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Fluid mechanics of the cochlea. Part 1

By M. B. LESSER† AND D. A. BERKLEY‡
Bell Telephone Laboratories, Whippany, New Jersey

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The physiology of the cochlea (part of the inner ear) is briefly examined in conjunction with a description of the 'place' theory of hearing. The role played by fluid motions is seen to be of importance, and some attempts to bring fluid mechanics into a theory of hearing are reviewed. Following some general fluid-mechanical considerations a potential flow model of the cochlea is examined in some detail. A basic difference between this and previous investigations is that here we treat an *enclosed* two-dimensional cavity as opposed to one-dimensional and open two-dimensional models studied earlier. Also the two time-scale aspect of the problem, as a possible explanation for nonlinear effects in hearing, has not previously been considered. Thus observations on mechanical models indicate that potential flow models are applicable for times of the same scale as the frequency of the driving acoustic inputs. For larger time scales mechanical models show streaming motions which dominate the qualitative flow picture. The analytical study of these effects is left for a future paper.

1. Introduction

The cochlea, part of the inner ear, is a small fluid-filled chamber which contains the biological structures that convert mechanical acoustic signals into neural signals. Of prime interest to the worker in mechanics is the fact that not only signal conversion but also signal processing takes place. Thus to fully understand the part played by the nervous system in our sense of hearing we must also unravel the mechanical aspects of audition.

A complete physiologically oriented description of the mammalian auditory system can be found in Wever & Lawrence (1953); we shall only give a short description of auditory physiology with emphasis on the cochlea. We then describe mechanical models used by several investigators in their pursuit of an understanding of auditory perception and also briefly review previous mathematical attempts to describe the function of the cochlea.

Figure 1 is a schematic representation of the peripheral auditory system, encompassing the outer, middle and inner ear. The essential role of the outer and middle ear appears to be that of an impedance matching device which transduces airborne acoustic energy into motion of the perilymphatic fluid contained within the cochlea. Perilymph is a fluid with approximately the same density and twice the viscosity of water. The airborne acoustic signal sets the eardrum into motion

† Present address: Bell Laboratories, Holmdel, N.J., U.S.A.
‡ Present address: Inst. CERAC, S.A., Ecublens, Switzerland.

which in turn causes motion of the middle ear bones. One of these bones, the stapes or stirrup, is attached to a membrane which covers the so-called oval window. Another membrane-covered opening in the cochlea, the round window, also opens to the middle ear. The cochlea itself consists of a tapered tube wound into a spiral. As can be seen from the cross-section shown in figure 2 this tube is divided into three ducts. The upper and lower ducts are connected to the middle ear via the oval and round windows respectively. The central section is separated

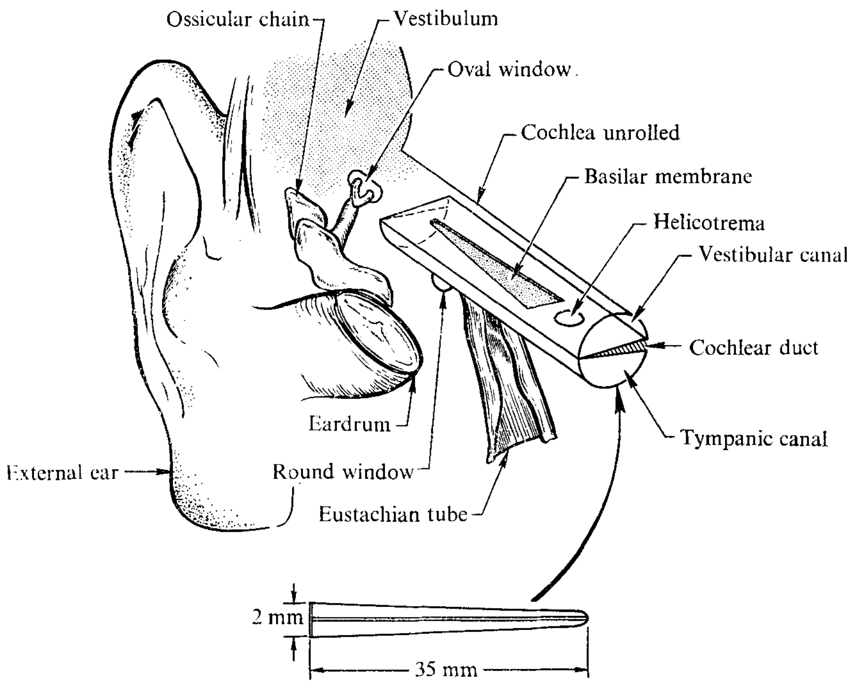

FIGURE 1. Schematic diagram of auditory system.

from the upper duct by an extremely thin membrane and from the lower duct by both a bony shelf and another membrane, the basilar membrane, which is attached to the shelf and the outer wall. On this latter membrane sits the organ of Corti in which are contained the sensory hair cells. The motion of the hair cells induces, by an only dimly understood process, an action potential or neural signal in attached nerve fibres. The basilar membrane is narrowest at the portion of the cochlea adjacent to the oval window, widening out, as indicated in figure 1, as the apical end is approached. At the apical end of the cochlea there is an opening, the helicotrema, joining the two outer ducts. Typical dimensions of a human inner ear are indicated in figure 1, where for clarity the cochlea has been unwound.

The so-called 'place' theory of hearing is currently the most generally accepted qualitative picture of the hearing process. This theory was first given both serious scientific consideration and popularization by Helmholtz (1895). According to the 'place' theory portions of the basilar membrane respond selectively to pure tones, the membrane's motion being greatest at a particular location along its length corresponding to the frequency of the exciting tone. Neurons attached to the hair cells in the part of the organ of Corti where the basilar membrane is undergoing the most extreme excursions are thus excited and hence, crudely speaking, the brain is informed as to what portion of the cochlea is undergoing the most disturbance. In this way a mapping is effected of frequency into position and as the basilar membrane is considered to have a variable stiffness, the stiffness being largest near the oval window and smallest at the apical end of the cochlea, high frequency tones map into a 'place' near the oval window and low frequency tones map into a 'place' near the cochlea apex.

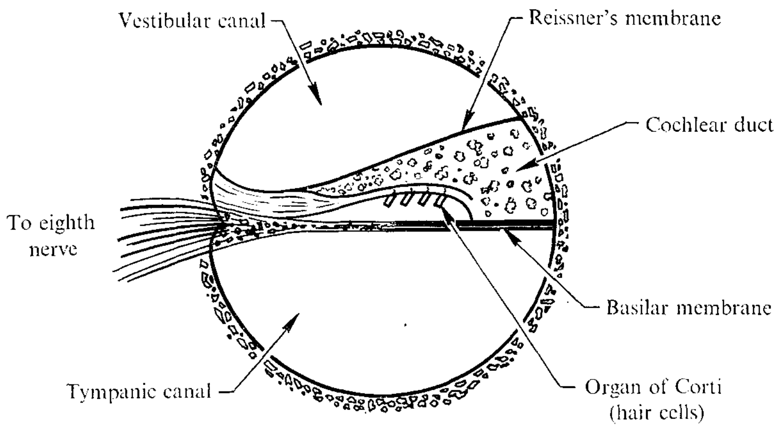

FIGURE 2. The cochlea in cross-section.

Békésy (1960), in his observations of motion in animal cochleae, reported that the steady-state response of the basilar membrane to a pure tone appeared to be a travelling wave which in the course of a period of oscillation moved with changing amplitude from the oval window towards the apex of the cochlea. The envelope of the wave was reported to peak at a 'place' dependent on the frequency of the driving tone; after this the wave amplitude rapidly decays.

The main purpose of Part 1 will be to discuss a two-dimensional mathematical model which yields the behaviour observed by Békésy. It will become evident that a good deal of work still remains to be done before we have a clear understanding of the mechanical aspects of the auditory signal processing which is performed in the cochlea. The model presented here, however, is felt to provide a logical basis for future efforts, about which we shall say more in the concluding section of the paper.

2. The Békésy–Tonndorf model

Before passing on to a discussion of the mathematical model we shall consider a mechanical analogue of the cochlea used by several investigators, but made most popular by Békésy and also by Tonndorf (1959). This model was principally used by Békésy for the purpose of planning his difficult physiological observations of actual cochlea motions. A typical model of the Békésy type is shown in figure 3. The upper and lower chambers correspond to their counterparts in the ear while the central chamber of the inner ear, the scala media, is represented by a metal plate with a triangular shaped cut to hold the 'basilar membrane' and a hole to simulate the helicotrema. Other parts corresponding to inner ear structures are indicated in the figure. From observations which he made on the cochlea, Békésy felt that most of the significant elastic behaviour of the scala media could be attributed to the basilar membrane, hence the simple representation used in the model. For an elastic material a rubber cement membrane was passed over the triangular cut. We note here that the basilar membrane's

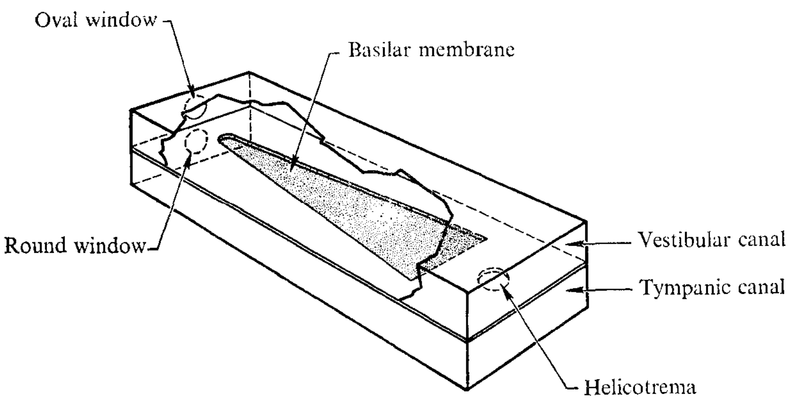

FIGURE 3. Fluid-mechanical model of the cochlea.

mechanical properties are only dimly known, however, it is fairly certain that it is not a membrane in the mechanical sense as indicated by the fact that when slits are made in the membrane the edges do not draw apart. Thus the basilar membrane does not appear to be under tension. Also, from a static measurement made by Békésy the stiffness of the basilar membrane appears to vary by a factor of 50 to 100 over the membrane's 35 mm length.

Observations on models of the type described showed the 'travelling' waves mentioned above. The flow field, which can be observed in the model by means of dispersed aluminium particles, is shown in the photograph presented in figure 4 (plate 1). This picture is a *time exposure* and hence shows *the flow over many cycles of motion* of the driving force. We see from the photograph that over the course of many cycles the particles drift in an eddy pattern. The origin of the drift appears to come from the 'place' where the membrane is undergoing its maximal excursions and indeed eddy's were used by Békésy to pick out the 'place' of maximal response. In the auditory literature these patterns are called Békésy eddies, and at one time or another they have been deemed responsible for many of the anomalous results of auditory research. A somewhat misleading calculation was made by Zwislocki (1948) in an effort to prove that the eddy is unimportant to audition. In this calculation he simply substituted the results of a crude one-dimensional theory into Bernoulli's equation and concluded that the nonlinear effect was of higher order. He did not account for the mechanism of the eddy or examine possible secular effects.

3. Assumptions for modelling

A number of investigators have proposed mathematical models which yield results that appear to agree, at least qualitatively, with the experimental results of Békésy. It is not our purpose to review this past research in detail here; however, we shall devote some discussion to it in order to clearly set out the differences, both in nature and in intent, of the present work. Our work differs in three essential ways from past theoretical endeavours. First, we differ in the type of mathematical model we use. We consider a *two-dimensional enclosed cavity*, containing a structure of *spatially variable elastic properties*. At least two of these features, but not all of them, are to be found in past formulations. The second difference is that we produce a *complete* (though partially numerical) solution to the problem as posed. All past theories were forced to relax the initial formulations in order to arrive at quantitative results. The third and perhaps most important difference lies in the intent of our work. The main aim of past mathematical theories appears to have been to reproduce as exactly as possible the experimental results of Békésy. We also have this as a subsidiary aim but feel that the important contribution of present day mechanics must allow for the realities of experimental difficulties in the field of audition. Some of these are that all the important mechanical parameters of the cochlea are not known, that Békésy's measurements were taken for only a few animals on dead tissue and at amplitude levels far in excess of normal hearing. Thus in our view the task of mechanics is to clearly show by rational calculation what type of physical phenomena result from a particular set of assumptions. We must answer questions such as whether viscosity is important in hearing and what type of nonlinearity can be important even at the low excitation levels prevalent in normal hearing. Before setting forth our remaining assumptions let us briefly discuss some of the previous research on cochlea mechanics.

One group of investigators, as exemplified by Peterson & Bogert (1950), Zwislocki (1965) and Hause (1963), have concentrated their efforts on so-called long wavelength theories, i.e. they assumed that because the length of the cochlea is approximately 35 times its diameter fluid motions normal to the surface of the scala media could be ignored. We shall devote some discussion to this point at the end of § 4. The essential point is that because the elastic properties undergo rapid change from the oval window to the cochlea apex another characteristic length is introduced which is of order of the cochlea diameter. Thus it is unrealistic to expect the flow to be one-dimensional, especially at the 'place' where the cochlea partition is undergoing maximal displacements in a direction transverse to itself. Two-dimensional motion is evident in model studies as made by Tonndorf (and also reproduced by us). At least one past investigator, Ranke, formulated several two-dimensional models. Unfortunately his work has been almost totally ignored, perhaps because in order to obtain solutions to his boundary-value problems he was forced to make numerous additional approximations, e.g. he was not able to treat a closed cavity. In one paper (Ranke 1950) he gives a review of his work and thoughts on the problem and also states that the problem of the Békésy eddy has received no hydromechanical explanation.

The remainder of our assumptions have for the most part been used in some previous investigation. Thus we shall unwind the spiral cochlea as indeed it is in alligators and the platypus. The central duct in the cochlea, which contains the organ of Corti and which is enclosed by Reissner's membrane and the basilar membrane, will be represented as a single elastic partition. Also the mechanical properties of the partition will be represented by the assumption that each point acts as a damped harmonic oscillator, point-to-point coupling being only through the surrounding fluid. Not enough is known to prove or disprove this assumption at present. The assumption is tantamount to representing the partition by a mechanical impedance $Z(x, \omega)$, where x denotes distance from the oval window along the partition. We note that such assumptions do yield good results in the description of walls in room response problems (Morse & Ingard 1968).

We take the perilymph to be incompressible (Peterson & Bogert treated it as compressible, but even in their calculations it is clear that compressibility is of minor importance) for if perilymph has about the same sound speed as water, which is likely, the wavelength of an acoustic signal at 5000 Hz (a high frequency for hearing) is about 30 cm while the cochlea is only 35 mm long. In the present paper we treat the flow as inviscid but with the difference that we consider this as a first step in an expansion procedure. This is important in regard to the mechanism of the Békésy eddy. Also, in regard to the question of viscous effects, it has been claimed that the fluid contained in the scala media, endolymph, is extremely viscous (Békésy 1960) however modern measurements indicate that the mechanical properties of endolymph are the same as perilymph (Tonndorf 1959).

One very notable feature of past work has been the assumption that nonlinear mechanical effects can be ignored. The motion of the basilar membrane is small, a displacement of 10^{-6} cm corresponding to normal amplitude sound (Békésy). In fact, man can detect sound corresponding to basilar membrane and eardrum displacements of 10^{-10} cm. As is well known small amplitude nonlinearities do exist in mechanics, though many of them are of a secular nature, i.e. they tend to become noticeable over long periods of time. Also, recent experiments, mainly in electrophysiology, indicate the presence of nonlinearities in cochlear mechanics (Goldstein 1967; Goblick & Pfeiffer 1969). It is a challenge to mechanics to find possible mechanisms that might explain these findings. The Békésy eddy is a secular type nonlinearity and probably not responsible for the experimental indications of nonlinear behaviour which make themselves felt over a time scale equal to a period of acoustic wave. As the Békésy eddy is to be understood as resulting from the combination of viscous and nonlinear effects, we consider our present *linear inviscid* calculation as the leading term in an asymptotic expansion procedure. This is especially important as we wish to understand the cochlea-model results where streaming is clearly present. Thus the flow pattern in a cochlea model excited by an oscillatory disturbance exhibits a steady streaming motion as well as motions typical of a fluid with a free surface. As the excitation is purely oscillatory, the steady motion must result from a nonlinear interaction. This type of behaviour is familiar from the theory of acoustic streaming (Batchelor 1967; Riley 1967) from which we see that the governing parameter for the streaming effect is the Strouhal number $S = \omega l/U_\infty$, where l is a typical length and U_∞ is the velocity amplitude of the driving oscillation. When $S \gg 1$ we expect to see a linear oscillatory boundary layer of thickness of $O(1/\sqrt{S})$. Nonlinear effects in the boundary layer drive a steady boundary layer which in turn drives an outer slow streaming motion (a Stokes flow). The magnitude of the outer streaming velocity is $O(1/S)$. Thus we expect that the streaming motion only affects the flow significantly after a number of acoustic periods. Also the oscillatory boundary layer has a thickness which is small compared with the cochlea diameter. We shall therefore proceed on the assumption that basilar membrane motion is primarily controlled by the outer or potential flow. A linearized theory is adequate on the time scale of an acoustic period since, for the range of frequencies of interest in auditory perception, physical measurements show (Békésy 1960) the maximum basilar membrane slope to be sufficiently small. In addition consistency of the numerical results (i.e. those also showing small membrane slope) supports use of the linearized equations. These considerations lead us to postulate as a reasonable mathematical model or, perhaps better, analogue of the cochlea, the potential cavity flow model presented below.

4. Mathematical model

In the present paper we shall investigate the simplest mathematical model which contains the *linear short time scale* aspects of cochlea behaviour. A future paper will discuss some of the nonlinear mechanical phenomena that may be of importance. We shall also ignore the helicotrema, as model experiments indicate that its main importance is in transient response (we shall confine our attention to steady-state response).

Thus, for the present we assume linearized two-dimensional potential flow in a configuration depicted in figure 5. The upper domain where $y > 0$ will be denoted by the subscript 1 while for $y < 0$ we will use the subscript 2. Where necessary we shall characterize the oval and round windows by a constant (in space) mechanical impedance. The fluid density is ρ, the potential is $\bar{\phi}$ with $\nabla\bar{\phi} = (\bar{u}, \bar{v})$, where $\bar{u}$ and $\bar{v}$ are the x and y fluid velocity components and $\bar{p}$ the fluid pressure. Thus the equations characterizing our model are

$$\nabla^2\bar{\phi}_1 = \nabla^2\bar{\phi}_2 = 0, \tag{1}$$

$$\bar{p}_1 + \rho(\partial\bar{\phi}_1/\partial t) = \bar{p}_2 + \rho(\partial\bar{\phi}_2/\partial t) = 0; \tag{2}$$

on $y = 0,\ 0 < x < L$

$$m(x)\,\partial^2\bar{\eta}/\partial t^2 + r(x)\,\partial\bar{\eta}/\partial t + k(x)\,\bar{\eta} = \bar{p}_2(x,0,t) - \bar{p}_1(x,0,t), \tag{3}$$

$$\partial\bar{\eta}/\partial t = \partial\bar{\phi}_1/\partial y = \partial\bar{\phi}_2/\partial y; \tag{4}$$

on $x = 0$, $0 < y < +l$

$$m_0\,\partial^2\bar{\xi}_1/\partial t^2 + r_0\,\partial\bar{\xi}_1/\partial t + k_0\,\bar{\xi}_1 = \bar{p}_0(t) - \bar{p}_1(0,y,t), \tag{5a}$$

or as an alternative but different condition

$$\bar{\xi}(y,t) = \bar{F}(y,t), \quad \text{a given function,} \tag{5b}$$

$$\partial\bar{\xi}_1/\partial t = \partial\bar{\phi}_1/\partial x; \tag{6}$$

on $x = 0$, $-l < y < 0$

$$m_0\,\partial^2\bar{\xi}_2/\partial t^2 + r_0\,\partial\bar{\xi}_2/\partial t + k_0\,\bar{\xi}_2 = -\bar{p}_2(0,y,t), \tag{7}$$

$$\partial\bar{\xi}_2/\partial t = \partial\bar{\phi}_2/\partial x, \tag{8}$$

while for $x = L$, $\partial\bar{\phi}_1/\partial x = \partial\bar{\phi}_2/\partial x = 0$ and for $|y| = l$, $\partial\bar{\phi}_1/\partial y = \partial\bar{\phi}_2/\partial y = 0$. In the above equations $m(x)$, $r(x)$ and $k(x)$ specify the basilar membrane's variable mechanical impedance, $m(x)$ denoting its mass per unit area, $r(x)$ its damping

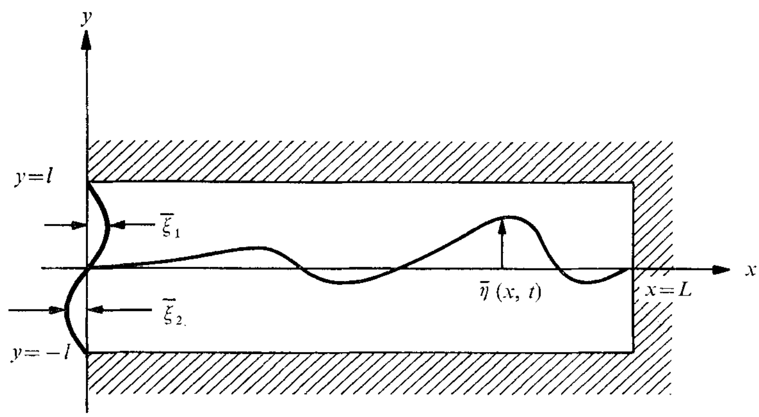

FIGURE 5. Potential flow model of the cochlea.

in dyne sec/cm³ and $k(x)$ its stiffness in dyne/cm³. The constant values of these parameters for the round and oval window are denoted by m_0, r_0 and k_0. Note from equations (5*a*, *b*) that we have the alternative of specifying either a driving pressure $\bar{p}_0(t)$ or a driving displacement (equivalent to stapes motion) $\bar{F}(y,t)$. It should be pointed out that such a choice will lead to different results for the equivalent input impedance of the cochlea as seen from the oval window. In our calculations we shall emphasize (5*b*) as being closer to the input action of the stapes. As our interest centres on the model's steady-state response to a pure tone, so that the driving terms have the form $\mathrm{Re}\{F(y)\,e^{st}\}$, where $s = i\omega$, we consider the frequency dependent equations

$$\nabla^2\phi_1 = \nabla^2\phi_2 = 0, \tag{9}$$

$$p_1 + \rho s\phi_1 = p_2 + \rho s\phi_2 = 0; \tag{10}$$

on $y = 0$, $0 < x < L$

$$sZ(x,s)\,\eta = p_2 - p_1, \tag{11}$$

$$s\eta = \partial\phi_1/\partial y = \partial\phi_2/\partial y; \tag{12}$$

on $x = 0, 0 < y < l$

$$sZ_0(s)\,\xi = p_0 - p_1 \tag{13a}$$

or

$$\xi = F, \tag{13b}$$

$$s\xi = \partial\phi/\partial x; \tag{14}$$

on $x = 0, \; -l < y < 0$

$$sZ_0(s)\,\xi = -p_2, \tag{15}$$

$$s\xi_2 = \partial\phi/\partial x, \tag{16}$$

where, for example, $\bar{\phi} = \mathrm{Re}\,(e^{st}\,\phi)$ and $Z = ms + k/s + r$.

The problem as presented can be simplified somewhat by re-defining the arbitrary time functions implied in the introduction of a velocity potential. Thus for region 2, where $-l < y < 0$, let $\xi' = -\xi$, $y' = -y$, $\phi' = -\phi_2 - p_0/\rho s$, $p' = -p_2 + p_0$. The equations in region 2 then become

$$\left(\frac{\partial^2}{\partial y'^2} + \frac{\partial^2}{\partial x^2}\right)\phi' = 0,$$

$$p' + \rho s\phi' = 0;$$

on $y' = 0, 0 < x < L$

$$sZ\eta = p_2 - p_1 = (p_0 - p') - p_1,$$

$$\partial\phi'/\partial y' = s\eta;$$

on $x = 0$

$$sZ_0\xi' = p_0 - p', \quad \partial\phi/\partial x = s\xi'.$$

Hence we have the identical boundary-value problem for the variables ϕ' and p' as functions of x and y' as for ϕ_1 and p_1 as functions of x and y, so that $\phi' = \phi_1$ and $p' = p_1$. The boundary condition on the surface $y = y' = 0$ is then

$$sZ\eta = p_0 - 2p_1$$

and we need only consider the *equivalent* one chamber boundary-value problem in the region $\mathscr{D}$, $0 \leqslant x \leqslant L$, $0 \leqslant y \leqslant l$:

$$\nabla^2\phi = 0, \quad p + \rho s\phi = 0;$$

on $y = 0$

$$\partial\phi/\partial y = s\eta, \quad s\eta Z = p_0 - 2p;$$

on $x = 0$

$$\partial\phi/\partial x = s\xi, \quad s\xi Z_0 = p_0 - p,$$

or *if* ξ *is specified*

$$U_0 = \xi/s = \partial\phi/\partial x.$$

In this latter case it can easily be seen that we must take $p_0 = 0$. As before, $\partial\phi/\partial x = 0$ on $x = L$ and $\partial\phi/\partial y = 0$ on $y = l$.

We thus arrive at the pressure input equivalent model

$$\nabla^2\phi = 0 \quad \text{in} \quad \mathscr{D}, \tag{17}$$

$$\partial\phi/\partial x - (\rho s/Z_0)\,\phi = p_0/Z_0 \quad \text{on} \quad x = 0, \tag{18}$$

$$\partial\phi/\partial y - (2\rho s/Z)\,\phi = p_0/Z \quad \text{on} \quad y = 0, \tag{19}$$

$$\partial\phi/\partial x = 0 \quad \text{on} \quad x = L, \tag{20}$$

and

$$\partial\phi/\partial y = 0 \quad \text{on} \quad y = l. \tag{21}$$

The boundary conditions for the velocity input model require

$$\partial\phi/\partial x = U_0(y) \quad \text{on} \quad x = 0 \tag{22}$$

and

$$\partial\phi/\partial y - (2\rho s/Z)\,\phi = 0 \quad \text{on} \quad y = 0. \tag{23}$$

The condition that the fluid is incompressible or, equivalently, the application of Green's theorem to the above equation shows that any solution must satisfy the condition

$$\int_0^l \frac{\partial\phi(0,y)}{\partial x}dy + \int_0^L \frac{\partial\phi(x,0)}{\partial y}dx = 0. \tag{24}$$

The above equations, when cast in non-dimensional variables, take the form

$$\left(\frac{\partial^2}{\partial\hat{x}^2}+\frac{\partial^2}{\partial\hat{y}^2}\right)\hat{\phi} = 0, \tag{25}$$

$$\partial\hat{\phi}/\partial\hat{y} = (2/\hat{Z})\,\hat{\phi} = 0 \quad \text{on} \quad \hat{y} = 0, \tag{26}$$

$$\partial\hat{\phi}/\partial\hat{y} = 0 \quad \text{on} \quad \hat{y} = \sqrt{\sigma}, \tag{27}$$

$$\partial\hat{\phi}/\partial\hat{x} = 1 \quad \text{on} \quad \hat{x} = 0, \tag{28}$$

and

$$\partial\hat{\phi}/\partial\hat{x} = 0 \quad \text{on} \quad \hat{x} = 1, \tag{29}$$

where

$$\hat{x} = x/L, \quad \hat{y} = y/L, \quad Z = Z/(\rho L s), \quad \hat{\phi} = \phi/(U_0 L), \quad \sigma^2 = l^2/L^2. \tag{30}$$

The boundary condition on $\hat{x} = 0$ is chosen for the case of a uniform imposed velocity, i.e. a piston such that $\overline{u}(0,y,t) = U_0\cos\omega t$. As the typical approach in theories of the cochlea has been to assume *a priori* one-dimensional flow on the grounds that $\sigma = l^2/L^2$ is small it is of some interest to briefly examine the validity of one-dimensional theory.

A formal derivation from the two-dimensional theory is easily obtained as a limit-process expansion in $\sigma \to 0$. Thus we define the long wavelength variables as

$$\tilde{x} = \hat{x}, \quad \tilde{y} = \hat{y}/\sqrt{\sigma}, \quad \tilde{Z} = \sqrt{\sigma}\,\hat{Z}, \quad \tilde{\phi} = \hat{\phi}. \tag{31}$$

The equations of motion in the above variables are

$$\left(\sigma\frac{\partial^2}{\partial\tilde{x}^2}+\frac{\partial^2}{\partial\tilde{y}^2}\right)\tilde{\phi} = 0, \tag{32}$$

$$\partial\tilde{\phi}/\partial\tilde{y} - (2\sigma/\tilde{Z})\,\tilde{\phi} = 0 \quad \text{on} \quad \tilde{y} = 0, \tag{33}$$

$$\partial\tilde{\phi}/\partial\tilde{y} = 0 \quad \text{on} \quad \tilde{y} = 1, \tag{34}$$

$$\partial\tilde{\phi}/\partial\tilde{x} = 1 \quad \text{on} \quad \tilde{x} = 0, \tag{35}$$

and

$$\partial\tilde{\phi}/\partial\tilde{x} = 0 \quad \text{on} \quad \tilde{x} = 1. \tag{36}$$

The variable $\tilde{Z}$ is of course a function of $\tilde{x}$ and σ. For the one-dimensional theory to result from the limit $\sigma \to 0$ it is necessary that $\tilde{Z}(\tilde{x},\sigma) = O(1)$ as $\sigma \to 0$. Then if

$$\tilde{\phi} = \tilde{\phi}^{(0)} + \sigma\tilde{\phi}^{(1)} + \dots \tag{37}$$

and

$$\lim_{\sigma\to 0}\tilde{Z} = \tilde{Z}^{(0)}(\tilde{x}), \tag{38}$$

it is a straightforward matter to show (see, for example, Stoker (1957, chapter II) for a similar derivation) that

$$\partial\tilde{\phi}^{(0)}/\partial\tilde{y} = 0$$

and
$$d^2\tilde{\phi}^{(0)}/d\tilde{x}^2 - (2/\tilde{Z}^{(0)})\,\tilde{\phi}^{(0)} = 0, \tag{39}$$

with
$$d\tilde{\phi}^{(0)}/d\tilde{x} = 1 \quad \text{on} \quad \tilde{x} = 0 \tag{40}$$

and
$$d\tilde{\phi}^{(0)}/d\tilde{x} = 0 \quad \text{on} \quad \tilde{x} = 1. \tag{41}$$

Thus the above result shows that a necessary condition for the one-dimensional theory to be plausible is that

$$\hat{Z} = \frac{Z}{\rho L s} = O(1/\surd\sigma) = O\left(\frac{L}{l}\right).$$

The meaning of this condition here can be seen clearly if we consider the case of a purely elastic wall with $Z = k/s$ and hence

$$\hat{Z} = k/\rho L s^2$$

or, with $s = i\omega$,

$$|\hat{Z}| = k/\rho L \omega^2.$$

Thus it is required in this case that

$$\frac{kl}{\rho}\frac{1}{\omega^2 L^2} = O(1).$$

Now $kl/\rho = C^2$, where C is the wave speed for the equivalent one-dimensional system (Lesser & Berkley 1970), hence C/ω represents a wavelength and the necessary condition for one-dimensional theory is that

$$\frac{C/\omega}{L} = O(1) \quad \text{as} \quad \sigma \to 0.$$

We can only expect a one-dimensional approach to work everywhere for small ω, as

$$C \sim 10^3 e^{-3x} \quad \text{and} \quad \frac{C/\omega}{L} = \frac{3\times 10^2 e^{-3x}}{\omega}.$$

Even for small ω we can expect trouble owing to the rapid variation of the magnitude of Z as x varies. Thus it is no surprise that the fluid motion in cochlea models appears to be two-dimensional.

Another approach to the calculation of the flow pattern would be via an approximation of the deep water wave type (Ranke 1950). For this type of approach to be valid, as can be seen by analogy with conventional water wave theory, the surface wave penetration depth $|Z/\rho s|$ should be small in comparison with the typical cross-sectional dimension of the cochlea (about 1 mm). If Z is due to a pure stiffness this is tantamount to having $k/(\rho\omega^2) \leqslant 0{\cdot}1$; however, for $\omega = 10^4$ we expect $0{\cdot}1 \geqslant k/(\rho\omega^2) \geqslant 0{\cdot}01$, over the length of the cochlea. We thus must obtain a solution for the enclosed geometry of figure 5.

5. Potential flow solutions

The solution to equations (25)–(29) for a specific $\hat{Z}$ is most easily obtained by the use of a truncated Fourier series which is determined by the best 'fit' to the mixed boundary condition (26). The method is straightforward and we only outline it here. Thus we assume

$$\hat{\phi} = \hat{x}(1-\tfrac{1}{2}\hat{x}) - \sqrt{(\sigma)}\,\hat{y}\left(1-\frac{1}{2\sqrt{\sigma}}\hat{y}\right) + \sum_{n=0}^{\infty} A_n \cosh\left[n\pi(\sqrt{\sigma}-\hat{y})\right]\cos n\pi\hat{x}.$$

It can easily be verified that this series automatically satisfies all the boundary conditions for the problem except on $\hat{y} = 0$. This latter condition takes the form

$$\sqrt{\sigma} + \sum_{0}^{\infty} n\pi A_n \sinh(n\pi\sqrt{\sigma})\cos(n\pi\hat{x}) - \frac{2}{\hat{Z}}\left\{\hat{x}(1-\tfrac{1}{2}\hat{x}) + \sum_{0}^{\infty} A_n \cosh(n\pi\sqrt{\sigma})\cos n\pi\hat{x}\right\} = 0.$$

If we truncate the series at $N+1$ terms and use the notation $A_n^{(N)}$ to denote the coefficients of the truncated series we can use the above equation and the orthogonality of the trigonometric functions to derive a closed set of equations for the $A_n^{(N)}$. As $N \to \infty$ we expect $A_n^{(N)} \to A_n$. The use of a variational principle for Laplace's equation and the Ritz procedure (Schechter 1967) leads to the same equations for the $A_n^{(N)}$. Thus we find

$$\sum_{n=0}^{n=N} A_n^{(N)} \alpha_{nm} = f_m,$$

where $$\alpha_{nm} = \cosh(n\pi\sqrt{\sigma})\int_0^1 \frac{\cos n\pi\hat{x}\cos m\pi\hat{x}}{\hat{Z}}\,d\hat{x} - \tfrac{1}{4}n\pi\sinh(n\pi\sqrt{\sigma})\,\delta_{nm},$$

and $$f_m = \tfrac{1}{2}\sqrt{(\sigma)}\,\delta_{m0} - \int_0^1 \frac{\hat{x}(1-\frac{1}{2}\hat{x})\cos m\pi\hat{x}}{\hat{Z}}\,d\hat{x}.$$

The procedure so outlined has given excellent results for a wide range of functional forms for $\hat{Z}(\hat{x}, s)$. The fast Fourier transform algorithm (Cooley & Tukey 1965) was used to expedite the evaluation of α_{nm} and f_m.

6. Comments on oscillating boundary layer

The potential flow solution given above can be considered as the first term in the outer expansion of the solution for large Strouhal number. It is a relatively easy matter to include the solution to this order of the appropriate inner expansion. These formal matters will be discussed more fully in a future paper. We content ourselves here by commenting that the inner expansion has no noticeable effect on the solution to this order. Noticeable effects are only produced when we look at terms of order 1/(Strouhal number) and steady motions occur with purely periodic forces at the oval window.

7. Results

A number of calculations were made using the above model to examine the effects of *various choices* for $Z(x, \omega)$. A typical case (similar to the Z used in Peterson & Bogert 1950; Zwislocki 1965; Hause 1963) chosen was

$$Z = i\omega m + K/(i\omega) + r,$$

with

$$m = 0{\cdot}05, \qquad K = 10^7 e^{-1{\cdot}5x} \;\text{ and }\; 10^9 e^{-3x}, \qquad \text{and} \quad r = 3000\, e^{-1{\cdot}5x}.$$

The results obtained are shown in figures 6, 7 and 8. In figure 6 we see the wave envelope plus a few plots of the wall shape at various times in the driving

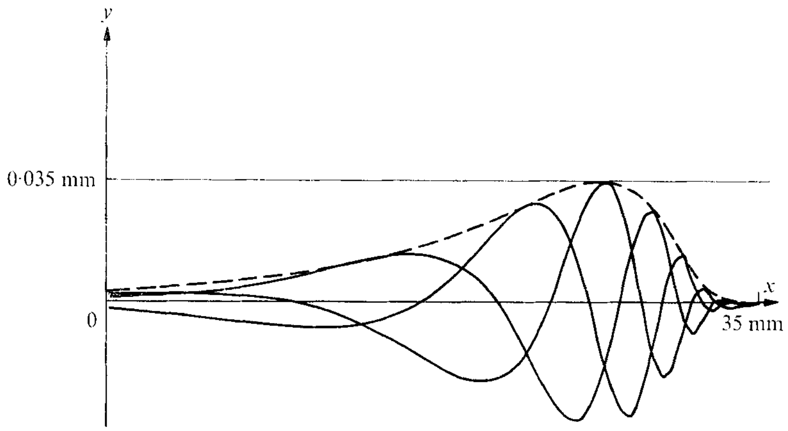

FIGURE 6. Wave envelope and motion of basilar membrane. $m = 0{\cdot}05$, $k = 10^7 e^{-1{\cdot}5x}$, $r = 3000e^{-1{\cdot}5x}$, $\omega = 1000$.

cycle. The qualitative behaviour observed by Békésy, i.e. the peaking of the profile amplitude at a particular 'place' on the wall can be easily seen in this figure. The variation of place with frequency is demonstrated in figure 7. In figure 8 we show a plot of particle paths for a number of particular fluid particles. Both the horizontal and vertical amplitudes of the particle orbits are equally magnified. The failure of the one-dimensional transmission line models, which predicts an essentially horizontal motion, is most evident in this figure.

As implied above the quantitative comparison with experimental results is tricky. The parameter $r(x)$ is not really understood in terms of the mechanics of the scala media and in past theories particular investigators have chosen it so as to yield agreement with Békésy's data. The particular choice of Z used above was a cross between that used by several past investigators. It should be no surprise that with its use we obtain reasonable agreement with the data of Békésy as shown in table 1 below. (We have used the figures from Békésy (1960, p. 448).) The one-dimensional or long wavelength theory of Zwislocki also achieves general agreement with Békésy; however we note the following quotation from Zwislocki (1965, p. 30): "There are no direct data for the acoustic resistance R_P. Consequently, its numerical value must be adjusted so that the theoretical computations agree with V. Békésy's dynamic measurements."

It is clear that to some extent the basic physics of the place effect is contained in both one- and two-dimensional theories, otherwise it would be unlikely that even with the freedom of adjusting constants we could come close to Békésy's measurements. In this light, fitting the theoretical results to Békésy's data could be interpreted as a measurement of the scala media equivalent impedance and

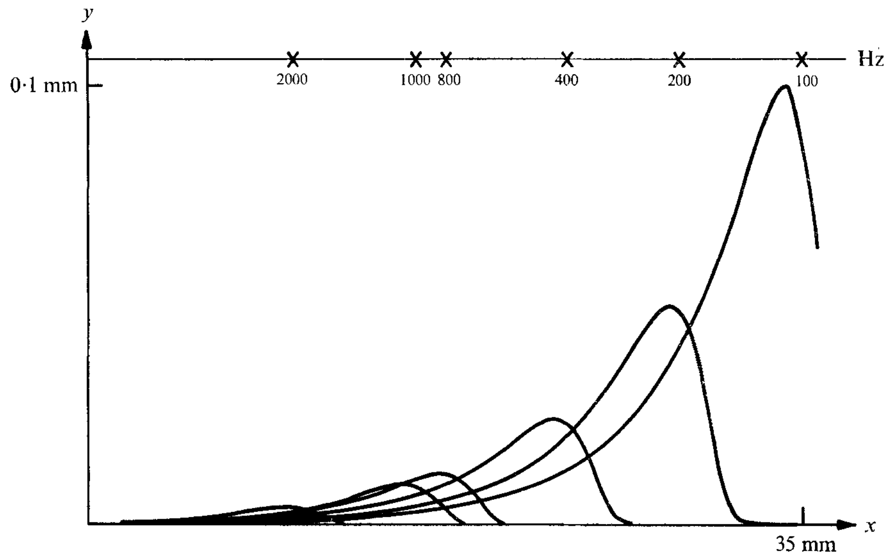

FIGURE 7. Unit velocity excitation at stapes, showing wave envelopes. $m = 0{\cdot}05$, $k = 10^9 e^{-3x}$, $r = 3000 e^{-1{\cdot}5x}$.

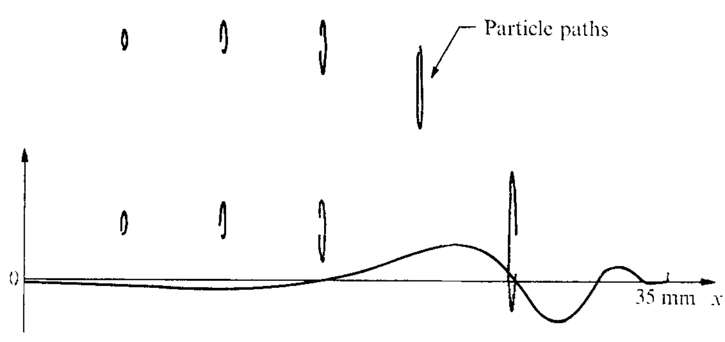

FIGURE 8. Paths of tracer particles. $m = 0{\cdot}05$, $k = 10^7 e^{-1{\cdot}5x}$, $r = 3000 e^{-1{\cdot}5x}$, $\omega = 1000$.

hence of $r(x)$. Certainly, if two-dimensional effects are significant in the region of the place, as they certainly are from both our and Tonndorf's model studies and our theoretical work, interpretation of the fitting of theoretical results to empirical data as a means of assessing the mechanical properties of the scala media necessitates a two-dimensional theory. An aspect of the two-dimensional calculations which is perhaps even more important is that they are needed as a foundation in the search for significant nonlinear effects.

Frequency in Hz	Distance of place from stapes: Békésy (mm)	Distance of place from stapes: Two-dimensional theory (Z from figure 7) (mm)
100	31	33
200	28	28
400	24	23
800	20	17

TABLE 1

Finally, we would like once more to stress the two time-scale nature of the problem. This is evident in a comparison between figures 4 and 8. Figure 4 (plate 1), which is a time exposure, shows the flow in a cochlea model over a number of periods of the excitation while figure 8 depicts the linear solution over a single period. The latter figure agrees very well with what is seen over this short time scale. The particle motion in figure 8, being over the long time scale, does not show the detailed particle orbits but an average over many periods. For the parameters appropriate to the actual cochlea the long time scale is of the order of a second and perceptions which take this time to register might well be influenced by nonlinear hydromechanical effects. Tonndorf has raised the possibility of nonlinear hydromechanical effects but seems to be unaware of the possibility of time integrative (secular) nonlinearities. This might be an important point in hearing because the amplitudes of motion involved indicate that simple amplitude dependent nonlinearities are not significant. The subtlety of nonlinear behaviour in the cochlea is indicated in the experimental work of Goldstein (1967) and of Goblick & Pfeiffer (1969), in which they exhibit some nonlinearities that are probably only weakly amplitude dependent. The final interpretation of these nonlinearities remains an open question in present day theory of audition.

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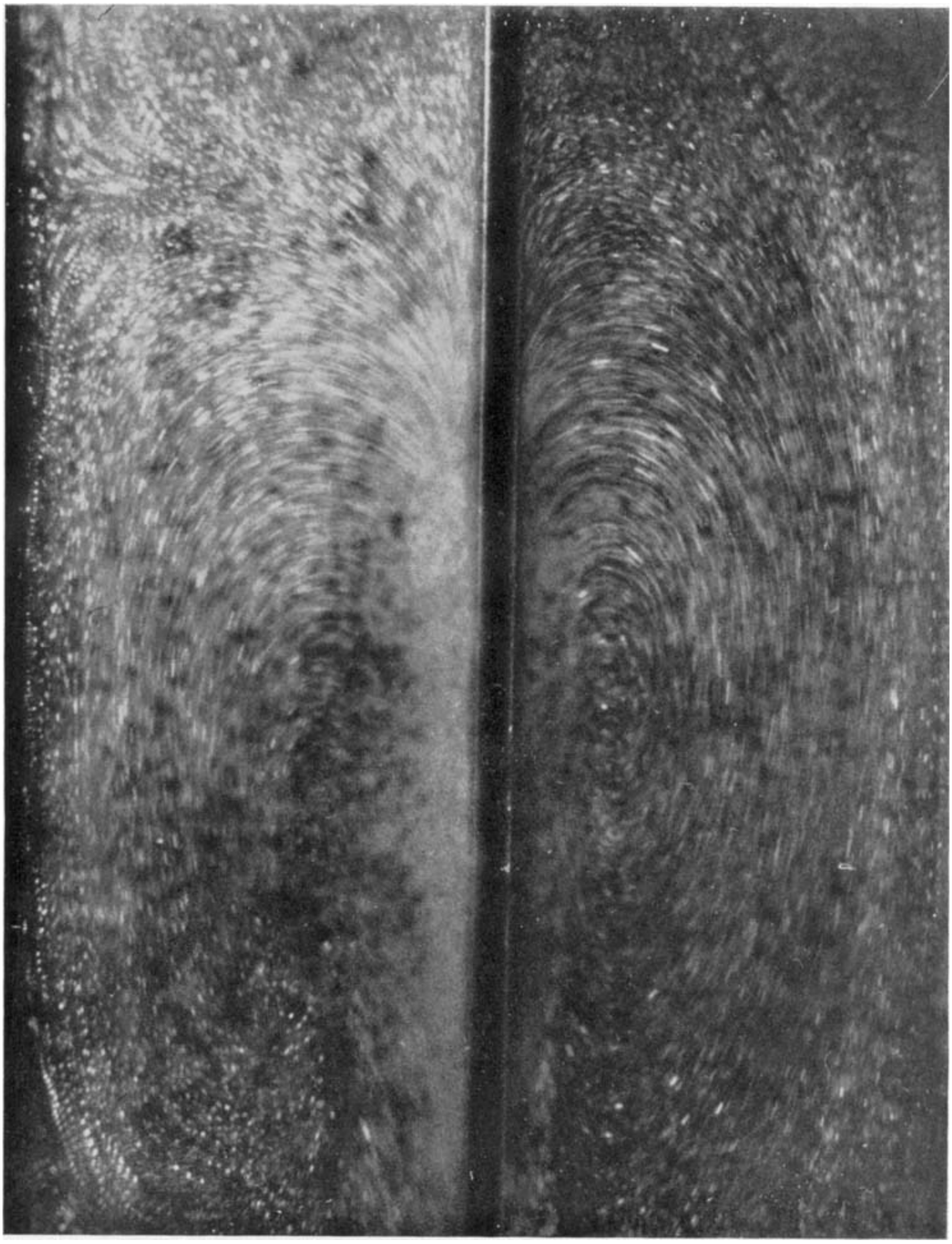

FIGURE 4. Time-averaged flow field in a fluid-mechanical model.

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