

On the adequacy of the Peterson-Bogert model and on the effects of viscosity in cochlear dynamics

M. A. VIERGEVER AND J. J. KALKER

Department of Mathematics, University of Technology, Delft, The Netherlands

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SUMMARY

Based on a simplified model of the cochlea a one-dimensional approach (the Peterson-Bogert model) is compared with a three-dimensional one. The results appear to be in agreement provided the impedance of the partition is large. This is true for low frequencies except in the region of maximum membrane amplitude. For low frequencies, moreover, the fluid can be considered as incompressible. The influence of the viscosity is investigated by localizing the entire viscous force in a boundary layer. This layer is shown to occur in the fluid. Besides it is concluded that the rotation is approximately largest where the membrane has its maximum amplitude. This can be an explanation for the appearance of eddies at that point.

1. Introduction

The cochlea is a part of the inner ear and consists of a spirally coiled tube, longitudinally divided into three parts: the scala vestibuli, the cochlear duct and the scala tympani. The smallest of these, the cochlear duct, is separated from the scala vestibuli by Reissner's membrane and from the scala tympani by the basilar membrane. It contains a highly viscous fluid, the endolymph. Von Békésy [1] has shown that the two membranes and the fluid move in unison, so that it is assumed generally that the cochlea can be represented by two channels divided by a single membrane, the cochlear partition, and bounded moreover by a rigid wall. Another simplification which seems to be permissible is that the spiral coiling can be dispensed with. At the basal end of the cochlea the scala vestibuli and the scala tympani are separated from the middle ear both by an opening covered with a membrane, the oval and round window respectively. Near the apex the partition terminates just before the end of the scalae; because of this the channels communicate through a small aperture called the helicotrema.

Knowing finally that the cross-sectional areas of the scalae are roughly equal with the exception of the immediate vicinity of the windows, we can represent the cochlea as indicated by Fig. 1.

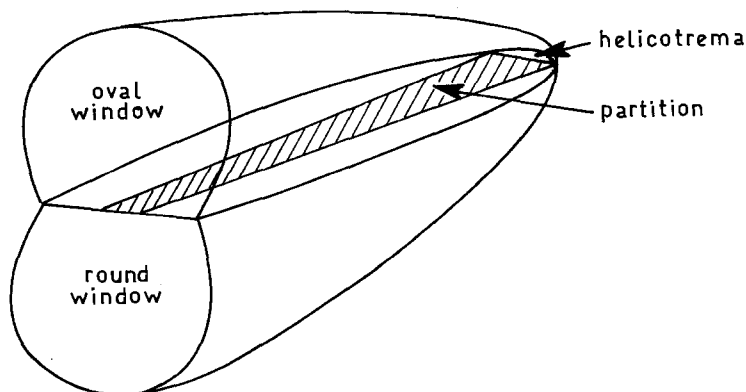


Figure 1.

The cross-sectional area being largest at the basal end and decreasing slowly towards the helicotrema has an average of 0.02 cm^2 . The width of the partition increases from 0.01 cm (windows) to 0.04 cm (hel.); the length of the cochlea is about 3.5 cm . The density of the perilymph is about 1 g/cm^3 , its viscosity $0.02 \text{ g/cm} \cdot \text{s}$. Of great importance for the dynamical behaviour of the cochlea are mass, resistance and stiffness of the partition. The order of magnitude of these quantities is known to a sufficient extent but the references disagree as to the exact values. Taken per unit area the mass increases slightly from the basal to the apical end, the order of magnitude being 0.1 g/cm^2 , the resistance and the stiffness decrease rapidly (order $10^3 \text{ g/cm}^2 \cdot \text{s}$ and 10^6 dyn/cm^3 respectively). These figures are due to [2, 6, 7, 11], all of which refer to experiments of Von Békésy.

Fluid motion in the cochlea is caused by the stapes, the last of the three middle-ear bones. In case of a sound vibration the stapes excites the oval window to which it is attached. The main effect of this is a deflection of the partition as a result of the pressure difference in the two scalae. This deflection can be considered decisive as to sound perception which is effectuated by the organ of Corti localized in the cochlear partition and supported by the basilar membrane.

To describe the dynamical phenomena in the cochlea a one-dimensional model is used almost without exception in which the viscosity of the perilymph is not taken into account. Only Peterson and Bogert [7] introduce viscosity in their equations but they do not draw any conclusions concerning its relevance. Klatt and Peterson [6] and especially Tonndorf [9] point out the possible importance of viscous effects, the latter because they could explain the observed non-linearities.

The purpose of this paper is two-fold: first the applicability of the one-dimensional (Peterson-Bogert) model will be checked on the basis of a simplified representation of the cochlea; next the influence of the viscosity will be examined.

2. The three-dimensional model

Since the geometry of the cochlea is too complicated to obtain results from a direct three-dimensional treatment a simplified representation is introduced namely a parallelepiped bisected by a membrane clamped at the edges, the cochlear partition (see fig. 2).

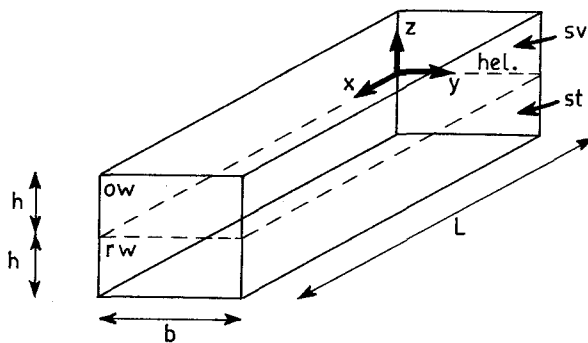


Figure 2.

The rectangular coordinate system is chosen in such a way that $x=0$ at the helicotrema (hel.), $x=l$ 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 $\tilde{p}(x, y, z, t)$ and $\tilde{\mathbf{v}}(x, y, z, t) = (\tilde{u}(x, y, z, t), \tilde{v}(x, y, z, t), \tilde{w}(x, y, z, t))$ the pressure and velocity in the fluid and by $\rho(x, y, z, t)$ its density. Then the continuity equation reads

$$\rho_t + \nabla \cdot (\rho \tilde{\mathbf{v}}) = 0. \quad (2.1)$$

The equation of motion for an inviscid fluid is

$$\rho \tilde{v}_t + \rho(\tilde{v} \cdot \nabla) \tilde{v} + \nabla \tilde{p} = 0. \tag{2.2}$$

(subscripts indicate partial differentiation with respect to the variables involved).

If the fluid is barotropic, that is, if the pressure \tilde{p} is a function of the density ρ only, (2.1) can be written in the form

$$\frac{1}{a^2} \tilde{p}_t + \frac{1}{a^2} (\tilde{v} \cdot \nabla \tilde{p}) + \rho \nabla \cdot \tilde{v} = 0, \tag{2.3}$$

in which $a(\rho) = d\tilde{p}/d\rho$ is the velocity of sound in the perilymph.

The substitution of ρ by its average ρ_0 , by which $a(\rho)$ likewise becomes a constant, leaves one non-linear term in each of the equations (2.2) and (2.3). These terms can be disregarded under the hypothesis of small velocities, so that

$$\frac{1}{\rho_0 a^2} \tilde{p}_t + \nabla \cdot \tilde{v} = 0, \tag{2.4}$$

$$\rho_0 \tilde{v}_t + \nabla \tilde{p} = 0. \tag{2.5}$$

We take only pure tones of frequency $f = \omega/2\pi$ into consideration and set

$$\tilde{p}(x, y, z, t) = p(x, y, z) e^{i\omega t}, \tag{2.6}$$

$$\tilde{v}(x, y, z, t) = v(x, y, z) e^{i\omega t}. \tag{2.7}$$

Then, writing $v = (u, v, w)$, we can simplify (2.4) and (2.5) as follows:

$$\frac{i\omega}{\rho_0 a^2} p + u_x + v_y + w_z = 0, \tag{2.8}$$

$$i\omega \rho_0 u + p_x = 0, \tag{2.9}$$

$$i\omega \rho_0 v + p_y = 0, \tag{2.10}$$

$$i\omega \rho_0 w + p_z = 0, \tag{2.11}$$

Equations (2.8)–(2.11) hold for both scala vestibuli (sv) and scala tympani (st).

We are interested mostly in the deflection of the partition. Since it is assumed generally that this depends on the pressure difference between the two channels only, we define

$$P(x, y, z) = p_{sv}(x, y, z) - p_{st}(x, y, -z). \tag{2.12}$$

It can be deduced easily from (2.8)–(2.11) that P satisfies the equation

$$\Delta P + \frac{\omega^2}{a^2} P = 0, \tag{2.13}$$

where Δ is the Laplace-operator.

To solve P from this equation, six boundary conditions are needed. Three of them can be obtained from the fact that the velocity component normal to the walls vanishes at the walls. Using (2.10), (2.11) and (2.12) we find

$$P_y(x, 0, z) = 0, \tag{2.14}$$

$$P_y(x, b, z) = 0, \tag{2.15}$$

$$P_z(x, y, h) = 0. \tag{2.16}$$

Because of the direct contact between the fluids in the scalae at the helicotrema, there can be no pressure difference at this point; hence it follows that

$$P(0, y, 0) = 0. \tag{2.17}$$

In addition we have the membrane equation

$$\zeta^* w(x, y, 0) = P(x, y, 0) \rightarrow 2P(x, y, 0) = \zeta P_z(x, y, 0). \tag{2.18}$$

In this equation is employed the impedance

$$\zeta = \frac{i\zeta^*}{\rho_0 \omega} = \frac{1}{\rho_0 \omega^2} (c - m\omega^2 + ik\omega), \tag{2.19}$$

with c, m, k stiffness, mass and resistance of the membrane per unit area. Finally we suppose $P(l, y, z)$ is known.

The solution of (2.13) satisfying (2.14)–(2.18) can be obtained by separation of variables. It reads

$$P(x, y, z) = \sum_{\alpha=0}^{\infty} \sum_{\beta=0}^{\infty} B_{\alpha,\beta} \sinh(\lambda_{\alpha,\beta} x) \cos\left(\frac{\alpha\pi y}{b}\right) \cos(\tau_{\beta}(h-z)) \tag{2.20}$$

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

$$\lambda_{\alpha,\beta}^2 = \left(\frac{\alpha\pi}{b}\right)^2 + \tau_{\beta}^2 - \frac{\omega^2}{a^2} \tag{2.21}$$

and the τ_{β} are roots of

$$\tau \operatorname{tg}(\tau h) = \frac{2}{\zeta}, \tag{2.22}$$

arranged towards increasing β according to increasing modulus; the quantities $\lambda_{\alpha,\beta}, \tau_{\beta}$ and ζ are complex. The coefficients $B_{\alpha,\beta}$ can be found from the window condition (i.e. $P(l, y, z)$ is known).

Define δ by

$$\delta = \frac{2h}{\zeta}. \tag{2.23}$$

With the aid of this (2.22) becomes

$$\tau h \operatorname{tg}(\tau h) = \delta, \tag{2.24}$$

so that for small $|\delta|$ the following approximations are valid:

$$\begin{aligned} \tau_0 h &= \delta^{\frac{1}{2}}, \\ \tau_{\beta} h &= \beta\pi + \frac{\delta}{\beta\pi}, \quad \beta = 1, 2, \dots \end{aligned} \tag{2.25}$$

Here, second and higher powers of δ have been neglected.

Employing (2.25), (2.20) can be written as

$$\begin{aligned} P(x, y, z) &= \sum_{\alpha=0}^{\infty} \left[B_{\alpha,0} \sinh(\lambda_{\alpha,0} x) \cos\left(\frac{\alpha\pi y}{b}\right) \cos\left(\frac{(h-z)\delta^{\frac{1}{2}}}{h}\right) + \right. \\ &\quad \left. + \sum_{\beta=1}^{\infty} B_{\alpha,\beta} \sinh(\lambda_{\alpha,\beta} x) \cos\left(\frac{\alpha\pi y}{b}\right) \cos\left(\frac{\beta\pi(h-z)}{h}\right) \right] + O(\delta). \end{aligned} \tag{2.26}$$

For a comparison with the one-dimensional model it is sufficient to consider p_{av} , that is, the average of $P(x, y, z)$ over a cross-section of the channel. Hence, p_{av} is given by

$$\begin{aligned} p_{av}(x) &= \frac{1}{bh} \int_{y=0}^b \int_{z=0}^h P(x, y, z) dy dz = \\ &= B_{0,0} \sinh(\lambda_{0,0} x) \frac{\sin \delta^{\frac{1}{2}}}{\delta^{\frac{1}{2}}} + O(\delta). \end{aligned} \tag{2.27}$$

Since $P(l, y, z)$ is prescribed, $p_{av}(l)$ is known. Obviously we can write for p_{av} , ignoring $O(\delta)$,

$$p_{av}(x) = p_{av}(l) \frac{\sinh(\lambda_{0,0}x)}{\sinh(\lambda_{0,0}l)} \tag{2.28}$$

with $\lambda_{0,0}$ given by

$$\lambda_{0,0}^2 = \tau_0^2 - \frac{\omega^2}{a^2}, \tag{2.29}$$

where τ_0^2 denotes the root of (2.22) with the smallest modulus.

Though we are interested mostly in the pressure difference we have considered the pressure sum also for the sake of completeness. Writing

$$Q(x, y, z) = p_{sv}(x, y, z) + p_{st}(x, y, -z) \tag{2.30}$$

we have to solve the equation

$$\Delta Q + \frac{\omega^2}{a^2} Q = 0 \tag{2.31}$$

subject to the boundary conditions

$$Q_y(x, 0, z) = 0, \tag{2.32}$$

$$Q_y(x, b, z) = 0, \tag{2.33}$$

$$Q_z(x, y, h) = 0, \tag{2.34}$$

$$Q_z(x, y, 0) = 0, \tag{2.35}$$

$$\int_{y=0}^b \int_{z=0}^h Q_x(0, y, z) dy dz = 0 \tag{2.36}$$

and $Q(l, y, z)$ prescribed. Equation (2.35) can be derived from (2.11) and its analogue for the scala tympani; (2.36) is due to the condition of zero axial flux at the helicotrema.

For our purpose only the cross-sectional average q_{av} of $Q(x, y, z)$ is important:

$$q_{av}(x) = q_{av}(l) \frac{\cosh(\omega x/a)}{\cosh(\omega l/a)}. \tag{2.37}$$

Here, $q_{av}(l)$ is known. It can be obtained easily from the prescribed $Q(l, y, z)$.

3. The one-dimensional model

The Peterson–Bogert equations for a cochlea of which the scalae are equal and have constant cross-sectional areas, are ([7]):

$$(p_{sv} - p_{st})_{xx} + \left(\frac{\omega^2}{a^2} - \frac{2}{\zeta h} \right) (p_{sv} - p_{st}) = 0, \tag{3.1}$$

$$(p_{sv} + p_{st})_{xx} + \frac{\omega^2}{a^2} (p_{sv} + p_{st}) = 0. \tag{3.2}$$

In this conception p_{sv} and p_{st} are homogeneous over the respective cross-sections. When

$$p(x) = p_{sv}(x) - p_{st}(x), \tag{3.3}$$

$$q(x) = p_{sv}(x) + p_{st}(x), \tag{3.4}$$

the boundary conditions for (3.1) which are in agreement with the three-dimensional case, are

$$p(0) = 0, \tag{3.5}$$

$$p(l) = p_{av}(l), \tag{3.6}$$

while (3.2) is liable to

$$q_x(0) = 0, \quad (3.7)$$

$$q(l) = q_{av}(l). \quad (3.8)$$

The solutions for p and q are

$$p(x) = p_{av}(l) \frac{\sinh(\theta x)}{\sinh(\theta l)}, \quad (3.9)$$

where θ is given by

$$\theta^2 = \frac{2}{\zeta h} - \frac{\omega^2}{a^2}, \quad (\theta, \zeta \text{ complex}) \quad (3.10)$$

$$q(x) = q_{av}(l) \frac{\cosh(\omega x/a)}{\cosh(\omega l/a)}. \quad (3.11)$$

4. Discussion

In view of the foregoing it is clear that the results for the pressure sum of the Peterson–Bogert model correspond with the three-dimensional results completely. When we look at the pressure difference, we see from eqs. (2.28), (2.29), (2.22) and (3.9), (3.10) that the one-dimensional model is an asymptotic approximation of the three-dimensional model by letting $|\tau_0 h| \rightarrow 0$, since (2.28) and (3.9) can be asymptotically equal only if $|\lambda_{0,0}| = |\theta|$. For this to hold, $\tau_0 \operatorname{tg}(\tau_0 h)$ needs to be replaced by $\tau_0^2 h$. This can be done approximately if $|\tau_0 h| \ll 1$, or, in other words, if $|\zeta h^{-1}| \gg 1$.

It can be expected that this criterion will be valid as well in the non-simplified model of the cochlea, because the geometry plays no part in it.

From (2.19) it is found that

$$|\zeta h^{-1}| = \frac{[(c - m\omega^2)^2 + k^2 \omega^2]^{\frac{1}{2}}}{\rho_0 \omega^2 h} = \frac{1}{\rho_0 h} \left(m^2 + \frac{k^2 - 2mc}{\omega^2} + \frac{c^2}{\omega^4} \right)^{\frac{1}{2}}. \quad (4.1)$$

The numerical values, used by Peterson and Bogert [2], [7] are

$$c = 1.72 \times 10^9 e^{2(x-1)} \text{ dyn/cm}^3, \quad k = 6.737 \times 10^3 e^{x-1} \text{ g/cm}^2 \cdot \text{s}, \\ m = 0.143 \text{ g/cm}^2, \quad \rho_0 = 1 \text{ g/cm}^3,$$

while $h \approx 0.1$ cm and $10^2 < \omega < 10^5$ c.p.s.

Regarding these values which are not very precise but do give us enough qualitative information, we can conclude that the Peterson–Bogert equations are inappropriate to describe the cochlear phenomena for high frequencies. Also, for low frequencies, the computed values near the position of maximal membrane amplitude (where $c \approx m\omega^2$, see e.g. [11]) may differ from the real ones.

Lastly it can be seen immediately from (2.21) and (2.29) that the compressibility is negligible as to the results of the pressure difference for low frequencies, namely $f \ll a|\tau_0|/2\pi$.

5. The viscous case

Since the equations for a viscous fluid cannot be dealt with as easily as in the non-viscous case the approach to this problem differs fundamentally from the former. Suppose the fluid can be considered as incompressible which is certainly justified for low frequencies. Then the continuity equation reads

$$\nabla \cdot \tilde{\mathbf{v}} = 0 \quad (5.1)$$

and the equation of motion reads

$$\rho \tilde{v}_t + \rho(\tilde{v} \cdot \nabla)\tilde{v} + \nabla \tilde{p} - \mu \Delta \tilde{v} = \theta, \tag{5.2}$$

where μ is the coefficient of viscosity.

When the non-linear quadratic velocity term is disregarded and only harmonic oscillations are considered, (5.2) becomes with the aid of (2.6)–(2.7)

$$i\omega \rho \mathbf{v} + \nabla p - \mu \Delta \mathbf{v} = \theta. \tag{5.3}$$

Decompose p and \mathbf{v} in an inviscid part (p_0, \mathbf{v}_0) and a perturbation (p_1, \mathbf{v}_1) as a result of the viscosity. Then (5.1) and (5.3) can be written as

$$\nabla \cdot (\mathbf{v}_0 + \mathbf{v}_1) = 0, \tag{5.4}$$

$$i\omega \rho (\mathbf{v}_0 + \mathbf{v}_1) + \nabla (p_0 + p_1) - \mu \Delta (\mathbf{v}_0 + \mathbf{v}_1) = \theta, \tag{5.5}$$

where p_0 and \mathbf{v}_0 satisfy the equations for an inviscid fluid (see Section 2). Moreover, because the inviscid flow is irrotational, we have

$$\nabla \times \mathbf{v}_0 = \theta, \tag{5.6}$$

so that the relation

$$\Delta \mathbf{v}_0 = \nabla \nabla \cdot \mathbf{v}_0 - \nabla \times (\nabla \times \mathbf{v}_0) \tag{5.7}$$

with the aid of (5.1) and (5.6) leads to

$$\Delta \mathbf{v}_0 = \theta. \tag{5.8}$$

Define ε and q_1 by

$$\varepsilon^2 = \frac{\mu}{\rho \omega}, \tag{5.9}$$

$$q_1 = \frac{p_1}{\rho \omega}. \tag{5.10}$$

In view of the foregoing, (5.4) and (5.5) simplify to

$$\nabla \cdot \mathbf{v}_1 = 0, \tag{5.11}$$

$$i \mathbf{v}_1 + \nabla q_1 - \varepsilon^2 \Delta \mathbf{v}_1 = \theta. \tag{5.12}$$

Inasmuch as (5.11) and (5.12) hold for both channels, it is sufficient to consider the scala vestibuli only.

Suppose that the inviscid flow is the main flow and the effects of viscosity are taken to be localized in a thin layer near the walls ($y=0, y=b, z=h$) and the membrane ($z=0$). The fact that boundary layers do play a role is evident from the following: knowing that $\rho \approx 1 \text{ g/cm}^3$ and $\mu \approx 0.02 \text{ g/cm} \cdot \text{s}$ one finds, when $f=30 \text{ Hz}$, that $\varepsilon=0.01 \text{ cm}$. This means that the thickness of the layer which will appear to be $O(\varepsilon)$, comes to about one tenth of the diameter of a scala ($\approx 1 \text{ mm}$). For large f ($\approx 10^4 \text{ Hz}$) the thickness is of order 0.01 mm , still one percent of the scala diameter.

Because we are interested in the effects in the neighbourhood of the partition only, we confine ourselves to the boundary layer near $z=0$. The flow in this layer is subject to the following hypotheses, already posed by Rayleigh [8]: the derivatives in the x - and y -directions are negligible with respect to those in the z -direction, whilst v and w are small compared to u . The reason for this is as follows: for the inviscid flow the z -component w_0 is equal to the membrane velocity on the partition, while $v_0 \approx 0$ since the flow is approximately axially directed, but $u_0 \neq 0$. Because of the no-slip condition we have therefore that $v_1 = w_1 = 0$ and $u_1 = -u_0 \neq 0$ on the partition, so that from the fact that $\mathbf{v}_1 \approx \theta$ outside the boundary layer it can be deduced that u_1 decreases strongly within the layer while v_1 and w_1 remain small.

Write out (5.11) and (5.12)

$$u_{1,x} + v_{1,y} + w_{1,z} = 0, \tag{5.13}$$

$$i u_1 + q_{1,x} - \varepsilon^2 (u_{1,xx} + u_{1,yy} + u_{1,zz}) = 0, \quad (5.14)$$

$$i v_1 + q_{1,y} - \varepsilon^2 (v_{1,xx} + v_{1,yy} + v_{1,zz}) = 0, \quad (5.15)$$

$$i w_1 + q_{1,z} - \varepsilon^2 (w_{1,xx} + w_{1,yy} + w_{1,zz}) = 0. \quad (5.16)$$

Starting from $\partial/\partial x = O(1)$, $\partial/\partial y = O(1)$ and $u_1 = O(1)$, (5.14) gives $\partial/\partial z = O(\varepsilon^{-1})$, if indeed the viscosity is a factor of some importance. Then (5.13) shows that $w_1 = O(\varepsilon)$ and hence $q_1 = O(\varepsilon^2)$, since when $q_1 = O(\varepsilon)$ it would follow that $q_{1,z} = O(1)$ which contradicts (5.16). With the above-mentioned estimates the most important component of (5.12), namely (5.14) can be simplified by neglecting $O(\varepsilon^2)$ with respect to $O(1)$:

$$i u_1 - \varepsilon^2 u_{1,zz} = 0 \quad (5.17)$$

with the boundary conditions

$$u(x, y, 0) = 0 \rightarrow u_1(x, y, 0) = -u_0(x, y, 0), \quad (5.18)$$

$$\lim_{z \rightarrow \infty} u_1(x, y, z) = 0. \quad (5.19)$$

The solution of (5.17) satisfying (5.18) and (5.19) is:

$$u_1(x, y, z) = -u_0(x, y, 0) \exp\left[-\frac{(1+i)z}{\varepsilon \cdot 2^{\frac{1}{2}}}\right]. \quad (5.20)$$

Now the assumptions made appear to be consistent. One can see clearly from (5.20) that the thickness of the boundary layer is of order ε .

On account of $\partial/\partial x, \partial/\partial y \ll \partial/\partial z$ and $v_1, w_1 \ll u_1$, the rotation is roughly equal to $\partial u_1/\partial z$, since the inviscid flow is irrotational. Thus, the magnitude of the rotation is given approximately by

$$\frac{1}{\varepsilon} |u_0(x, y, 0)| e^{-z/\varepsilon} \quad (5.21)$$

This is maximal with regard to z when $z=0$ (i.e. on the partition) and with regard to x when $|u_0(x, y, 0)|$, that is $|p_{0,x}(x, y, 0)|$ is largest. The calculations of Peterson and Bogert [2], [7] and of Hubbard and Geisler [5] show that $\partial p/\partial x$ is maximal near the helicotrema for low frequencies. For high frequencies the maximum moves towards the windows. It is presumably located in the region where the membrane has its maximum amplitude.

This picture is in complete accordance with the experiments of Von Békésy [1] concerning the localization of the observed eddies and with the statement of Tonndorf [9] that boundary layers in consequence of viscous effects would play a part in this. The most important influence of viscosity therefore seems to consist in the creation of vortices near the position of maximum partition amplitude, but no quantitative conclusions regarding this can be drawn.

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