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A two-dimensional model for the cochlea

I. The exact approach

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SUMMARY
A two-dimensional model for the cochlea is developed. An integral equation is derived that describes the pressure difference between the scalae. For the main quantity, the transmembrane pressure, an ordinary differential equation is obtained, which appears to be an improvement of the well-known Peterson-Bogert equation. The results are valid for all frequencies; an assumption of long or short wavelengths is not necessary at all.

1. Introduction

During a long period mathematical models of the cochlea have been basically one-dimensional [4, 7, 17, 18]. The reasons for this are obvious: the length of the cochlea, i.e. the distance from the windows to the helicotrema, is very large compared to the diameter of a scala (≈ 3.5 cm and ≈ 0.1 cm respectively), while the computations are substantially more simple in the one-dimensional case. The implication is the neglect of any other than axial particle velocity in the fluid. The deviations as a consequence of this simplification were assumed to be negligible. The authors showed [14] that this is correct for large values of the partition impedance, which corresponds with low frequencies of the input signal. For high frequencies the one-dimensional model is inaccurate; then the cross-sectional dimensions are no longer small in comparison with the length of the generated waves.

Ranke is the only investigator who developed short-wave theories. In the summary of his work [9] he also discussed the difficulty of an analysis of the three-dimensional fluid interaction with the basilar membrane.

Only recently attention was drawn to more-dimensional models. Steele [13] designed a three-dimensional model of which the scala walls are tapered and used the taper angle as a small parameter for an asymptotic expansion of perilymph and basilar membrane motion. The main feature of his model however, is the independent motion of the arches of Corti and the remaining portion of the basilar membrane. He obtains results in both short-wave and long-wave regions. Lesser and Berkley [6] and very recently Siebert [11] and Van Dijk [3] set up two-dimensional models using a method somewhat similar to the one we will outline in the sequel. The purpose of our work was to develop a two-dimensional model and to compare the results with those of one-dimensional models. In the appendix, it is shown that the neglect of variations in the direction along the width of the membrane does not alter the character of the solution, whereas the neglect of variations in the direction perpendicular to the partition causes essential deviations of the exact solution. This explains why we chose for a two-dimensional model.

2. The model

Peterson and Bogert [2, 7] designed a model for the cochlea, against which one of the main objections is that the vertical particle velocity in the perilymph (that is, the velocity component in the direction of the membrane deflection) is neglected. In the introduction it was stated already that this can be a good approximation only for long waves; these occur in the cochlea for frequencies < 1 kHz (see [13]). For high frequencies the one-dimensional approach is inadequate.

We have made an attempt to meet this objection by means of a two-dimensional model in which the axial and vertical directions are taken into account. Variations in the third direction, that along the width of the membrane, are likely to be small and besides of little interest to the motion of the partition, in which we are above all interested.

In this work we confine ourselves to linear phenomena; the driving forces and the resulting responses are taken to be so small that non-linear effects are excluded. In addition three *a priori* assumptions are introduced: the spiral coiling can be dispensed with, the scalae walls are rigid and all parts of the scala media (Reissner's membrane, endolymph, tectorial membrane, organ of Corti, basilar membrane) move in unison. The reasonableness of these hypotheses is shown by Von Békésy [1], although especially the third is open to doubt in our opinion (*cf.* [13, 15]). Two minor simplifications are made; their principal importance lies in the facilitation of the calculations. First, the heights of the scalae are taken to be equal and constant, which according to Wever [16] is correct in relation to the other, rapidly varying, quantities except at the basal end; second, the cochlea is extended to infinity, as has been done before by Klatt and Peterson [4]. Then the cochlea can be represented by Fig. 1.

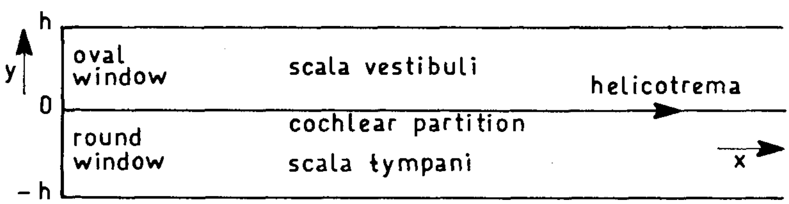

Fig. 1.

The fluid is considered to be incompressible and inviscid. The former assumption is correct except for frequencies over about 10 kHz, the latter has a small weight as to membrane motion, though it could affect considerably the creation of vortices in the perilymph near the point of maximum membrane amplitude [14]. We will pay attention to the compressibility and to the viscosity in a later paper.

Let x and y be the axial and vertical coordinate respectively ($x=0$ at the windows, $y=0$ at the partition, $y=\pm h$ at the walls); t is the time variable. Denote by $\tilde{p}(x, y;\ t)$ and $\tilde{\boldsymbol{v}}(x, y;\ t)$ the pressure and the velocity in the perilymph and by ρ its density. In view of the foregoing the continuity equation reads

$$\nabla\cdot\tilde{\boldsymbol{v}}=0\,, \tag{2.1}$$

and the equation of motion is given by

$$\rho\,\tilde{\boldsymbol{v}}_t+\nabla\tilde{p}=\boldsymbol{0}\,. \tag{2.2}$$

Subscripts denote partial differentiation with respect to the variable involved. We take into account only harmonic oscillations of the input signal of frequency $\omega/2\pi$. Thus we set

$$\tilde{\boldsymbol{v}}(x, y;\ t)=\boldsymbol{v}(x, y)\mathrm{e}^{i\omega t}\,, \tag{2.3}$$

$$\tilde{p}(x, y;\ t)=p(x, y)\mathrm{e}^{i\omega t}\,. \tag{2.4}$$

Our main interest is the displacement of the partition. Hence we define the difference pressure P by

$$P(x, y)=p^{\mathrm{st}}(x, -y)-p^{\mathrm{sv}}(x, y)\,, \qquad (y>0) \tag{2.5}$$

in which the indices st and sv stand for scala tympani and scala vestibuli respectively. It can be deduced from (2.1)–(2.5) that

$$P_{xx}(x, y) + P_{yy}(x, y) = 0\,. \tag{2.6}$$

Since $P(x, y)$ is defined for $y>0$, we can confine ourselves to look upon the scala vestibuli; it is represented as an infinite strip in the z-plane (Fig. 2), when $z=x+jy$ is a complex variable. We emphasize the difference between i- and j-complex.

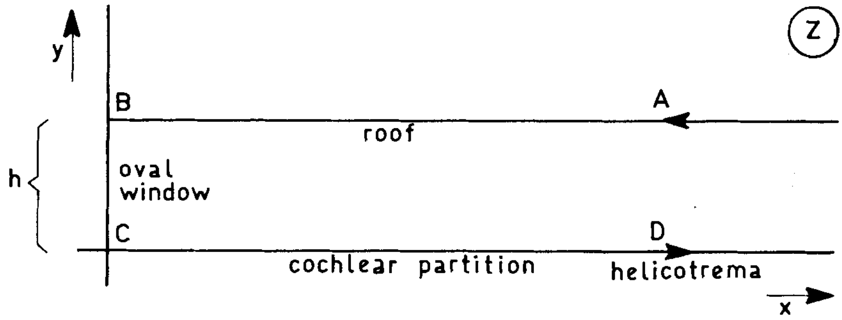

Fig. 2.

The next step is the determination of the boundary conditions for eq. (2.6). The first is found from the vanishing of the y-component of the velocity on the roof. With the aid of (2.2), (2.4) and (2.5), this leads to

$$P_y(x, h) = 0\,. \tag{2.7}$$

The window condition can be given in various forms. Mostly the difference pressure $P(0, y)$ just inside the cochlea is prescribed, sometimes its normal derivative $P_x(0, y)$, which is proportial to the axial difference velocity, or the ratio between $P(0, y)$ and $P_x(0, y)$. These conditions are afflicted with the objection that they are all unrealistic; better, if less easy to acquire, would be a relation between the pressure difference across the windows and the axial difference velocity at $x=0$. The difficulty here is that we want to avoid the appearance in the equations of any other pressure than $P(x, y)$. To this end we set that the stapes exerts a pressure $p_s(y)$ upon the oval window; knowing that the middle ear does not exert a pressure upon the round window, we see that $p_s(y)$ is the middle-ear analogue for $P(0, y)$. Hence we find for the equilibrium at the windows

$$p_s(y) - P(0, y) = Z(y)\,P_x(0, y)\,, \tag{2.8}$$

where $Z(y)$ is the difference impedance of the windows. It cannot be expressed in terms of the distinct impedances of oval and round window, unless these are equal. In that case $Z(y)$ is equal to both impedances. When $Z(y)$ cannot be ascertained, we use the alternative window condition

$$P_x(0, y) = f(y)\,, \tag{2.8.a}$$

where $f(y)$ is a known function. The physical interpretation of this is that the axial difference velocity at $x=0$ is prescribed.

The boundary condition at the partition has the same form as (2.8). It is assumed that the membrane moves only as a result of the pressure difference between the scalae. When $\tilde{w}(x, t)$ is the membrane velocity and $m(x)$, $k(x)$ and $c(x)$ are mass, resistance and stiffness of the membrane per unit area, we obtain

$$P(x, 0) = m(x)\,\tilde{w}_t(x, t) + k(x)\,\tilde{w}(x, t) + c(x) \int \tilde{w}(x, t)\,dt\,. \tag{2.9}$$

The following relation holds, since only harmonic oscillations are considered:

$$\tilde{w}(x, t) = w(x)e^{i\omega t}. \quad (2.10)$$

With the help of (2.10) and the relation between $w(x)$ and $P_y(x, 0)$, eq. (2.9) can be written as

$$2P(x, 0) + \zeta(x)P_y(x, 0) = 0. \quad (2.11)$$

Here $\zeta(x)$ is the impedance of the cochlear partition:

$$\zeta(x) = [c(x) - \omega^2 m(x) + i\omega k(x)]/(\rho\omega^2). \quad (2.12)$$

Finally, we have the condition

$$\lim_{x\to\infty} P(x, 0) = 0, \quad (2.13)$$

for, at the helicotrema all static pressure variations are equalized because of the direct contact between the scalae.

Summarizing, we have to find a function $P(x, y)$, harmonic in the interior of an infinite strip in the complex z-plane, and satisfying the conditions (2.7), (2.8), (2.11) and (2.13). The solution of this problem can be found easily with the method of separation of variables, as has been done in [14]. A necessary condition for the existence of this solution is, however, that the impedance of the cochlear partition, given by (2.12), is independent of the axial coordinate x. Since this would be a far too drastic simplification, we try to tackle the problem in such a way that this restriction can be avoided. To this end the region in the z-plane is mapped conformally on to the upper half of a w-plane ($w = u + jv$) such that the boundary of the strip is mapped into the u-axis (see Fig. 3). The primed points A′, B′, C′, D′ correspond to the unprimed A, B, C, D in Fig. 2.

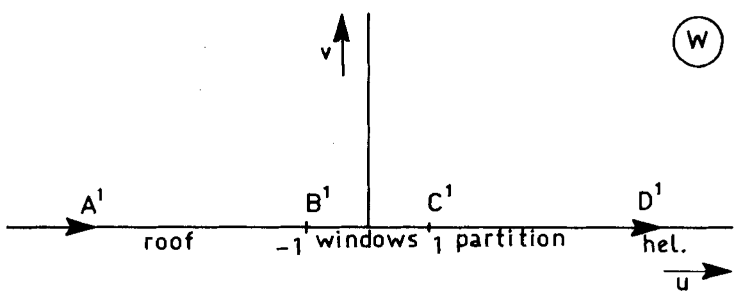

Fig. 3.

The required transformation is

$$w = \cosh(\pi z/h), \quad (2.14)$$

with the inverse transformation

$$z = h/\pi \operatorname{arccosh} w = h/\pi \ln(w + (w^2 - 1)^{\frac{1}{2}}). \quad (2.15)$$

The branch of the logarithm is determined by $z = 0$ when $w = 1$, that of the square root by $(w^2 - 1)^{\frac{1}{2}} > 0$ when w is real, $w > 1$.

Denote the image of $P(x, y)$ in the w-plane by $Q(u, v)$. The conditions that Q must satisfy are derived by straightforward calculations from (2.7), (2.8), (2.11) and (2.13). Herewith are employed the relations

$$P_x = Q_u u_x + Q_v v_x, \qquad P_y = Q_u u_y + Q_v v_y, \quad (2.16)$$

together with the expressions for u and v that can be deduced from (2.14):

$$u = \cosh(\pi x/h)\cos(\pi y/h), \qquad v = \sinh(\pi x/h)\sin(\pi y/h). \quad (2.17)$$

Setting that $p_s(y)$, $Z(y)$ and $\zeta(x)$ are transformed into $\chi(u)$, $\eta(u)$ and $\psi(u)$, the problem can be formulated as follows: To find a function $Q(u, v)$, harmonic in the upper half of the w-plane with the exception of the real axis and satisfying on this axis the conditions

$$Q_v = 0\,, \qquad -\infty < u < -1\,, \tag{2.18}$$

$$Q_v + \frac{hQ}{\pi(1-u^2)^{\frac{1}{2}}\eta} = \frac{h\chi}{\pi(1-u^2)^{\frac{1}{2}}\eta}\,, \qquad -1 < u < 1\,, \tag{2.19}$$

$$Q_v + \frac{2hQ}{\pi(u^2-1)^{\frac{1}{2}}\psi} = 0\,, \qquad 1 < u < \infty\,, \tag{2.20}$$

$$Q = 0\,, \qquad u \to \infty\,. \tag{2.21}$$

We impose on $\psi(u)$ the restriction that (2.21) is automatically satisfied when (2.20) is satisfied. Then we have a mixed boundary value problem for the real axis, since (2.18)–(2.21) pass into

$$Q_v(u, 0) + a(u)Q(u, 0) = b(u)\,, \tag{2.22}$$

with $\alpha(u)$ and $b(u)$ piecewise continuous functions, which are indeterminate in the isolated points $u = -1$ and $u = 1$ only.

The solution of the problem can be expressed in the form of a logarithmic potential [8]

$$Q(u, v) = -\int_{-\infty}^{\infty} F(\sigma)\ln|u-\sigma+jv|\,d\sigma\,,^{\star} \tag{2.23}$$

where $F(\sigma)$ is a real-valued function of σ that satisfies the integral equation

$$-\pi F(\sigma) - \int_{-\infty}^{\infty} a(\sigma)F(t)\ln|\sigma-t|\,dt = b(\sigma)\,. \tag{2.24}$$

For, consider $Q(u, v)$ as the real part of a complex function $\Omega(w)$:

$$\Omega(w) = -\int_{-\infty}^{\infty} F(\sigma)\ln(w-\sigma)\,d\sigma\,. \tag{2.25}$$

Its derivative with respect to w reads

$$\frac{d\Omega}{dw} = -\int_{-\infty}^{\infty} \frac{F(\sigma)}{w-\sigma}\,d\sigma\,, \tag{2.26}$$

from which we get

$$\frac{\partial Q}{\partial v} = -\operatorname{im}\frac{d\Omega}{dw} = -\int_{-\infty}^{\infty} \frac{vF(\sigma)}{(u-\sigma)^2+v^2}\,d\sigma\,. \tag{2.27}$$

When F satisfies the rather weak restriction

$$\int_{-\infty}^{\infty} \frac{|F(\sigma)|}{1+|\sigma|}\,d\sigma < +\infty\,, \tag{2.28}$$

it holds that, for any continuity point u of F (see [5]),

$$F(u) = \operatorname*{Lim}_{v\to 0} \frac{v}{\pi}\int_{-\infty}^{\infty} \frac{F(\sigma)}{(u-\sigma)^2+v^2}\,d\sigma\,, \tag{2.29}$$

which, substituted in (2.27) gives

$$Q_v(u, 0) = -\pi F(u)\,, \tag{2.30}$$

again for any continuity point of F.

Insertion of (2.30) and (2.23) into (2.22) leads to (2.24).

⋆ The integrals in this section are to be viewed upon as principal value integrals, when there is a singularity on the path of integration.

We are interested in the values of Q at the window and especially at the cochlear partition. The values of the pressure and the velocity in the interior of the fluid are less important. The determination of the interior values encounters, however, no insurmountable difficulties and can therefore be done, if required.

Now eqs. (2.23) and (2.24) can be combined into

$$\pi F(u) = a(u)Q(u,0) - b(u)\,, \tag{2.31}$$

leaving the integral equation

$$Q(u,0) = -\frac{1}{\pi}\int_{-\infty}^{\infty} [a(\sigma)Q(\sigma,0) - b(\sigma)]\ln|u-\sigma|\,d\sigma \tag{2.32}$$

Substituting the values of $a(\sigma)$ and $b(\sigma)$ at the distinct intervals, we arrive at

$$Q(u,0) = -\frac{h}{\pi^2}\int_{-1}^{1}\frac{Q(\sigma,0)-\chi(\sigma)}{(1-\sigma^2)^{\frac{1}{2}}\eta(\sigma)}\ln|u-\sigma|\,d\sigma - \frac{2h}{\pi^2}\int_{1}^{\infty}\frac{Q(\sigma,0)\ln|u-\sigma|}{(\sigma^2-1)^{\frac{1}{2}}\psi(\sigma)}\,d\sigma \tag{2.33}$$

Returning to the original coordinates and noting that

$$Q(\cosh(\pi x/h), 0) = P(x,0)\,, \tag{2.34}$$
$$Q(\cos(\pi y/h), 0) = P(0,y)\,, \tag{2.35}$$
$$\psi(\cosh(\pi x/h)) = \zeta(x)\,, \tag{2.36}$$
$$\chi(\cos(\pi y/h)) = p_s(y)\,, \tag{2.37}$$
$$\eta(\cos(\pi y/h)) = Z(y)\,, \tag{2.38}$$

we obtain the integral equations

$$P(0,y) = \frac{1}{\pi}\int_{\alpha=0}^{h}\frac{p_s(\alpha)-P(0,\alpha)}{Z(\alpha)}\ln|\cos(\pi y/h)-\cos(\pi\alpha/h)|\,d\alpha + $$
$$-\frac{2}{\pi}\int_{\beta=0}^{\infty}\frac{P(\beta,0)}{\zeta(\beta)}\ln(\cosh(\pi\beta/h)-\cos(\pi y/h))\,d\beta\,, \tag{2.39}$$
$$P(x,0) = \frac{1}{\pi}\int_{\alpha=0}^{h}\frac{p_s(\alpha)-P(0,\alpha)}{Z(\alpha)}\ln(\cosh(\pi x/h)-\cos(\pi\alpha/h))\,d\alpha + $$
$$-\frac{2}{\pi}\int_{\beta=0}^{\infty}\frac{P(\beta,0)}{\zeta(\beta)}\ln|\cosh(\pi x/h)-\cosh(\pi\beta/h)|\,d\beta\,. \tag{2.40}$$

From eqs. (2.39) and (2.40) the pressure difference along the windows and the basilar membrane can be solved. The singularities in the integrals are logarithmic and hence present no great difficulties in the calculations. When it is impossible to determine $Z(y)$, (2.8.a) is used instead of (2.8); then $[p_s(\alpha)-P(0,\alpha)]/Z(\alpha)$ must be replaced by $f(\alpha)$ in both (2.39) and (2.40).

3. Comparison with a one-dimensional model

In this section we will investigate whether the described two-dimensional approach leads to an improvement of the well-known one-dimensional models. First off it is clear that the values of the pressure difference along the windows and in the interior of the fluid will be more realistic than the corresponding values in the one-dimensional case, where uniformity of all quantities over the cross-section of the scalae has been assumed. Our main interest, however, is the motion of the basilar membrane. To make a comparison with the one-dimensional models, we try to derive an ordinary differential equation for the variable $P(x,0)$ from (2.40).

We set

$$I_1 = \frac{1}{\pi}\int_{\alpha=0}^{h} \frac{p_s(\alpha)-P(0,\alpha)}{Z(\alpha)} \ln(\cosh(\pi x/h)-\cos(\pi\alpha/h))\,d\alpha\,, \tag{3.1}$$

$$I_2 = -\frac{2}{\pi}\int_{\beta=0}^{\infty} \frac{P(\beta,0)}{\zeta(\beta)} \ln|\cosh(\pi x/h)-\cosh(\pi\beta/h)|\,d\beta\,. \tag{3.2}$$

We differentiate I_1 twice with respect to x and find for $x\neq 0$

$$\frac{d^2 I_1}{dx^2} = \frac{\pi}{h^2}\int_{\alpha=0}^{h} \frac{p_s(\alpha)-P(0,\alpha)}{Z(\alpha)} \cdot \frac{1-\cosh(\pi x/h)\cos(\pi\alpha/h)}{[\cosh(\pi x/h)-\cos(\pi\alpha/h)]^2}\,d\alpha\,, \tag{3.3}$$

so that

$$\frac{d^2 I_1}{dx^2} = O(\mathrm{e}^{-\pi x/h}) \quad \text{as} \quad x\to\infty\,. \tag{3.4}$$

Besides we find

$$I_2 = -\frac{2}{\pi}\int_{\beta=0}^{\infty} \frac{P(\beta,0)}{\zeta(\beta)}\left[\ln 2+\ln\left\{\sinh\frac{\pi}{2h}(x+\beta)\right\}+\ln\left\{\sinh\frac{\pi}{2h}|x-\beta|\right\}\right]d\beta =$$

$$= -\frac{2}{\pi}\int_{\beta=0}^{\infty} \frac{P(\beta,0)}{\zeta(\beta)}\left[-\ln 2+\frac{\pi}{2h}(x+\beta)+\ln(1-\mathrm{e}^{-\pi(x+\beta)/h})+\frac{\pi}{2h}|x-\beta|+\right.$$

$$\left.+\ln(1-\mathrm{e}^{-\pi|x-\beta|/h})\right]d\beta\,, \tag{3.5}$$

from which it can be derived that

$$\frac{d^2 I_2}{dx^2} = \frac{-2P(x,0)}{h\zeta(x)} - \frac{2}{\pi}\frac{d^2}{dx^2}\left\{\int_{\beta=0}^{\infty}\frac{P(\beta,0)}{\zeta(\beta)}\ln(1-\mathrm{e}^{-\pi|x-\beta|/h})\,d\beta\right\}+O(\mathrm{e}^{-\pi x/h})\,. \tag{3.6}$$

We consider the integral

$$I_3 = \int_{\beta=0}^{\infty}\frac{P(\beta,0)}{\zeta(\beta)}\ln(1-\mathrm{e}^{-\pi|x-\beta|/h})\,d\beta\,. \tag{3.7}$$

By means of the substitution $\beta=h\gamma/\pi+x$, and writing $w(x)$ instead of $P(x,0)/\zeta(x)$, we get

$$I_3 = \frac{h}{\pi}\int_{\gamma=-\pi x/h}^{\infty} w(x+h\gamma/\pi)\ln(1-\mathrm{e}^{-|\gamma|})\,d\gamma$$

$$= \frac{h}{\pi}\int_{\gamma=0}^{\pi x/h} w(x-h\gamma/\pi)\ln(1-\mathrm{e}^{-\gamma})\,d\gamma + \frac{h}{\pi}\int_{\gamma=0}^{\infty} w(x+h\gamma/\pi)\ln(1-\mathrm{e}^{-\gamma})\,d\gamma\,. \tag{3.8}$$

We expand $w(x-h\gamma/\pi)$ and $w(x+h\gamma/\pi)$ in a truncated Taylor series around x:

$$I_3 = \frac{h}{\pi}w(x)\left\{\int_{\gamma=0}^{\pi x/h}\ln(1-\mathrm{e}^{-\gamma})\,d\gamma + \int_{\gamma=0}^{\infty}\ln(1-\mathrm{e}^{-\gamma})\,d\gamma\right\} +$$

$$+\frac{h^3}{2\pi^3}\int_{\gamma=0}^{\pi x/h} w_{xx}(x-h\vartheta_1\gamma/\pi)\,\gamma^2\ln(1-\mathrm{e}^{-\gamma})\,d\gamma$$

$$+\frac{h^3}{2\pi^3}\int_{\gamma=0}^{\infty} w_{xx}(x+h\vartheta_2\gamma/\pi)\,\gamma^2\ln(1-\mathrm{e}^{-\gamma})\,d\gamma \qquad (0<\vartheta_1<1\,,\ 0<\vartheta_2<1)\,. \tag{3.9}$$

Since (see a.o. [10, 12])

$$\int_{\gamma=0}^{\infty}\ln(1-\mathrm{e}^{-\gamma})\,d\gamma = \int_{\vartheta=0}^{1}\frac{\ln(1-\vartheta)}{\vartheta}\,d\vartheta = -\frac{\pi^2}{6}, \tag{3.10}$$

eq. (3.9) can be written as

$$I_3 = -\tfrac{1}{3}h\pi w(x) + \frac{h^3}{2\pi^3}\left[\int_{\gamma=0}^{\pi x/h} w_{xx}(x-h\vartheta_1\gamma/\pi)\gamma^2 \ln(1-e^{-\gamma})d\gamma + \right.$$

$$\left. + \int_{\gamma=0}^{\infty} w_{xx}(x+h\vartheta_2\gamma/\pi)\gamma^2 \ln(1-e^{-\gamma})d\gamma\right] + O(e^{-\pi x/h}). \tag{3.11}$$

Hence, eq. (3.6) simplifies to

$$\frac{d^2 I_2}{dx^2} = -\frac{2}{h}w(x) + \frac{2h}{3}w_{xx}(x) - \frac{h^3}{\pi^4}\left[\int_{\gamma=0}^{\pi x/h} w_{xxxx}(x-h\vartheta_1\gamma/\pi)\gamma^2 \ln(1-e^{-\gamma})d\gamma + \right.$$

$$\left. + \int_{\gamma=0}^{\infty} w_{xxxx}(x+h\vartheta_2\gamma/\pi)\gamma^2 \ln(1-e^{-\gamma})d\gamma\right] + O(e^{-\pi x/h}). \tag{3.12}$$

Using (3.4) and (3.12) we can replace (2.40) by

$$hP_{xx}(x,0) + 2w(x) - \tfrac{2}{3}h^2 w_{xx}(x) + O(e^{-\pi x/h}) =$$

$$= \frac{h^4}{\pi^4}\left[-\int_{\gamma=0}^{\pi x/h} w_{xxxx}(x-h\vartheta_1\gamma/\pi)\gamma^2 \ln(1-e^{-\gamma})d\gamma\right.$$

$$\left. - \int_{\gamma=0}^{\infty} w_{xxxx}(x+h\vartheta_2\gamma/\pi)\gamma^2 \ln(1-e^{-\gamma})d\gamma\right]. \tag{3.13}$$

The right hand side is majorized by

$$\frac{h^4}{\pi^4}\left| \max_{\substack{0<\vartheta_1<1 \\ 0\leq\gamma\leq\pi x/h}} w_{xxxx}(x-h\vartheta_1\gamma/\pi)\int_{\gamma=0}^{\pi x/h} \gamma^2 \ln(1-e^{-\gamma})d\gamma + \right.$$

$$\left. + \max_{\substack{0<\vartheta_2<1 \\ 0\leq\gamma<\infty}} w_{xxxx}(x+h\vartheta_2\gamma/\pi)\int_{\gamma=0}^{\infty} \gamma^2 \ln(1-e^{-\gamma})d\gamma\right| \leq$$

$$\leq \frac{2h^4}{\pi^4}\left| \max_{0\leq\xi<\infty} w_{xxxx}(\xi)\int_{\gamma=0}^{\infty} \gamma^2 \ln(1-e^{-\gamma})d\gamma\right| + O(e^{-\pi x/h}) \tag{3.14}$$

We compute the integral in (3.14) by partial integration:

$$\int_{\gamma=0}^{\infty} \gamma^2 \ln(1-e^{-\gamma})d\gamma = \tfrac{1}{3}\gamma^3 \ln(1-e^{-\gamma})\Big|_{\gamma=0}^{\infty} - \tfrac{1}{3}\int_{\gamma=0}^{\infty} \frac{\gamma^3}{e^{\gamma}-1}d\gamma. \tag{3.15}$$

The integral in the right hand side is equal to $\pi^4/15$ (*cf.* [10, 12]), so we find

$$\int_{\gamma=0}^{\infty} \gamma^2 \ln(1-e^{-\gamma})d\gamma = -\frac{\pi^4}{45}. \tag{3.16}$$

Substitution of (3.16) in (3.14) makes clear that the right hand side of (3.13) is majorized by $2h^4 A/45 + O(e^{-\pi x/h})$, where

$$A = \left| \max_{0 \leq \xi < \infty} w_{xxxx}(\xi) \right| .$$

For large x, $O(e^{-\pi x/h})$ is negligible. Moreover we assume that A is bounded. Because $|w(x)|$ is bounded (it is proportional to the magnitude of the membrane velocity) and h is small ($\simeq 0.1$ cm), it seems reasonable to neglect the right hand side of (3.13). Writing $p(x)$ for $P(x, 0)$, we arrive at

$$hp_{xx} + 2p/\zeta - \tfrac{2}{3}h^2(p/\zeta)_{xx} = 0 . \tag{3.17}$$

It is not possible to prove that the neglect of the right hand side of (3.13) is correct. We can, however, compute $w(x)$ numerically from (3.17) and check if $w_{xxxx}(x)$, thus obtained, does not contradict our hypothesis.* The differential equation (3.17) holds good for large x, viz. for $x \geq kh$ with $k \simeq 2$. It requires two boundary conditions to be solved. The first is, in accordance with (2.13):

$$\operatorname*{Lim}_{x \to \infty} p(x) = 0 . \tag{3.18}$$

Another condition for the difference pressure cannot be found for $x \to \infty$, so that the second boundary value must be given at $x = 0$, where (3.17) is not valid. It can be expected that the average pressure plays an important role in the pressure distribution. In fact all one-dimensional models are based on the uniformity of the pressure over a cross-section of a scala. Therefore, to get an insight in the nature of the boundary condition at $x = 0$, we compute

$$\overline{P(0, y)} = h^{-1} \int_0^h P(0, y)dy$$

from (2.39). The result is:

$$\overline{P(0, y)} = -\frac{\ln 2}{\pi} \int_{\alpha=0}^{h} \frac{p_s(\alpha) - P(0, \alpha)}{Z(\alpha)} d\alpha + 2 \int_{\beta=0}^{\infty} \left(\frac{\ln 2}{\pi} - \frac{\beta}{h} \right) w(\beta) d\beta , \tag{3.19}$$

where $w(\beta)$ is written instead of $P(\beta, 0)/\zeta(\beta)$.

We try to obtain the required boundary condition for (3.17) at $x = 0$ directly from (2.40). With the help of (3.5) and (3.12), eq. (2.40) changes into

$$\begin{aligned} P(x, 0) &= \frac{1}{\pi} \int_{\alpha=0}^{h} \frac{p_s(\alpha) - P(0, \alpha)}{Z(\alpha)} (-\ln 2 + \pi x/h) d\alpha \\ &\quad - \frac{2}{\pi} \int_{\beta=0}^{\infty} w(\beta)(-\ln 2 + \pi x/h + \ln|1 - e^{\pi(\beta - x)/h}|) d\beta + O(e^{-\pi x/h}) \\ &= \frac{1}{\pi} \int_{\beta=0}^{h} \frac{p_s(\alpha) - P(0, \alpha)}{Z(\alpha)} (-\ln 2 + \pi x/h) d\alpha - \frac{2}{h} \int_{\beta=x}^{\infty} (\beta - x) w(\beta) d\beta + \\ &\quad - \frac{2}{\pi} \int_{\beta=0}^{\infty} (-\ln 2 + \pi x/h) w(\beta) d\beta + \frac{2h}{3} w(x) + O(h^3 w_{xx}) + O(e^{-\pi x/h}) . \end{aligned} \tag{3.20}$$

We neglect $O(h^3 w_{xx}) + O(e^{-\pi x/h})$. Since the same neglects were made in the derivation of (3.17) and since moreover the remaining part of the right hand side in (3.20) satisfies (3.17), the sought boundary value $p(0)$ for (3.17) is equal to this part of $P(0, 0)$:

$$\begin{aligned} p(0) &= -\frac{\ln 2}{\pi} \int_{\alpha=0}^{h} \frac{p_s(\alpha) - P(0, \alpha)}{Z(\alpha)} d\alpha + \\ &\quad + 2 \int_{\beta=0}^{\infty} \left(\frac{\ln 2}{\pi} - \frac{\beta}{h} \right) w(\beta) d\beta + \frac{2h}{3} w(0) . \end{aligned} \tag{3.21}$$

* Preliminary numerical results justify our assumption.

Using (3.19) we get

$$p(0) = \frac{\overline{P(0, y)}}{1 - 2h/(3\zeta(0))}. \tag{3.22}$$

The Peterson–Bogert equation for a cochlea with constant scala height is [7]:

$$hp_{xx} + 2p/\zeta = 0\,, \tag{3.23}$$

which corresponds with (3.17), when we ignore $O(h^3 w_{xx})$ in that equation.

The first boundary condition for eq. (3.23) is (3.18); in the same way as above it is found that the other condition must read

$$p(0) = \overline{P(0, y)}\,. \tag{3.24}$$

This could be expected since the main hypothesis of the Peterson–Bogert model is the uniformity of the pressure over the cross-section of the scalae. It has been proved here that the model, up to its degree of accuracy, is consistent with the two-dimensional theory.

In the foregoing we assumed that the difference pressure $P(0, y)$ at the basal end is known. In Section 2, however, the window condition (2.8) was used with the alternative (2.8.a). The meaning of the latter condition is that $P_x(0, y)$ is prescribed, that of the former that there exists a given relation between $P(0, y)$ and $P_x(0, y)$. Eq. (2.8.a) can be translated in a condition for (3.17) easily; from (2.40) it follows that

$$P_x(x, 0) = \frac{1}{h}\int_{\alpha=0}^{h} P_x(0, \alpha)\frac{\sinh(\pi x/h)\,d\alpha}{\cosh(\pi x/h) - \cos(\pi\alpha/h)} - \frac{2}{h}\int_{\beta=0}^{\infty} w(\beta)\frac{\sinh(\pi x/h)\,d\beta}{\cosh(\pi x/h) - \cosh(\pi\beta/h)}$$

$$= \overline{P_x(0, y)} + \frac{dI_2}{dx} + O(\mathrm{e}^{-\pi x/h})\,. \tag{3.25}$$

From (3.5) it is found that

$$\frac{dI_2}{dx} = -\frac{1}{h}\int_{\beta=0}^{\infty} w(\beta)d\beta - \frac{1}{h}\int_{\beta=0}^{x} w(\beta)d\beta + \frac{1}{h}\int_{\beta=x}^{\infty} w(\beta)d\beta - \frac{2}{\pi}\frac{dI_3}{dx} + O(\mathrm{e}^{-\pi x/h}) \tag{3.26}$$

with I_3 defined in (3.7). With the same neglects as made in the derivation of (3.17), we arrive at

$$P_x(x, 0) = \overline{P_x(0, y)} - \frac{1}{h}\int_{\beta=0}^{\infty} w(\beta)d\beta - \frac{1}{h}\int_{\beta=0}^{x} w(\beta)d\beta + \frac{1}{h}\int_{\beta=x}^{\infty} w(\beta)d\beta + \frac{2h}{3}w_x(X)\,. \tag{3.27}$$

Now $p(0)$ is equal to $P(0, 0)$ and $p_x(0)$ to $P_x(0, 0)$, on the same grounds as used before in this section:

$$p_x(0) = \overline{P_x(0, y)} + \frac{2h}{3}(p/\zeta)_x|_{x=0}\,, \tag{3.28}$$

or, written elsewise

$$\left(1 - \frac{2h}{3\zeta(0)}\right)p_x(0) + \frac{2h\zeta_x(0)}{3\zeta^2(0)}p(0) = \overline{P_x(0, y)}\,. \tag{3.29}$$

When (2.8) is used, we can obtain a condition analogous to (3.29) only when $Z(y)$ is a constant. In that case (2.8) gives

$$\overline{p_s(y)} - \overline{P(0, y)} = Z\,\overline{P_x(0, y)}\,, \tag{3.30}$$

so that we have, utilizing (3.22) and (3.29):

$$\overline{p_s(y)} - \left(1 - \frac{2h}{3\zeta(0)}\right)p(0) = Z\left[\left(1 - \frac{2h}{3\zeta(0)}\right)p_x(0) + \frac{2h\zeta_x(0)}{3\zeta^2(0)}p(0)\right]. \tag{3.31}$$

The corresponding boundary conditions for (3.23) are

$$\overline{p_s(y)} - p(0) = Zp_x(0)\,, \tag{3.32}$$

when (2.8) is used, and

$$p_x(0) = \overline{P_x(0, y)}\,, \tag{3.33}$$

when (2.8.a) is used.

Now we have obtained the desired conditions for the ordinary differential equations as a function of the prescribed conditions in the two-dimensional case. We emphasize that both eqs. (3.17) and (3.23) have, apart from the error of $O(h^2P/\zeta)$ and $O(h^4(P/\zeta)_{xx})$ respectively, an inaccuracy of $O(e^{-\pi x/h})$. Consequently neither equation describes the pressure adequately in the immediate vicinity ($\simeq 2$ mm) of the windows. This is no limitation of the solution really, since the model itself does not represent the cochlea adequately at the basal end. There the assumption of equal and constant scala heights is not valid, as was stated already in Section 2. Fortunately this area is relatively unimportant from a physical point of view.

4. Discussion, conclusions and introduction to part II

We have developed a two-dimensional model for the cochlea; the dimension along the width of the membrane was not taken into account. Two fairly simple integral equations, (2.39) and (2.40), were obtained. We did not solve these equations numerically, but proceeded analytically and found that the integral equations led to a second order ordinary differential equation for the transmembrane pressure, viz. (3.17). This equation is shown to be more accurate than the Peterson–Bogert equation (3.23), which can be considered as representative for one-dimensional models. The agreement as well as the difference between the two equations are clear immediately when (3.17) is written in a different form:

$$h\left[\left(1 - \frac{2h}{3\zeta}\right)p\right]_{xx} + 2p/\zeta = 0 \tag{4.1}$$

We see that the equations (3.23) and (4.1) coincide for small values of $|h/\zeta|$, whereas the difference becomes significant when $|h/\zeta| = O(1)$. This result corresponds completely with the statement made in [14].

It is important to know that for frequencies > 500 Hz the modulus of ζ is of order h in the region of maximum membrane amplitude, and for frequencies over 10 kHz in the entire cochlea.

It is noteworthy that the results of our model are valid for all frequencies, so that no longer a short-wave or a long-wave approximation is required. An increased accuracy can be obtained by retaining more terms in the Taylor series in (3.9). Yet this is not advisable, since it would lead to an insignificant gain in accuracy at the cost of an increased order of the differential equation and consequently more boundary conditions. We will return to this subject in part II.

In this first part the exact approach of the two-dimensional model was outlined. In the second part we will describe a heuristic approach which is somewhat less rigorous than the exact one, but leads faster to the same results.

We will also give the results of the numerical calculations of eqs. (3.17) and (3.23). Besides, the model will be extended in various ways. First, a variable scala height is considered; second, the compressibility and the viscosity are taken into account. Finally, further possible extensions will be discussed such as replacement of the membrane by a plate, which seems to be more realistic, and extension to a three-dimensional model.

Appendix

We introduce a simplified representation of the cochlea, namely a parallelepiped bisected by a membrane, the cochlear partition.

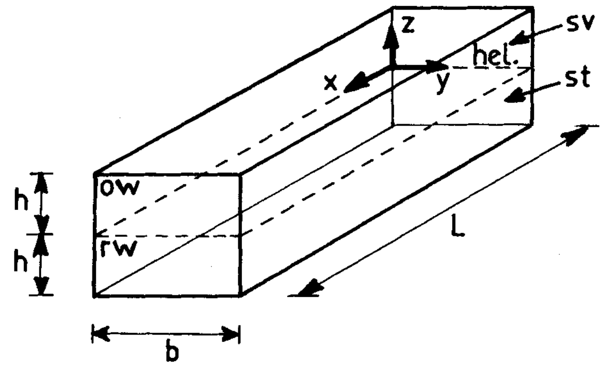

Fig. 4.

The rectangular coordinate system is chosen in such a way that $x=0$ at the helicotrema, $x=L$ at the windows (ow: oval window, rw: round window) and $y=0$, $y=b$, $z=-h$ and $z=h$ at the walls.

The scala vestibuli is the part of the figure with $z>0$, the scala tympani that with $z<0$, while the partition is located at $z=0$. It is assumed that the motion of the partition is negligible as compared to the dimensions of the cochlea. The time variable is t. Denote by $P(x, y, z, t)$ the difference pressure in the fluid and assume that the fluid is incompressible and inviscid.

Then the solution, obtained in [14] for a constant impedance ζ of the membrane and harmonic oscillations of the input signal reads

$$P(x, y, z, t) = \sum_{\alpha=0}^{\infty} \sum_{\beta=0}^{\infty} B_{\alpha,\beta} \sinh(\lambda_{\alpha,\beta} x) \cos(\alpha\pi y/b) \cos\{\tau_\beta(h-z)\} e^{i\omega t}, \tag{A1}$$

with $\alpha, \beta = 0, 1, 2, \ldots$ Further

$$\lambda_{\alpha,\beta}^2 = (\alpha\pi/b)^2 + \tau_\beta^2, \tag{A2}$$

and the τ_β are roots of

$$\tau \operatorname{tg}(\tau h) = -2/\zeta, \tag{A3}$$

arranged towards increasing β according to increasing modulus; the quantities $\lambda_{\alpha,\beta}$, τ_β and ζ are complex. The coefficients $B_{\alpha,\beta}$ can be found from the window condition (e.g. $P(L, y, z, t)$ is known); $\omega/2\pi$ is the frequency of the input signal. The impedance ζ is given by

$$\zeta = \frac{1}{\rho\omega^2}(c - m\omega^2 + ik\omega), \tag{A4}$$

where c, m and k are stiffness, mass and resistance per unit area of the membrane and ρ is the density of the fluid.

We compute the average $P_A(x, z, t)$ of $P(x, y, z, t)$ over the width of the membrane:

$$\begin{aligned} P_A(x, z, t) &= \frac{1}{b}\int_{y=0}^{b} P(x, y, z, t)\,dy \\ &= \sum_{\beta=0}^{\infty} B_{0,\beta} \sinh(\lambda_{0,\beta} x) \cos\{\tau_\beta(h-z)\} e^{i\omega t}. \end{aligned} \tag{A5}$$

From (A2) we see that

$$|\lambda_{0,\beta}| = |\tau_\beta|. \tag{A6}$$

Now consider the two-dimensional equivalent of Fig. 4.

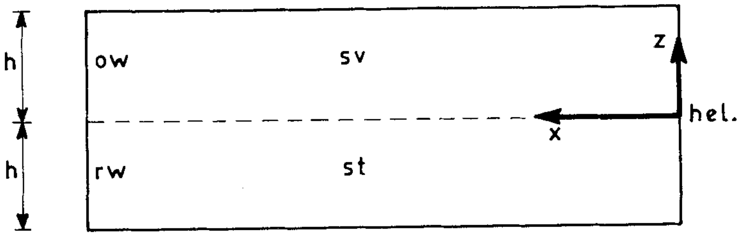

Fig.5.

When ζ is a constant, the solution can be found once more with the method of separation of variables. Let $P(x, z, t)$ be the difference pressure and consider the fluid as incompressible and inviscid. Then the solution is:

$$P(x, z, t) = \sum_{\gamma=0}^{\infty} B(\lambda_\gamma) \sinh(\lambda_\gamma x) \cos\{\lambda_\gamma(h-z)\} e^{i\omega t}, \tag{A7}$$

where the λ_γ are roots of

$$\lambda \operatorname{tg}(\lambda h) = -2/\zeta, \tag{A8}$$

arranged towards increasing γ according to increasing modulus; ζ is given by (A4) and the coefficients $B(\lambda_\gamma)$ have to be determined from the window condition.

A comparison between (A5) and (A7) shows clearly that the nature of the solution remains unchanged by the neglect of the dimension along the width of the membrane. When moreover the direction perpendicular to the membrane is neglected, the solution is violated essentially, as has been shown in [14]. It can be expected that this behaviour is valid as well when the partition impedance ζ is dependent on the axial coordinate x.

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