrane pressure of 1 dyn/cm^2, the velocity is shown to be smaller than 10^{-2} cm/s, while its spatial derivatives do not exceed the value of 10^{-1} c.g.s.-units. Thus the second term is of order 10^{-3} dyn/cm^3; the first and the third term however are both of order 1 dyn/cm^3. The ratio of the order of magnitude of the non-linear effects and that of the linear phenomena is larger than 10^{-2}, according to experiments concerning non-linearities (see e.g. [6, 9]). Therefore the second left hand term of (2.3) is negligible. To illustrate this result, we shall investigate in the sequel the introduction of non-linear terms in the Peterson–Bogert model [8]. The model is characterized by the assumption that long waves develop in the cochlea as a consequence of oval window excitation by the stapes. This means that the wavelength is large compared with the cross-sectional dimensions of the cochlea. As a result of this the pressure p and the velocity v of the fluid particles are homogeneous over a cross-section of a scala. Actually this holds to a good approximation only for frequencies < 1 kHz (see [12]). Moreover it was assumed that non-linear effects can be ignored and that the deflection of the partition is completely determined by the pressure difference between the two channels.

Maintaining the two other hypotheses of the Peterson–Bogert model we shall investigate here the effect of retaining the non-linearities in the equation of motion and in the continuity equation. The fluid is considered as compressible.

The continuity equation, given by (2.1), is integrated over a control volume V enclosed by a surface S; n is the outward unit normal on S. We find, utilizing the divergence theorem of Gauss:

$$\iiint_V \frac{\partial \rho}{\partial t} dV + \iint_S (\rho v) \cdot n \, dS = 0 .$$ (2.4)

Consider a control volume in the scala vestibuli as drawn in Fig. 1. Since the model is basically one-dimensional, we introduce only the axial coordinate x ($x=0$ at the helicotrema, $x=L$ at the windows). The width of the partition is $b(x)$, while $A(x)$ is the cross-section of a scala. In the figure A_x an b_x stand for dA/dx and db/dx respectively.

Assume that the displacement of the partition is so small that the resulting changes in S_1 and V are negligible; hence $S_1 = b \, dx$ and $V = A \, dx$. We define the density $\rho_{sv}(x, t)$ and the axial velocity $u_{sv}(x, t)$, both homogeneous over the cross-section of the scala vestibuli, and further $w(x, t)$, the vertical displacement of the partition, reckoned positive in case of a motion in the
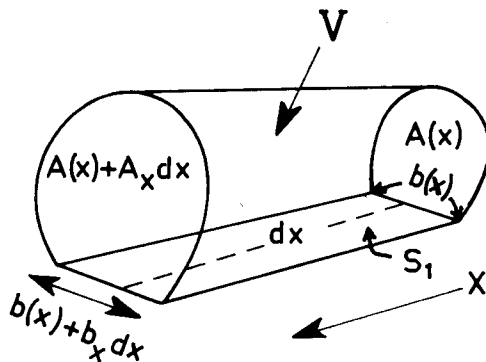

Figure 1.

direction of the scala tympani. Using these concepts, (2.4) leads to

$$A \frac{\partial \rho_{sv}}{\partial t} + b\rho_{sv}w + \frac{\partial}{\partial x}(A\rho_{sv}u_{sv}) = 0 . \tag{2.5}$$

Now suppose that in the cochlea the pressure p is a function of the density ρ only, which holds for most fluids. Then we can define $a(\rho)$, the velocity of sound in the perilymph, by

$$\frac{dp}{d\rho} = a^2 . \tag{2.6}$$

We assume that $a(\rho)$ is constant; this is correct with a very high degree of accuracy. Let ρ_0 be the average value of ρ and p_0 the corresponding pressure. Then we can write

$$\rho = \rho_0 + \frac{1}{a^2}(p - p_0) . \tag{2.7}$$

Denote by $p_{sv}(x; t)$ the pressure in the scala vestibuli. It is homogeneous over a cross-section like ρ_{sv} and u_{sv}. By means of (2.6) and (2.7) we change (2.5) into

$$\frac{1}{a^2}\left[A \frac{\partial p_{sv}}{\partial t} + b(p_{sv} - p_0)w + \frac{\partial}{\partial x}\{A(p_{sv} - p_0)u_{sv}\}\right] + \rho_0 bw + \rho_0 \frac{\partial}{\partial x}(Au_{sv}) = 0 . \tag{2.8}$$

The equation of motion for the scala vestibuli is found from (2.3). Using once more (2.6) and (2.7) it reads

$$\frac{1}{a^2}\left[(p_{sv} - p_0)\frac{\partial u_{sv}}{\partial t} + \tfrac{1}{2}(p_{sv} - p_0)\frac{\partial}{\partial x}u_{sv}^2\right] + \rho_0 \frac{\partial u_{sv}}{\partial t} + \frac{\partial}{\partial x}(p_{sv} + \tfrac{1}{2}\rho_0 u_{sv}^2) = 0 . \tag{2.9}$$

The analogues of (2.8) and (2.9) for the scala tympani are:

$$\frac{1}{a^2}\left[A \frac{\partial p_{st}}{\partial t} + b(p_0 - p_{st})w + \frac{\partial}{\partial x}\{A(p_{st} - p_0)u_{st}\}\right] - \rho_0 bw + \rho_0 \frac{\partial}{\partial x}(Au_{st}) = 0 , \tag{2.10}$$

$$\frac{1}{a^2}\left[(p_{st} - p_0)\frac{\partial u_{st}}{\partial t} + \tfrac{1}{2}(p_{st} - p_0)\frac{\partial}{\partial x}u_{st}^2\right] + \rho_0 \frac{\partial u_{st}}{\partial t} + \frac{\partial}{\partial x}(p_{st} + \tfrac{1}{2}\rho_0 u_{st}^2) = 0 . \tag{2.11}$$

Here, p_{st} and u_{st} are the values of pressure and axial velocity, homogeneous over the cross-section of the scala tympani. It has been assumed for the sake of simplicity only that the cross-sections of the channels are equal. This is in good agreement with reality, except for the neighbourhood ($\simeq 0.3$ cm) of the windows. It is clear that x is also the axial coordinate for the scala tympani.

The system is completed by the membrane equation

$$p_{sv} - p_{st} = m \frac{\partial w}{\partial t} + kw + c \int w \, dt , \tag{2.12}$$

in which $m(x)$, $k(x)$ and $c(x)$ are mass, resistance and stiffness of the partition per unit area.

We need boundary and initial values to solve this system in the unknowns p_{sv}, p_{st}, u_{sv}, u_{st} and w.

In the linear case the initial conditions could be avoided by the restriction to harmonic oscillations. The same approach would be unsatisfactory here, inasmuch as the response of the quantities involved is not harmonic because of the non-linear terms. It is possible however, on account of the external force (oval window excitation by the stapes), to regard the cochlea at rest at $t = 0$. This hypothesis determines the initial conditions. Of the four necessary boundary conditions, two are given at the helicotrema, where both the pressure difference and the axial flux are zero, so that

$$p_{sv}(0, t) - p_{st}(0, t) = 0 , \tag{2.13}$$

$$u_{sv}(0, t) + u_{st}(0, t) = 0 . \tag{2.14}$$

The latter equation can be written in this simple form because the scalae have equal cross-sections. The two other conditions can be either $p_{sv}(L, t)$ and $p_{st}(L, t)$ prescribed [12], or known impedances of oval and round window [10], or a mixture of these, e.g. $p_{sv}(L, t) - p_{st}(L, t)$ and round window impedance known [5, 7, 8]. Until now there has not been any doubt as to the linearity of these values; we assume that they are not non-linear sources (see Section 5). With the aforesaid conditions the system (2.8)–(2.12) can be resolved.

We want to investigate the suggestion that the effects of the non-linearities on p_{sv}, p_{st}, u_{sv}, u_{st} and w are merely consequences of the compressibility of the fluid. To this end we consider the incompressible case $(a = \infty)$; then the system (2.8)–(2.12) simplifies considerably. After the introduction of the variables p_+, p_-, u_+ and u_- by

$$p_+(x, t) = p_{sv}(x, t) + p_{st}(x, t), \tag{2.15}$$

$$p_-(x, t) = p_{sv}(x, t) - p_{st}(x, t), \tag{2.16}$$

$$u_+(x, t) = u_{sv}(x, t) + u_{st}(x, t), \tag{2.17}$$

$$u_-(x, t) = u_{sv}(x, t) - u_{st}(x, t), \tag{2.18}$$

it can be written in the following way:

$$\frac{\partial}{\partial x}(Au_+) = 0, \tag{2.19}$$

$$\frac{\partial}{\partial x}(Au_-) + 2bw = 0, \tag{2.20}$$

$$\rho_0 \frac{\partial u_+}{\partial t} + \frac{\partial}{\partial x}\left[p_+ + \tfrac{1}{4}\rho_0(u_-^2 + u_+^2)\right] = 0, \tag{2.21}$$

$$\rho_0 \frac{\partial u_-}{\partial t} + \frac{\partial}{\partial x}(p_- + \tfrac{1}{2}\rho_0 u_- u_+) = 0, \tag{2.22}$$

$$p_- = m \frac{\partial w}{\partial t} + kw + c \int w\, dt. \tag{2.23}$$

From (2.14) and (2.19) it is derived that

$$u_+(x, t) = 0. \tag{2.24}$$

Hence (2.21) and (2.22) simplify to

$$\frac{\partial}{\partial x}(p_+ + \tfrac{1}{4}\rho_0 u_-^2) = 0, \tag{2.25}$$

$$\rho_0 \frac{\partial u_-}{\partial t} + \frac{\partial p_-}{\partial x} = 0. \tag{2.26}$$

From (2.20), (2.23) and (2.26) we can find p_-, u_- and w by regarding harmonic oscillations and solving the remaining ordinary differential equations with the help of boundary conditions (2.13) and for instance $p_-(L, t)$ known. Subsequently p_+ can be computed from (2.25):

$$p^+ = -\tfrac{1}{4}\rho_0 u_-^2 + F(t), \tag{2.27}$$

in which $F(t)$ is an unknown function that has to be determined from the boundary conditions.

We see that p_-, u_- and w are completely linear, as well as of course u_+; p_+ is non-linear. Yet this does not contradict our former statement that the non-linearities investigated in this section are negligible. Above all it is obvious that p_+ is almost linear, since the first term on the right-hand side in (2.27) is very small because of the small velocities in the cochlea. Moreover we are interested mainly in the deflection of the partition in which p_+ does not play a part. The non-linearities in the equation of motion and in the continuity equation are thus clearly

compressibility effects. The compressibility of the perilymph is small. It can even be ignored at low and middle-high frequencies (< 7 kHz, see [5]). The non-linearities are therefore small effects of a small quantity. Hence they cannot be a satisfactory explanation for the non-linear behaviour of the cochlea.

3. Sources within the perilymph; the viscous case

In Section 2 the influence of non-linear sources within the perilymph has been investigated under the neglect of the viscosity of the perilymph. This quantity has been examined already by the authors in [14]. Its principal effect is the existence of a boundary layer along the walls and the membrane. The entire viscous force is localized in this layer, while the main flow is considered as inviscid. The same approach will be used here. The reason is that the order of magnitude of the non-linear term can be considerably larger in the layer than in the inviscid perilymph, since v and especially the derivative of the axial velocity in the direction perpendicular to the walls c.q. the membrane will reach much higher values because of the no-slip condition.

The fluid is regarded as incompressible on account of the insignificance of the compressibility as has been noted already in the previous section. Then the equation of motion is

$$\rho \frac{\partial v}{\partial t} + \rho (v \cdot \nabla) v + \nabla p - \mu \Delta v = 0, \tag{3.1}$$

where μ is the coefficient of viscosity.

Decompose p and v in an inviscid part (p_0, v_0) and a perturbation (p_1, v_1) as a consequence of the viscosity. It follows that

$$\rho \frac{\partial (v_0 + v_1)}{\partial t} + \rho ((v_0 + v_1) \cdot \nabla)(v_0 + v_1) + \nabla (p_0 + p_1) - \mu \Delta (v_0 + v_1) = 0. \tag{3.2}$$

For the main flow the equation of an inviscid fluid holds:

$$\rho \frac{\partial v_0}{\partial t} + \rho (v_0 \cdot \nabla) v_0 + \nabla p_0 = 0. \tag{3.3}$$

It is not necessary to assume *a priori* that the mainflow is irrotational; since it is supposed, however, in the course of the derivation that the cochlea was at rest at $t=0$, we can set $\Delta v_0 = 0$ at once as well. For, the vorticity of a vortex tube is unchanged during the motion, as has been posed already by Helmholtz. Hence $\nabla x v_0 = 0$. Moreover $\nabla \cdot v_0 = 0$ because of the incompressibility of the fluid. From these two relations it follows immediately that v_0 satisfies Laplace's equation. In view of the above the remainder of (3.2) is:

$$\frac{\partial v_1}{\partial t} + (v_0 \cdot \nabla) v_1 + (v_1 \cdot \nabla) v_0 + (v_1 \cdot \nabla) v_1 + \frac{1}{\rho} \nabla p - \frac{\mu}{\rho} \Delta v_1 = 0. \tag{3.4}$$
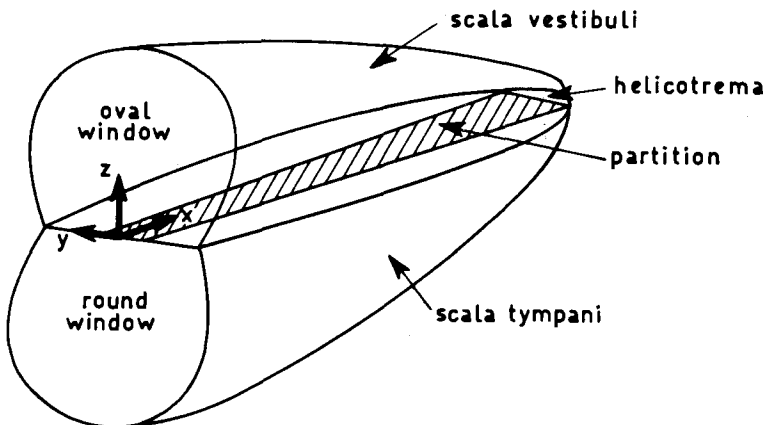

Figure 2.

Consider Fig. 2, which represents the uncoiled cochlea. The coordinate system is chosen in such a way that the z-axis is perpendicular to the plane of the partition ($z=0$); the x- and y-axis are located in this plane, in axial and lateral direction respectively. We are as usual merely interested in the phenomena in the neighbourhood of the membrane. The only boundary layer that will be considered is hence the one along the $z=0$ plane. In this layer the velocity u_1 is much larger than v_1 and w_1 and moreover the z-derivative of the perturbed quantities (v_1, p_1) far exceeds the other two in magnitude. For a more precise description we refer to [14].

As a result of the above, the most important component of (3.4) for our purpose is the axial one. Substituting v, the kinematic viscosity, for μ/ρ we can write it as

$$\frac{\partial u_1}{\partial t} + u_0 \frac{\partial u_1}{\partial x} + v_0 \frac{\partial u_1}{\partial y} + w_0 \frac{\partial u_1}{\partial z} + u_1 \frac{\partial u_0}{\partial x} + v_1 \frac{\partial u_0}{\partial y} + w_1 \frac{\partial u_0}{\partial z} +$$

$$+ u_1 \frac{\partial u_1}{\partial x} + v_1 \frac{\partial u_1}{\partial y} + w_1 \frac{\partial u_1}{\partial z} + \frac{1}{\rho} \frac{\partial p_1}{\partial x} - \left(\frac{\partial^2 u_1}{\partial x^2} + \frac{\partial^2 u_1}{\partial y^2} + \frac{\partial^2 u_1}{\partial z^2} \right) = 0 . \qquad (3.5)$$

An estimation of the various terms in this equation has been made in [13]. It is deduced there that (3.5) simplifies to

$$\frac{\partial u_1}{\partial t} + w_0 \frac{\partial u_1}{\partial z} - v \frac{\partial^2 u_1}{\partial z^2} = 0 \qquad (3.6)$$

with the solution

$$u_1(x, y, z; t) = u_{1,0}(x, y, z; t) + 10^{-1}\omega^{-\frac{1}{2}}\mathscr{L}^{-1}\left\{ (vs)^{-\frac{1}{2}} \int_0^z \mathscr{L}\left\{ \hat{w}_m(x, y; t) u_{1,0}(x, y, z; t) \right\} \right.$$

$$\left. \sinh\left[(s/v)^{\frac{1}{2}}(z-\lambda) \right] d\lambda \right\} + O(10^{-2}\omega^{-1}) . \qquad (3.7)$$

Here, $\mathscr{L}\{f\}$ is the Laplace transform of f with respect to t and $\mathscr{L}^{-1}\{F\}$ the inverse Laplace transform of F; ω is 2π times the frequency of the input signal, $\hat{w}_m(x, y; t)$ is the membrane velocity and $u_{1,0}(x, y, z; t)$ is given by

$$u_{1,0}(x, y, z; t) = -\tfrac{1}{2}(\pi v)^{-\frac{1}{2}} z \int_0^t u_0(x, y, 0; \tau)(t-\tau)^{-\frac{3}{2}} \exp\left[-\frac{z^2}{4v(t-\tau)} \right] d\tau , \qquad (3.8)$$

in which $u_0(x, y, 0; \tau)$ is the axial velocity along the partition in case the perilymph is inviscid. It can be derived easily from the results of Section 2 that this quantity is linear. Hence the first term on the right-hand side is linear; it corresponds to the expression for the axial boundary layer velocity that has been found in [14] when harmonic oscillations are regarded. The second term is non-linear. It cannot explain on itself the observed non-linearities, however, since it is completely insignificant for high frequencies. Even for low frequencies ($10^2 < \omega < 10^3$ c.p.s.) it is unlikely to play a part. For the membrane velocity is then considerably smaller than its upper bound of 10^{-2} cm/s, as can be derived from the calculations of [2, 7]. In view of the results of the Sections 2 and 3 we state that the effect of non-linear sources within the perilymph is negligible.

4. Non-linearities within the cochlear duct

In cochlear models the scala media is usually considered as a single membrane, in accordance with the experiments of von Békésy [1, 2]. The cochlea can be represented then by Fig. 2 (see Section 3). It is assumed generally that the membrane is rigid in the x- and y-directions and that its displacement $\chi(x, y; t)$ in the z-direction is determined completely by the pressure difference between the scalae. Let be $p_{sv}(x, y, z; t)$ and $p_{st}(x, y, z; t)$ the pressure in the scala vestibuli and the scala tympani respectively, and $m(x, y)$, $k(x, y)$ and $c(x, y)$ mass, resistance and stiffness of the membrane per unit area. When χ is positive in the positive z-direction the equation of motion is given by

$$p_{st}(x, y, 0; t) - p_{sv}(x, y, 0; t) =$$

$$= m(x, y) \frac{\partial^2 \chi(x, y; t)}{\partial t^2} + k(x, y) \frac{\partial \chi(x, y; t)}{\partial t} + c(x, y)\chi(x, y; t) . \qquad (4.1)$$

It is obvious that in this conception only m, k and c can be non-linear sources. It is however not possible to gain any insight in the nature of these non-linearities when the cochlear duct is regarded as a single structure. Consider therefore a cross-section of the partition, which is roughly triangular (Fig. 3).

B : Basilar membrane
C : Organ of Corti
E : Endolymph
H : Hair cells
R : Reissner's membrane
ST : Scala tympani
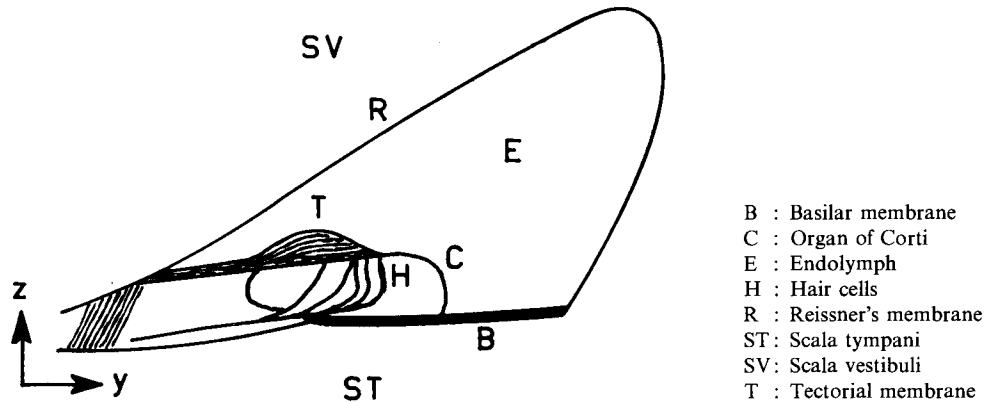SV : Scala vestibuli
T : Tectorial membrane

Figure 3.

The structure of the scala media is too complicated to be conceived in a simple mathematical model in which all the various parts are considered separately. Therefore we will take into consideration Reissner's membrane, the endolymph and the basilar membrane in the sequel, but ignore the organ of Corti, the haircells and the tectorial membrane. The reason for this is that we want to investigate above all the effect upon the membrane equation of endolymph motion in more than one direction. In relation to this aspect the ignored elements do not bear any importance. Another far less severe simplification is that all quantities are averaged over the width of the partition. Now the problem is actually two-dimensional (x, z).

The following y-averaged variables are defined:

$p_e(x, z; t)$: pressure in the endolymph
$p_{sv}(x; t)$ pressure on Reissner's membrane in perilymph
$p_{st}(x; t)$: pressure on basilar membrane in perilymph
$u_e(x, z; t)$: endolymph velocity in x-direction
$w_e(x, z; t)$: endolymph velocity in z-direction
σ: density of the endolymph
η: endolymph viscosity
$\tau(x, z; t)$: shear stress in the endolymph
$m_B(x)$: mass of the basilar membrane per unit area
$k_B(x)$: resistance of the basilar membrane per unit area
$c_B(x)$: stiffness of the basilar membrane per unit area
$\chi_B(x; t)$: displacement (in the z-direction) of the basilar membrane
$m_R(x)$: mass of Reissner's membrane per unit area
$k_R(x)$: resistance of Reissner's membrane per unit area
$c_R(x)$: stiffness of Reissner's membrane per unit area
$\chi_R(x; t)$: displacement (in the z-direction) of Reissner's membrane.

We suppose that the basilar membrane is located at $z=0$, and that its displacement is negligible with respect to the height $D(x)$ of the partition. Reissner's membrane is located at $z=D(x)$; the positive z-direction is that from the scala tympani towards the scala vestibuli.

In view of the foregoing we can represent the cochlear duct as in Fig. 4. The equation of continuity is

$$\frac{\partial u_e}{\partial x} + \frac{\partial w_e}{\partial z} = 0 . \qquad (4.2)$$
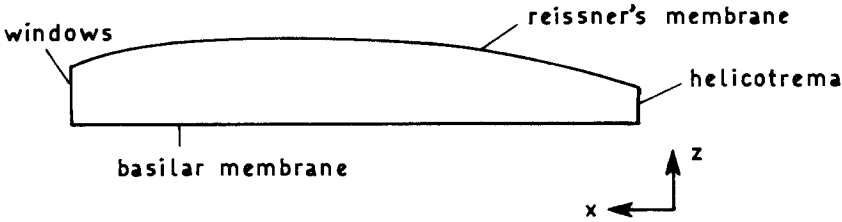
Figure 4.

Our purpose is a comparison with the original membrane equation (4.1). To this end the equilibrium of forces in the x-direction will appear to be irrelevant. We are merely interested in that in the z-direction. It is expressed by

$$\sigma \frac{dw_e}{dt} + \frac{\partial p_e}{\partial z} - \frac{\partial \tau}{\partial x} = 0 \,. \tag{4.3}$$

The boundary conditions are

$$p_{st}(x;t) - p_e(x, 0;t) = m_B(x) \frac{\partial^2 \chi_B(x,t)}{\partial t^2} + k_B(x) \frac{\partial \chi_B(x;t)}{\partial t} + c_B(x) \chi_B(x;t) \,, \tag{4.4}$$

$$p_e(x, D(x);t) - p_{sv}(x;t) = m_R(x) \frac{\partial^2 \chi_R(x,t)}{\partial t^2} + k_R(x) \frac{\partial \chi_R(x,t)}{\partial t} + c_R(x) \chi_R(x;t) \,. \tag{4.5}$$

Here it was assumed that the membranes can move in the z-direction only. This is approximately correct since the distance between the membranes varies only slowly with x. Application of the relation

$$\tau(x, z;t) = \eta \left(\frac{\partial w_e(x, z;t)}{\partial x} + \frac{\partial u_e(x, z;t)}{\partial z} \right) \,. \tag{4.6}$$

and integration of (4.3) leads, with the aid of the no-slip condition, to

$$p_e(x, D(x);t) - p_e(x, 0;t) = \int_{z=0}^{D(x)} \left(\eta \frac{\partial^2 w_e(x, z;t)}{\partial x^2} - \sigma \frac{dw_e(x, z;t)}{dt} \right) dz \,. \tag{4.7}$$

Both $u_e(x, 0;t)$ and $u_e(x, D(x);t)$ vanish because of the no-slip condition.
   Besides we note the identities

$$\frac{\partial \chi_B(x,t)}{\partial t} = w_e(x, 0;t) \,, \tag{4.8}$$

$$\frac{\partial \chi_R(x,t)}{\partial t} = w_e(x, D(x);t) \,. \tag{4.9}$$

From eqs. (4.4)–(4.9) the pressure difference $p_{st}-p_{sv}$ can be determined:

$$p_{st}(x;t) - p_{sv}(x;t) = m_B(x) \frac{\partial w_e(x, 0;t)}{\partial t} +$$

$$+ \sigma \int_{z=0}^{D(x)} \left(\frac{\partial w_e(x, z;t)}{\partial t} + u_e(x, z;t) \frac{\partial w_e(x, z;t)}{\partial x} + w_e(x, z;t) \frac{\partial w_e(x, z;t)}{\partial z} \right) dz +$$

$$+ m_R(x) \frac{\partial w_e(x, D(x);t)}{\partial t} + k_B(x) w_e(x, 0;t) - \eta \int_{z=0}^{D(x)} \frac{\partial^2 w_e(x, z;t)}{\partial x^2} dz +$$

$$+ k_R(x) w_e(x, D(x);t) + c_B(x) \int w_e(x, 0;t) dt + c_R(x) \int w_e(x, D(x);t) dt \,. \tag{4.10}$$

This is the alternative for the simple membrane equation (4.1). When the horizontal velocity u_e in the endolymph is equal to zero, it follows from (4.2) that $\partial w_e/\partial z = 0$, so that $w_e(x, z; t)$ is a function $w_e(x; t)$ of x and t only for all $z \in [0, D(x)]$. Then (4.10) would simplify to

$$p_{st}(x; t) - p_{sv}(x; t) = [m_B(x) + \sigma D(x) + m_R(x)] \frac{\partial w_e(x; t)}{\partial t} + [k_B(x) + k_R(x)] w_e(x; t) +$$

$$- \eta D(x) \frac{\partial^2 w_e(x; t)}{\partial x^2} + [c_B(x) + c_R(x)] \int w_e(x; t) dt . \qquad (4.11)$$

The principal difference with (4.1) lies in the term $\eta D(x) \partial^2 w_e(x; t)/\partial x^2$, by which the damping differs essentially from that in the membrane equation. The other terms match completely. Eq. (4.11) seems to be a better way of describing the behaviour of the scala media than eq. (4.1) in the case that the endolymph is assumed to move in the z-direction only.

To obtain an impression of the non-linearities within the partition we return to (4.10). The first three terms on the right-hand side refer to mass, the second set of three to resistance, and the last two to stiffness. Only one term is clearly non-linear, namely the second which represents the inertial force due to the mass of the endolymph. One term is essentially linear, *viz.* the fifth which represents the damping due to the internal friction of the endolymph. The other terms are linear only when the coefficients m, k and c are linear. Non-linearities in these quantities would imply that they are dependent on the velocity; this is very unlikely to be the case for m_B and m_R, whilst moreover these masses are negligible with respect to that of the endolymph.

The resistance of Reissner's membrane and of the basilar membrane are, though possibly non-linear, small as compared with the internal friction of the endolymph as a consequence of the viscosity [2, 4]. On account of this, the damping of the partition can be looked upon as linear.

Von Békésy [1, 2] has investigated the stiffness of the cochlear partition. He found that with increasing amplitude of vibration the stiffness also increases, whereas the phase difference between the stapes and the point of measurement decreases, that is, the wave length becomes larger, the maximum amplitude becomes less peaked and relatively smaller and the pattern of vibration is displaced towards the helicotrema. Thus the non-linear phenomena observed by Rhode [9] seem to be explained; Von Békésy, however, proved that the deviation from the linear character appears only with an amplitude of vibration which lies above the threshold of feeling in normal hearing. Hence the elasticity of the membrane cannot be a source of non-linear events.

The only non-linear term left after this inquiry is the second term on the right-hand side of equation (5.9). It is however obvious that the velocities u_e and w_e have the same order of magnitude; u_e is presumably even smaller on account of the no-slip condition on Reissner's membrane and on the basilar membrane. Consequently the order of magnitude of the non-linearity is at most the same as the similar one in the perilymph. Since the latter was shown to be negligible, we must conclude that the present one can be neglected also. It means that neither sources within the endolymph nor the mechanical properties (mass, resistance, stiffness) of the basilar membrane and Reissner's membrane contribute to the understanding of cochlear non-linearity.

5. Discussion and conclusions

In the foregoing we have investigated three kinds of non-linearities, namely sources within the perilymph, sources within the endolymph and the impedances of Reissner's membrane and the basilar membrane. None of them was found to be significant enough for a satisfactory ex-planation of the observed non-linearities. Hence the non-linear effects must have been elimin-ated by the simplifications that we made. Four of them were drastic enough to account for the elimination; they will be examined in the sequel.

First, it was assumed *a priori* that the spiral coiling can be dispensed with. Von Békésy [2]

states that this assumption is hardly open to doubt since the cochlea of several animals, as for instance the anteater, is practically uncoiled. Yet, we consider the assumption premature because, as far as known to the authors, the experiments from which the non-linear behaviour was found were carried out upon animals that do have a spiral coiled cochlea.

Second, we made the hypothesis that the impedances of the windows are linear, especially that of the oval window. To our knowledge this linearity has never been questioned before. It is however quite possible that the oval window impedance is a source of non-linearity. Therefore this quantity deserves more attention then it got so far.

Third, we supposed that Reissner's membrane and the basilar membrane can move in one direction only, *viz.* perpendicular to the basilar membrane. The principal motion of Reissner's membrane is of course perpendicular to the membrane itself, but the deviation caused by this can be neglected appositely because of the small variation in the height of the cochlear duct. The inferred assumption of rigidity of the membranes in their own planes can be defended by the fact that they are hinged (or possibly even clamped) at the edges to a bony shelf.

Fourth, the tectorial membrane, the haircells and the organ of Corti were ignored. The reason for this simplification was a purely mathematical one; it was not supported by any physical background.

Resuming we see that neither sources within the perilymph or the endolymph nor the impedance or motion in their own planes of Reissner's membrane and the basilar membrane are plausible explanations of the non-linear phenomena. Two of the remaining possible non-linear sources, the oval window impedance and the spiral coiling, are as yet insufficiently investigated. Therefore we cannot draw any conclusions concerning their significance. The last possibility has been investigated by Steele [11]. He suggests that the outer lip of the tectorial membrane is an important source of non-linearity. The reason is that the lip is very flexible while the central portion of the membrane is stiff. As a consequence of this a non-linear valving action takes place by which a directed flow of the sub-tectorial membrane fluid against the inner hair cells is established. In view of our results we endorse this suggestion.

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