HARMONIC OSCILLATIONS OF THE CUPULA IN THE VESTIBULAR CANAL

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Our analysis of the endolymph flow in the vestibular canal within a thin torus rotating about its axis with an angular velocity $\omega(t)$ demonstrates that the walls of the canal may be regarded at a first approximation as locally plane. In this case, the system of equations describing the fluid motion in the canal degenerates into a single equation. If the membrane model for the cupula is considered, then the dynamic equations for the cupula–endolymph system are completely integrable. Some amplitude-frequency and phase-frequency characteristics of the model are obtained in the form of algebraic relations.

Introduction. A system of model equations describing the joint dynamics of the cupula (an intracanal partition) and of the endolymph (a viscous fluid) within the rotating vestibular canal should be derived during the process of mathematical modeling of functions of the vestibular canal. One of the widely used methods for analyzing the influence of the fluid on the dynamics of the cupula is an approximate estimation of hydrodynamic forces followed by introducing these forces (taken in integral form) into the equation of motion of the cupula.

In this paper, we consider the fundamental equations for mathematical modeling of the cupula–endolymph system (its phenomenological model was first proposed by Steinhausen in 1933 [1]). As a result, a mathematical model of this system is obtained in the linear approximation on the basis of the dimensional analysis of the dynamic equations with the corresponding initial and boundary conditions.

1. Anatomy and physiology of the vestibular canal. An isolated semicircular canal of the vestibular apparatus is a thin curved duct filled with the endolymph (a viscous incompressible fluid). Both ends of the duct are open and lowered into a reservoir (the utricle). One of the ends of the duct is sharply expanded in the immediate neighborhood of the utricle, forming an ampulla and narrowing down to the initial diameter. The cupula (an elastic partition) lies inside the ampulla and is attached to the ampullary walls on the crista (a sensory base) in such a way that it is capable of shifting in response to the motion of the endolymph within the canal. The subcupular space (a fluid interlayer ranging in thickness from 2 to 5 μm) exists between the cupula and the crista. See [2] for a more detailed description of the anatomy of the canal and appropriate references.

The rotation of the semicircular canal with acceleration directed perpendicularly to the plane of the canal leads to the displacement of the endolymph and, as a consequence, to the deflection of the cupula. The displacement of the cupula relative to the crista causes the deformation of sensitive hairs of the cupula and the change of receptor potential of a cell. In its turn, this change modulates the frequency of impulses in the vestibular nerve. The signal coded by the change of impulse frequency in the vestibular nerve comes to vestibular nuclei of the brain. These nuclei provide the processing and transmission of data on the angular motion. Three semicircular canals positioned in mutually perpendicular planes would suffice to obtain these data.

2. Dynamics of the viscous fluid within the rotating vestibular canal. Let us consider the endolymph dynamics in a semicircular canal of the toroidal form. Suppose a thin torus of outer radius R and inner radius a rotates about its axis with a given angular velocity $\omega(t)$. The Cartesian system XYZ with the origin O at the center of the torus is associated with the torus formed by rotating the circle of radius a (lying in the plane XZ) about the Z-axis.

Let r and λ be the polar coordinates in the plane of the cross section of the torus and θ be the angular coordinate of this section measured from the X-axis. Then, the coordinates r, λ, θ and x, y, z are related as follows:

$$x = (R + r\cos\lambda)\cos\theta, \quad y = (R + r\cos\lambda)\sin\theta, \quad z = r\sin\lambda$$

The fluid motion in the torus is described by the Navier–Stokes equation

$$\frac{d\boldsymbol{V}}{dt} = \boldsymbol{F} - \frac{1}{\rho}\,\mathrm{grad}\,p + \nu\,\nabla^2\boldsymbol{V} \tag{1}$$

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and by the continuity equation

$$\operatorname{div} \boldsymbol{V} = 0 \tag{2}$$

Here $\boldsymbol{V}$ is the absolute velocity of the fluid, $\boldsymbol{F}$ is the mass-force vector, p is the fluid pressure, ρ is the density of the endolymph, μ is its viscosity, and $\nu = \mu/\rho$ is the fluid kinematic viscosity. Let us introduce the following nondimensional variables:

$$r = ar', \quad \frac{a}{R} = \varepsilon, \quad \boldsymbol{V} = V_{\mathrm{m}} \boldsymbol{V}', \quad \mathrm{Re} = \frac{a V_{\mathrm{m}}}{\nu}, \quad t = \frac{a}{V_{\mathrm{m}}}\,\tau, \quad h = 1 + \varepsilon r' \cos\lambda, \quad p = \rho V_{\mathrm{m}} p' \tag{3}$$

Taking into account (3) and the formula $\boldsymbol{F} = 0$, we rewrite equation (1) in the form

$$\frac{d\boldsymbol{V}'}{d\tau} = -\operatorname{grad} p' + \mathrm{Re}^{-1} \nabla^2 \boldsymbol{V}' \tag{4}$$

Projecting (4) on the axes of the rotating toroidal system r, λ, θ, we obtain

$$\begin{aligned}
&\frac{\partial V_r'}{\partial \tau} + V_r' \frac{\partial V_r'}{\partial r'} + \frac{V_\lambda'}{r'} \frac{\partial V_r'}{\partial \lambda} + \frac{\varepsilon V_\theta'}{h} \frac{\partial V_r'}{\partial \theta} - \frac{(V_\lambda')^2}{r'} - \frac{\varepsilon \cos\lambda}{h} (V_\theta')^2 = -\frac{\partial p'}{\partial r'} \\
&\quad + \frac{\mathrm{Re}^{-1}}{h r'} \left\{ \varepsilon \frac{\partial}{\partial \theta} \left[\frac{r'}{h} \left(\varepsilon \frac{\partial V_r'}{\partial \theta} - h \frac{\partial V_\theta'}{\partial r'} - \varepsilon \cos\lambda\, V_\theta' \right) \right] - \frac{\partial}{\partial \lambda} \left[h \left(\frac{\partial V_\lambda'}{\partial r'} + \frac{V_\lambda'}{r'} - \frac{1}{r'} \frac{\partial V_r'}{\partial \lambda} \right) \right] \right\} \\
&\frac{\partial V_\lambda'}{\partial \tau} + V_r' \frac{\partial V_\lambda'}{\partial r'} + \frac{V_\lambda'}{r'} \frac{\partial V_\lambda'}{\partial \lambda} + \frac{\varepsilon V_\theta'}{h} \frac{\partial V_\lambda'}{\partial \theta} + \frac{V_r' V_\lambda'}{r'} + \frac{\varepsilon \sin\lambda}{h} (V_\theta')^2 = -\frac{1}{r'} \frac{\partial p'}{\partial \lambda} \\
&\quad + \frac{\mathrm{Re}^{-1}}{h} \left\{ \varepsilon \frac{\partial}{\partial \theta} \left[\frac{1}{r' h} \left(\varepsilon r' \frac{\partial V_\lambda'}{\partial \theta} - h \frac{\partial V_\theta'}{\partial \lambda} + \varepsilon r' \sin\lambda\, V_\theta' \right) \right] + \frac{\partial}{\partial r'} \left[h \left(\frac{\partial V_\lambda'}{\partial r'} + \frac{V_\lambda'}{r'} - \frac{1}{r'} \frac{\partial V_r'}{\partial \lambda} \right) \right] \right\} \\
&\frac{\partial V_\theta'}{\partial \tau} + V_r' \frac{\partial V_\theta'}{\partial r'} + \frac{V_\lambda'}{r'} \frac{\partial V_\theta'}{\partial \lambda} + \frac{\varepsilon V_\theta'}{h} \frac{\partial V_\theta'}{\partial \theta} + \frac{\varepsilon V_\theta'}{h} (V_r' \cos\lambda - V_\lambda' \sin\lambda) = -\frac{\varepsilon}{h} \frac{\partial p'}{\partial \theta} \\
&\quad + \frac{\mathrm{Re}^{-1}}{r'} \left\{ \frac{\partial}{\partial \lambda} \left[\frac{1}{r' h} \left(h \frac{\partial V_\theta'}{\partial \lambda} - \varepsilon r' \sin\lambda\, V_\theta' - \varepsilon r' \frac{\partial V_\lambda'}{\partial \theta} \right) \right] - \frac{\partial}{\partial r'} \left[\frac{r'}{h} \left(\varepsilon \frac{\partial V_r'}{\partial \theta} - h \frac{\partial V_\theta'}{\partial r'} - \varepsilon \cos\lambda\, V_\theta' \right) \right] \right\}
\end{aligned} \tag{5}$$

where V_r', V_λ', and V_θ' are the projections of the fluid dimensionless velocity $\boldsymbol{V}'$ on the axes r, λ, and θ. The continuity equation (2) can be written down in nondimensional form as follows:

$$\frac{\partial V_r'}{\partial r'} + \frac{V_r'(1 + 2\varepsilon r' \cos\lambda)}{r' h} + \frac{1}{r'} \frac{\partial V_\lambda'}{\partial \lambda} - \frac{\varepsilon \sin\lambda}{h} V_\lambda' + \frac{\varepsilon}{h} \frac{\partial V_\theta'}{\partial \theta} = 0 \tag{6}$$

Suppose $\boldsymbol{u}$ is the fluid velocity relative to the walls of the semicircular canal, u_r, u_λ are the transverse components of the relative velocity in the plane of the cross section of the torus, and u is the velocity component along the curved axis of the canal. Then,

$$V_r = u_r, \quad V_\lambda = u_\lambda, \quad V_\theta = u + \omega\,(R + r\cos\lambda) \tag{7}$$

Since the cross section of the canal is sufficiently small $\left(\dfrac{a}{R} \sim \varepsilon\right)$, its walls are smooth, and the appearance of secondary flows is improbable, we set

$$\frac{u_r}{u} = O\left(\varepsilon^2\right), \quad \frac{u_\lambda}{u} = O\left(\varepsilon^2\right)$$

and simplify system (5), (6) with regard to (3) and (7). If we ignore the terms of order ε^2, then from equation (6) we obtain

$$\frac{\partial V_\theta'}{\partial \theta} = 0 \tag{8}$$

As a result, equations (5) take the form

$$\begin{cases} \varepsilon \dfrac{(V_\theta')^2}{h} \cos\lambda = \dfrac{\partial p'}{\partial r'} \\[2ex] \varepsilon \dfrac{(V_\theta')^2}{h} \sin\lambda = -\dfrac{1}{r'} \dfrac{\partial p'}{\partial \lambda} \end{cases} \tag{9}$$

$$\frac{\partial V'_\theta}{\partial \tau} = -\frac{\varepsilon}{h}\frac{\partial p'}{\partial \theta} + \mathrm{Re}^{-1}\left[\frac{1}{r'}\frac{\partial}{\partial r'}\left(r'\frac{\partial V'_\theta}{\partial r'}\right)\right] \tag{10}$$

See [3] for more detailed mathematical manipulations.

It is assumed that the symmetry of the flow with respect to the angle λ exists in system (8)–(10). Ignoring the terms of order ε^2, from equations (8) and (10) we get $\dfrac{\partial p'}{\partial \theta} = \varphi(\tau)$; hence, system (9), (10) is decomposed into two independent parts (9) and (10). The relations ($ds = R\,d\theta$)

$$\frac{\varepsilon}{d\theta} = \frac{a}{ds} = \frac{1}{ds'} \quad (s = as')$$

are valid for the dimensionless variables ε and $d\theta$ near the cupula. Therefore, near the cupula we should take $\dfrac{\partial p'}{\partial s'}$ instead of $\varphi(t)$ and write down equation (10) in the form

$$\frac{\partial V'_\theta}{\partial \tau} = -\frac{1}{h}\frac{\partial p'}{\partial s'} + \mathrm{Re}^{-1}\left[\frac{1}{r'}\frac{\partial}{\partial r'}\left(r'\frac{\partial V'_\theta}{\partial r'}\right)\right]$$

Turning back to the dimensional variables, we obtain

$$\frac{\partial u}{\partial t} + \dot{\omega}R = -\frac{1}{\rho}\frac{\partial p}{\partial s} + \nu\left(\frac{\partial^2 u}{\partial r^2} + \frac{1}{r}\frac{\partial u}{\partial r}\right) \tag{11}$$

where

$$\frac{1}{\rho}\frac{\partial p}{\partial s} = f(t)$$

Thus, our analysis of the motion of the endolymph within the toroidal rotating vestibular canal leads to solving equation (11) with the corresponding initial and boundary conditions. The pressure gradient $\dfrac{\partial p}{\partial s}$ entering into equation (11) is determined from the boundary condition at the cupula.

3. Harmonic oscillations of the cupula–membrane in the toroidal vestibular canal. Let us consider the toroidal vestibular canal filled with a viscous incompressible fluid and rotating about its axis with an angular velocity $\omega(t)$. It is assumed that the cupula is a weighable membrane attached to the ampullary walls in such a way that the possibilities for leakage of the fluid are eliminated. The membrane has the density ρ, thickness 2δ, and stiffness T. Now we consider transverse oscillations of the membrane when its displacement $\xi(r,t)$ from the equilibrium position is directed perpendicularly to the plane of the undeflected membrane. The function $\xi(r,t)$ specifies a shape of the membrane, which is symmetric with respect to λ and has its maximal deflection when $r = 0$.

The transverse oscillations of the membrane are described by the equation

$$2\delta\rho\left(\ddot{\xi} + \dot{V}_t\right) = T\nabla^2\xi + (p_1 - p_2) \tag{12}$$

with the boundary conditions

$$\xi(a,t) = 0, \quad \frac{\partial \xi}{\partial r}(0,t) = 0$$

and with the corresponding initial conditions. Here $V_t = \omega R$ is the transient velocity of the canal, $(p_1 - p_2)$ is the pressure drop across the cupula, and the dot indicates the time differentiation. At the cupula we have $u(r,t) = \dot{\xi}(r,t)$ (i.e., the velocities of the fluid and cupula are equal). Setting $u = \dot{\xi}(r,t)$ in equation (11) and expressing $(p_1 - p_2)$ from this equation, from (11) and (12) we can obtain

$$l\rho\left(\ddot{\xi} + \dot{V}_t\right) = T\nabla^2\xi + (l - 2\delta)\,\rho\nu\nabla^2\dot{\xi} \tag{13}$$

where l is the length of the vestibular canal. Dividing equation (13) by $l\rho$ and ignoring the terms of order ε $\left(\dfrac{2\delta}{l} \sim \varepsilon\right)$, we get

$$\ddot{\xi} + \dot{V}_t = \nabla^2\left(\frac{T}{\rho l}\xi + \nu\dot{\xi}\right) \tag{14}$$

Let us consider the oscillations of the membrane in response to the periodic stimulus $V_n = d\cos\sigma t$. According to (14), the displacement of the membrane in the absolute coordinate system $\zeta(r,t)$ (where $\ddot{\zeta} = \ddot{\xi} + \dot{\omega}R$) satisfies the equation

$$\ddot{\zeta} = \nabla^2\left(\frac{T}{\rho l}\zeta + \nu\dot{\zeta}\right) \tag{15}$$

and the boundary conditions

$$\dot{\zeta}(a,t) = V_t, \quad \frac{\partial\zeta}{\partial r}(0,t) = 0 \tag{16}$$

It can be shown that for a thin torus the equality $\nabla^2 = \dfrac{\partial^2}{\partial r^2}$ is a sufficient approximation of the Laplace operator. Then, equation (15) may be written down in the form

$$T_0\zeta'' + \nu\dot{\zeta}' - \ddot{\zeta} = 0 \tag{17}$$

where $T_0 = \dfrac{T}{\rho l}$ and the prime indicates the differentiation with respect to r.

As is known, the periodic mode of the motion takes place in response to a periodic signal when the transient process in the cupula–endolymph system is damping. This motion has the frequency equal to a frequency of the forcing stimulus and the relative phase that depends on the frequency of the input signal. Therefore, the steady-state oscillations of the cupula are sought in the form

$$\zeta(r,t) = A(r)\sin\sigma t + B(r)\cos\sigma t \tag{18}$$

From relations (17) and (18) we get

$$T_0A'' + \sigma^2 A - \nu\sigma B'' = 0, \quad \nu\sigma A'' + \sigma^2 B + T_0 B'' = 0 \tag{19}$$

Setting $A = A_0 e^{kr}$ and $B = B_0 e^{kr}$, we obtain the following four linearly independent solutions of equation (17):

$$\zeta_1 = e^{k_1 r + i\sigma t}, \quad \zeta_2 = e^{-k_1 r + i\sigma t}, \quad \zeta_3 = e^{k_2 r - i\sigma t}, \quad \zeta_4 = e^{-k_2 r + i\sigma t} \tag{20}$$

Here $A_0 = \pm iB_0$, $c^2 = T_0^2 + \nu^2\sigma^2$, $\sin\alpha = \dfrac{T_0}{c}$, $\cos\alpha = \dfrac{\nu\sigma}{c}$, $k_1 = \dfrac{\sigma}{\sqrt{c}}\left(-\sin\dfrac{\alpha}{2} + i\cos\dfrac{\alpha}{2}\right) = -M + iN$, and $k_2 = \dfrac{\sigma}{\sqrt{c}}\left(\sin\dfrac{\alpha}{2} + i\cos\dfrac{\alpha}{2}\right) = M + iN$. Equation (17) has the general solution

$$\zeta = \sum_{n=1}^{4} c_n\zeta_n \tag{21}$$

Substituting (20) into (21), separating the real and imaginary parts, and combining them, we obtain the required solution. The unknown coefficients in this solution are determined from boundary conditions (16) (see [3]).

As a result, the deflection of the membrane under the action of the periodic stimulus $V_t = d\cos\sigma t$ is as follows:

$$\begin{aligned}\zeta(r,t) = {} & \frac{d}{\sigma\left(\operatorname{sh}^2 Ma + \cos^2 Na\right)} \\ & \times \{\cos\sigma t(\operatorname{sh} Ma\sin Na\operatorname{ch} Mr\cos Nr - \operatorname{ch} Ma\cos Na\operatorname{sh} Mr\sin Nr) \\ & + \sin\sigma t(\operatorname{ch} Ma\cos Na\operatorname{ch} Mr\cos Nr + \operatorname{sh} Ma\sin Na\operatorname{sh} Mr\sin Nr)\}\end{aligned}$$

When $r = 0$, the maximal deflection of the cupula is

$$\zeta(0,t) = \frac{d}{\sigma\left(\operatorname{sh}^2 Ma + \cos^2 Na\right)}\{\operatorname{sh} Ma\sin Na\cos\sigma t + \operatorname{ch} Ma\cos Na\sin\sigma t\} \tag{22}$$

Formula (22) may be written in the form $\zeta(0,t) = Q(\sigma)\sin(\sigma t + \varphi)$, where

$$\left|\frac{Q}{\zeta_c}\right| = \frac{1}{\sqrt{\operatorname{sh}^2 Ma + \cos^2 Na}}, \quad \tan\varphi = \operatorname{th} Ma\tan Na \tag{23}$$

Formula (23) expresses the amplitude and the phase of oscillations of the membranous center, depending on the frequency of the periodic stimulus.

The amplitude and the phase of oscillations of the membranous center relative to the walls of the vestibular canal are determined by the formulas

$$A = \left|\frac{\xi}{\zeta_c}\right| = \frac{\operatorname{ch} Ma + \cos Na}{\sqrt{\operatorname{sh}^2 Ma + \cos^2 Na}}, \quad \tan\varphi_{\mathrm{rel}} = \frac{\operatorname{th} Ma \tan Na}{1 + \dfrac{\operatorname{sh}^2 Ma + \cos^2 Na}{\operatorname{ch} Ma \cos Na}} \tag{24}$$

Here ζ_c is the amplitude of transient motion of these walls.

4. Dynamics of the cupula–membrane in the canal of variable section. Let us consider a toroidal vestibular canal whose end is widened by a factor of k. Both the ends of the torus are open and lowered into a reservoir (the utricle). Let $a_0 = ka$ $(k > 1)$ be the radius of the ampulla and l_1 be the length of the utricle. The cupula–membrane completely overlaps the cross section of the ampulla and its displacement $\xi(r,t)$ from the equilibrium position is subject to equation (12) and the boundary conditions

$$\xi(a_0, t) = 0, \quad \frac{\partial\xi}{\partial r}(0,t) = 0 \tag{25}$$

The pressure difference $(p_1 - p_2)$ at both sides of the cupula is specified by the pressure drop across the utricle and the narrow part of the vestibular canal. Let us estimate the pressure drop across the canal, using the equation of endolymph dynamics (11). Taking into account (3), these equations can be written down in nondimensional form as follows:

$$\begin{gathered} \frac{1}{r'}\frac{\partial}{\partial r'}\left(r'\frac{\partial u'}{\partial r'}\right) - \mathrm{Re}\,\frac{\partial u'}{\partial \tau} = \mathrm{Re}\,\frac{Rh\dot\omega}{V_{cp}} + \frac{\mathrm{Re}}{h}\frac{\partial p'}{\partial s'} \\ u'|_{r'=1} = 0 \end{gathered} \tag{26}$$

The exact solution of this equation is given in [8]. Following the paper [8], we seek a solution to equation (26) in the form

$$u'(r',\tau) = \sum_{n=1}^{\infty} u_n(\tau)\, J_0(\beta_n r') \tag{27}$$

where $J_0(\beta_n r')$ is the Bessel function of zero order and β_n are the eigenvalues of this function.

Note that the right-hand side of equation (26) depends only on the time τ. Assuming that $\dot\omega(\tau)$ and $\dfrac{\partial p'}{\partial s'}(\tau)$ are harmonic time functions, we replace this right-hand side by a harmonic function $g\,e^{ip\tau}$ $(p\tau = \sigma t)$. Then, from equations (26) and (27) we obtain

$$J_0(\beta_n r') = J_{0n}, \quad \sum_{n=1}^{\infty}\left\{\beta_n^2 J_{0n} u_n + \mathrm{Re}\, J_{0n}\frac{\partial u_n}{\partial\tau}\right\} = g\,e^{ip\tau} \tag{28}$$

Let us multiply equation (28) by J_{0m} $(m = 1, 2, \ldots)$ and integrate it over the area of the cross section of the canal. Using the property of orthogonality of Bessel functions, we obtain

$$\frac{\partial u_n}{\partial \tau} + \alpha_n u_n = g_n e^{ip\tau}, \quad n = 1, 2, \ldots$$

$$\alpha_n = \frac{\beta_n^2}{\mathrm{Re}}, \quad g_n = \frac{g \displaystyle\iint_A J_{0n}\, dA}{\mathrm{Re} \displaystyle\iint_A J_{0n}^2\, dA}$$

Hence,

$$u_n(\tau) = \frac{g_n}{\alpha_n + ip}\, e^{ip\tau}, \quad n = 1, 2, \ldots \tag{29}$$

From (27) and (29) we find the following expression for the dimensionless velocity of the fluid:

$$u'(r',\tau) = 2g\, e^{ip\tau} \sum_{n=1}^{\infty} \frac{J_{0n}(\beta_n r')}{\beta_n J_1(\beta_n)\,(\beta_n^2 + i\,\mathrm{St})} \tag{30}$$

Here $\mathrm{St} = \dfrac{a^2\sigma}{\nu}$ is the Stokes number and J_1 is the first-order Bessel function.

The viscous shear-stress factor κ introduced in [8] by the formula

$$\kappa = -\pi \frac{\displaystyle\int_{\partial A} \frac{\partial u'}{\partial r'}\, d\lambda}{\displaystyle\iint_A u'\, dA}$$

can be obtained from (30) as

$$\kappa = \pi \frac{\displaystyle\sum_{n=1}^{\infty} \frac{1}{\beta_n^2 + i\,\mathrm{St}}}{\displaystyle\sum_{n=1}^{\infty} \frac{1}{\beta_n^2\,(\beta_n^2 + i\,\mathrm{St})}} \tag{31}$$

The factor κ can be considered as a nondimensional analog of the forces of viscous shear at the lateral surface of the vestibular canal. These forces cause the motion of the endolymph in the canal, inducing the pressure drop across the cupula. The factor κ characterizes the influence of the shape of the cross-section fluid velocity profile on the viscous drag of the duct walls.

If the Poiseuille flow in a straight circular pipe is considered, then $\kappa_{\mathrm{P}} = 8\pi$. It follows from (31) that the factor κ depends on the number St and, hence, on the frequency of a forcing stimulus σ. The dependence of the real part of $\dfrac{\kappa}{8\pi}$ on the number St is represented in Figure 1. This dependence on the frequency σ (the axolotl) is shown in Figure 2. The following parameters were used for the axolotl: $a = 0.0175$ cm and $\nu = 0.0085$ cm/s. The summation was performed up to the 10000th term.

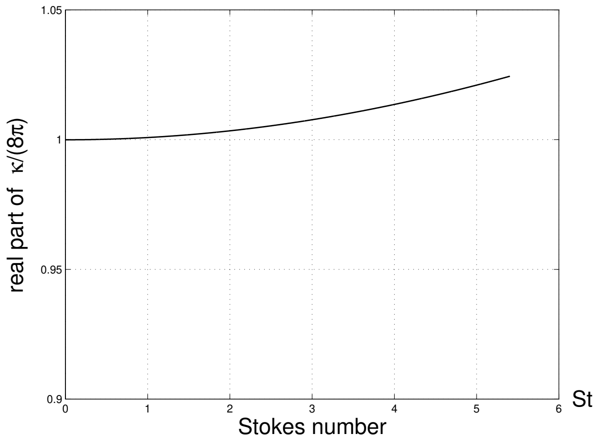

Fig. 1. The shear-stress factor κ is shown relative to the steady laminar flow value $\kappa_{\mathrm{P}} = 8\pi$ as a function of Stokes number

As is seen from these graphs, the factor κ differs practically little from κ_{P} over the physiological range of frequencies. Indeed, if $\mathrm{St} < 2.3$, then $\kappa/\kappa_{\mathrm{P}} < 1.005$; the frequency σ of the forcing stimulus can be varied from 0 to 10 Hz. Hence, when formulating a mathematical model for dynamics of the vestibular canal in the physiological range of frequencies, we can restrict ourselves to an approximate solution (i.e., to the Poiseuille flow for the narrow part of the vestibular canal).

In order to determine the pressure drop across the narrow part of the vestibular canal, we use this flow and the approximate value (given by $\rho\, l_1 R\, \dot{\omega}$) for the pressure drop in the utricle [9]. As a result, we obtain the pressure difference $(p_1 - p_2)$ across the cupula. Let us substitute this difference into equation (12). Following [10], we solve equation (12) with boundary conditions (25). Finally, the displacement $\xi(r,t)$ of the cupula–membrane

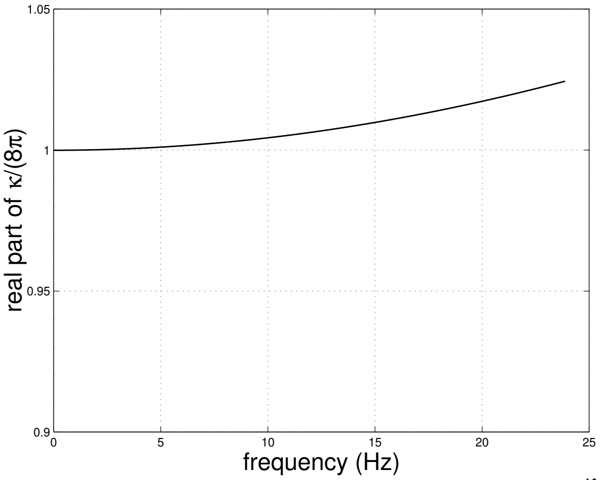

Fig. 2. The frequency dependence of the real part of the shear-stress factor $\frac{\kappa}{8\pi}$ is shown for the case of sinusoidal flow in the pipe

can be written down in the form

$$\begin{aligned} &\xi(r,t) = 2\,M(t)\left(1-\frac{r^2}{a_0^2}\right), \quad 0 \leqslant r \leqslant a_0 \\ &\ddot{M} + \frac{8\nu}{a^2}\,\dot{M} + \frac{8T}{\rho l k^4 m}\,M = -\frac{1}{k^2}\left(1+\frac{l_1}{l}\right)\dot{\omega} R \end{aligned} \tag{32}$$

Here m is the fluid mass of the semicircular canal.

Thus, it was shown that the very complex problem consisting in the study of interaction between the endolymph and the cupula in the toroidal duct with the ampulla and utricle can be reduced to simple equations (32) or to algebraic relations (24) over the physiological range of frequencies.

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