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# The fluid mechanics of the semicircular canals

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A mathematical model for the unsteady fluid-dynamic response of the semicircular canals is developed. The endolymph is assumed to be an incompressible Newtonian fluid and the presence and effects of both the utricle and the cupula are specifically accounted for. A first approximate solution is obtained using a singular perturbation method. It is shown that the canal can be modelled as a heavily damped, second-order system which behaves as an angular-velocity meter. A comparison of the model response with experimental results is made; fairly good agreement is found.

## 1. Introduction

The semicircular canals are the primary transducer for the sensing of angular motions. As such, they are part of the organs of equilibrium. The importance of these organs for the successful functioning of the human body is obvious. The semicircular canals have, therefore, attracted the attention of physiologists, sensory psychologists and physicians over the years. From the very beginning, physical scientists have been consulted to provide an explanation of the mechanics of this fascinating organ.

The advent of aerospace flight with its new demands on the human organism has accelerated the pace of vestibular research. It has become apparent that, while the semicircular canals are an engineering system of some elegance, they are capable of producing disorienting sensations when subjected to non-physiological motion. This knowledge has helped aerospace planners to avoid situations which might prove discomforting or disabling to the pilot or astronaut.

This alone is an adequate reason for wishing to study the mechanics of the canals, but a further incentive comes from the fact that a full understanding of the mechanics of healthy semicircular canals may contribute to the diagnosis and treatment of canals in a diseased state.

## 2. Anatomy and physiology

The semicircular canals are located, along with the organ of hearing, in the inner ear. There are three sets of canals on each side of the head (see figure 1, plate 1). They are oriented in almost mutually orthogonal planes so that rotation about any axis may be properly sensed. As shown, each canal consists of two parts: an outer canal, which is a channel carved in bone, and an inner, membranous canal. The inner canal is filled with a fluid called *endolymph*. The space between the membranous and bony canal is filled with *perilymph*, a fluid different in composition from endolymph.

One end of each semicircular *duct* is enlarged to form its *ampulla*. The ampulla nearly fills the cross-section of the bony canal and terminates on the *utricle*. The ampulla contains the *cupula*, a gelatinous dividing partition with the same density as endolymph. The cupula fills the entire cross-section of the ampulla, thus interrupting the otherwise continuous fluid path through the duct, utricle and ampulla.

The cupula is the system transducer. It is connected to nervous tissue at its base. Mechanical deflexion of the cupula is converted into electrical impulses which transmit the state of angular motion along the vestibular nerve to the central nervous system.

Qualitatively, the manner in which the canals work is as follows. An angular acceleration of the head causes the bony canals and the membranous structure attached to them to accelerate in a similar manner. The inertia of the endolymph, however, causes it to lag behind the motion of the head. Thus there is a flow of endolymph relative to the duct walls. This flow deflects the cupula, initiating the electrical impulses to the brain.

## 3. Review of the literature

The theory that angular acceleration produces an inertially induced flow of endolymph was first proposed independently by Mach (1875), Breuer (1874) and Crum Brown (1874). They did not, however, develop a mathematical model for the flow problem; there was even doubt on the part of some that fluid would flow at all in the very narrow ducts of the semicircular canals.' Gaede (1922) and Schmaltz (1931) were perhaps the first to attempt a mathematical description of flow in the canals. Their efforts are of limited utility however, since they ignored the presence of the cupula and utricle. (In all fairness to these investigators, we should point out that it was not known at the time that the cupula filled the entire cross-section of the ampulla.)

The first to propose the model used today was Wilhelm Steinhausen (1933), who suggested that the canals respond to angular acceleration in the same manner as would a heavily damped torsion pendulum. The mathematical formulation of this idea, which in the literature has come to be known as the 'torsion pendulum equation', may be written in the form

$$I\ddot{\theta}+B\dot{\theta}+K\theta=-I\alpha, \tag{1}$$

where $\theta$, $\dot{\theta}$ and $\ddot{\theta}$ represent respectively the mean angular displacement, mean angular velocity and mean angular acceleration of the endolymph relative to the duct and $\alpha$ is the component of the angular acceleration of the head perpendicular to the plane of the canal. The coefficient $I$ is the inertia term defined by the mass and distribution of the endolymph. The damping coefficient $B$

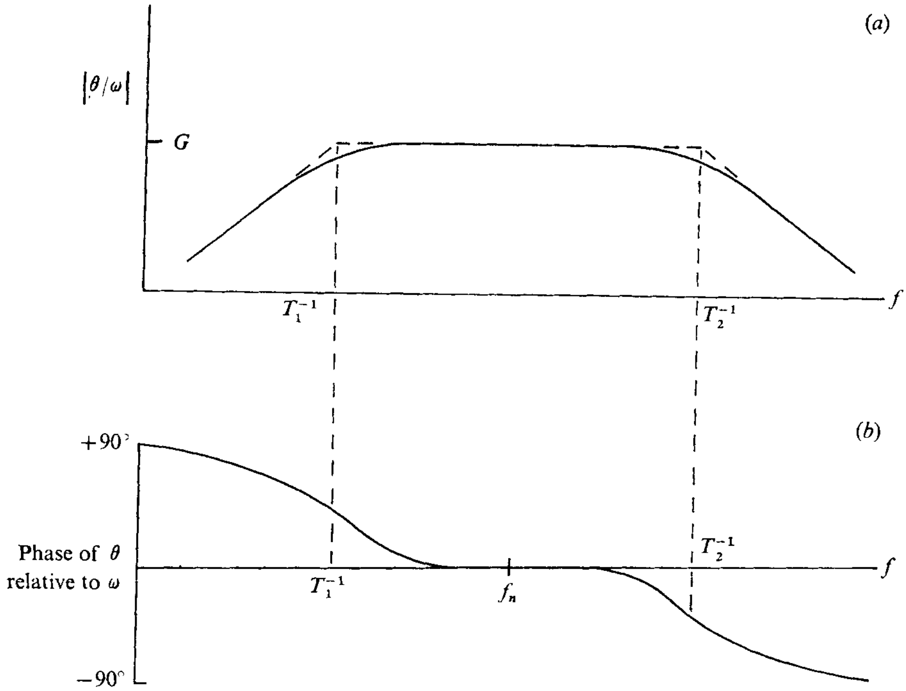


FIGURE 2. Bode plots of the gain and phase lag between the displacement of the endolymph $\theta$ and the angular velocity $\omega$ as a function of the frequency $f$ of sinusoidal oscillation.

denotes the ratio of torque resulting from viscous forces to the mean angular velocity of the endolymph. The stiffness of the cupula is represented by $K$.

The Laplace transform of (1) leads to

$$\theta(s) = -I\alpha(s)/(Is^2+Bs+K), \tag{2}$$

where $\theta(s)$ and $\alpha(s)$ are the Laplace transforms of $\theta(t)$ and $\alpha(t)$. Since the system is heavily overdamped, a convenient and sufficiently accurate form of (2) is

$$\theta(s) = \frac{-\alpha(s)}{(s+T_1^{-1})(s+T_2^{-1})}, \tag{3}$$

where $T_1$ = 'long' time constant $\simeq B/K$, $T_2$ = 'short' time constant $\simeq I/B$ and $T_2 \ll T_1$.

Another convenient form of (2) is obtained by writing down the transfer function from the angular velocity $\omega$ to $\theta$:

$$\frac{\theta}{\omega}(s) = \frac{-s}{(s+T_1^{-1})(s+T_2^{-1})}. \tag{4}$$

The usefulness of such a formulation is seen when we display the frequency response of the system described by (4) in terms of Bode plots. Figure 2(a) is a plot of the logarithm of the ratio of the amplitudes of $\theta$ and $\omega$ as a function of frequency. The phase lag between $\theta$ and $\omega$ is plotted in figure 2(b). It is clear from these graphs that the semicircular canal functions as an angular-velocity meter over the range $2/T_1$ to $1/2T_2$, which, as we shall show below, includes the range of physiological activity.

Since the response of the canals to any input will be governed by $T_1$ and $T_2$, much effort has been expended in attempting to determine these two time constants. One of the problems associated with all of these attempts is the determination of the coefficient $B$, which appears in both $T_1$ and $T_2$. $B$ is invariably calculated assuming Poiseuille flow (see, for example, Schmaltz 1931; van Egmond, Groen & Jongkees 1949; Mayne 1965). But $B$ is a constant only for steady flow, and the inertially induced flow in the semicircular canals is anything but steady. To clarify this issue, we have re-examined the fluid dynamics of semicircular canals.

## 4. Formulation of the problem

We now examine the fluid mechanics of a single canal. The membranous semicircular canal duct is approximated for initial study by a section of a rigid torus filled with an incompressible Newtonian fluid. For the purpose of this analysis, the perilymph is assumed to have no effect on the deflexion of the cupula. The governing equation for the flow of fluid in the duct is the classical Navier–Stokes equation

$$\partial \mathbf{v}/\partial t + \mathbf{v} \cdot \nabla \mathbf{v} = -\rho^{-1}\nabla p + \mathbf{F} + \nu \nabla^2 \mathbf{v}, \tag{5}$$

where $\mathbf{v}$ is the velocity of the fluid with respect to an inertial reference frame, $\rho$ is the density, $p$ is the pressure, $\mathbf{F}$ is the body force and $\nu$ is the kinematic viscosity.

We are interested in the flow of fluid with respect to the duct. Therefore we introduce the symbol $\mathbf{u}$, which will represent the velocity of the fluid relative to the duct wall. If $\mathbf{v}_w$ is the velocity of the wall, then

$$\mathbf{v} = \mathbf{u} + \mathbf{v}_w. \tag{6}$$

Now the velocity of a given point on the duct wall is given by

$$\mathbf{v}_w = \mathbf{v}_c + \boldsymbol{\omega} \times (\mathbf{R} + \mathbf{r}), \tag{7}$$

where $\mathbf{v}_c$ is the velocity of the centre of curvature of the duct, $\boldsymbol{\omega}$ is the angular velocity of the canal, $\mathbf{R}$ is the position vector of the centre of the duct with respect to the centre of curvature, and $\mathbf{r}$ is the position vector of the point on the duct wall with respect to the centre of the duct (see figure 3). Since $|\mathbf{r}|/|\mathbf{R}| \ll 1$, we can approximate $\mathbf{v}_w$ by

$$\mathbf{v}_w \simeq \mathbf{v}_c + \boldsymbol{\omega} \times \mathbf{R}. \tag{8}$$

Therefore

$$\mathbf{v} = \mathbf{u} + \mathbf{v}_c + \boldsymbol{\omega} \times \mathbf{R}. \tag{9}$$

Substituting (9) into (5) we obtain

$$\partial \mathbf{u}/\partial t + \mathbf{u} \cdot \nabla \mathbf{u} + \mathbf{a}_c + \boldsymbol{\alpha} \times \mathbf{R} + \boldsymbol{\omega} \times (\boldsymbol{\omega} \times R) = -\rho^{-1}\nabla p + \mathbf{F} + \nu \nabla^2 \mathbf{u}, \tag{10}$$

where $\mathbf{a}_c$ is the acceleration of the centre of curvature of the duct and $\boldsymbol{\alpha}$ is the angular acceleration of the canal.

Let the pressure gradient $\nabla p$ be split into two parts:

$$\nabla p = \nabla p' + \nabla p'', \tag{11}$$

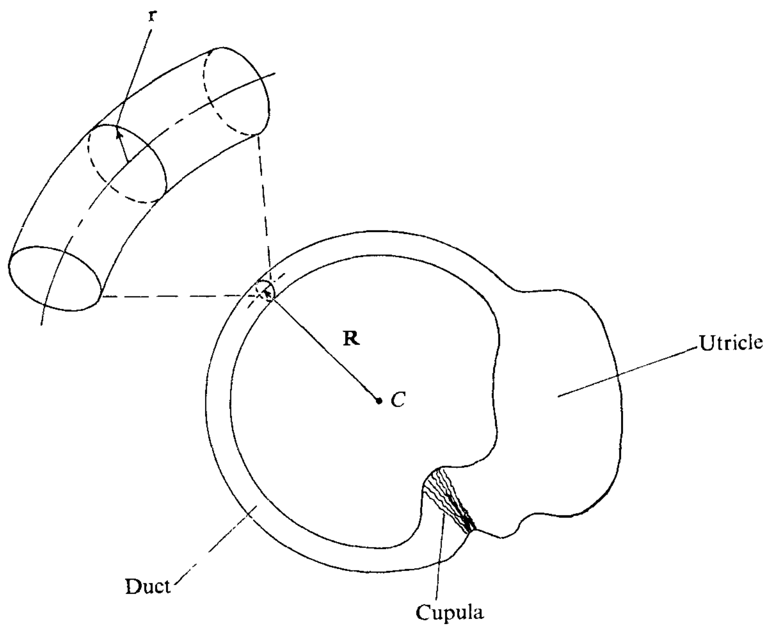


FIGURE 3. A schematic diagram of a single semicircular canal. $\mathbf{R}$ is a vector from $C$ to the centre of the duct and $\mathbf{r}$ is a vector from the tip of $\mathbf{R}$ to the duct wall.

where $\nabla p''$ is the pressure gradient associated with $\mathbf{a}_c$, i.e.

$$\mathbf{a}_c = -\rho^{-1}\nabla p''. \tag{12}$$

This is the same sort of pressure gradient as would arise if the canal were standing in a gravity field. The acceleration $\mathbf{a}_c$ thus leads to no net flow within the canals.

Subtracting $\mathbf{a}_c$ from the left-hand side of (10) and $-\nabla p''/\rho$ from the right side we obtain

$$\partial \mathbf{u}/\partial t + \mathbf{u}\,.\,\nabla\mathbf{u} + \boldsymbol{\alpha}\times\mathbf{R} + \boldsymbol{\omega}\times(\boldsymbol{\omega}\times\mathbf{R}) = -\rho^{-1}\nabla p' + \mathbf{F} + \nu\nabla^2\mathbf{u}. \tag{13}$$

Since $|\mathbf{r}|/|\mathbf{R}| \ll 1$, we may express this equation in cylindrical co-ordinates. The axial component is then

$$\frac{\partial u}{\partial t} + R\alpha = -\frac{1}{\rho}\frac{\partial p}{\partial z} + \frac{\nu}{r}\frac{\partial}{\partial r}\left(r\frac{\partial u}{\partial r}\right), \tag{14}$$

where $r$ is the radial co-ordinate, $z$ is the axial co-ordinate, $u$ is the velocity of the fluid in the axial direction relative to the duct wall, $R$ is the radius of curvature, $\alpha$ is the component of $\boldsymbol{\alpha}$ perpendicular to the canal and $\partial p/\partial z$ is the axial component of $\nabla p'$.

We now consider the possible sources of a pressure gradient. The first source we shall examine is the cupula. The cupula, when deflected, exerts a restoring force on the fluid. We model the cupula as a membrane with linear stiffness $K = \Delta p/\Delta V$, where $\Delta p$ is the pressure difference across the cupula and $\Delta V$ is its volumetric displacement. If the angle subtended by the membranous duct is denoted by $\beta$, the pressure gradient in the duct produced by the cupula is

$$\partial p/\partial z = K\Delta V/\beta R. \tag{15}$$

Now

$$\Delta V = 2\pi \int_0^t \int_0^a u(r,t)\, r\, dr\, dt, \tag{16}$$

in which $a$ is the radius of the duct.

A pressure gradient in the duct is also produced by the presence of the utricle. The size of this contribution may be assessed in the following manner. A cylinder of length $l$ being accelerated through inertial space at a rate $\ddot{s}$ will have a pressure difference between its ends of

$$\Delta p = \rho \ddot{s} l. \tag{17}$$

If the utricle had closed ends, the pressure difference due to rotational motion only could be approximated by

$$\Delta p \simeq \rho \gamma R^2 \alpha, \tag{18}$$

where $\gamma$ is the angle subtended by the utricle. Van Buskirk (1976) has shown that the small acceleration of the fluid in the utricle relative to the walls may be ignored. He has also shown that the pressure drop in the fluid as it moves from the larger utricle into the narrow duct is negligible. Therefore (18) is an accurate approximation and the pressure gradient in the duct due to the presence of the utricle and ampulla is

$$\partial p/\partial z = (\gamma/\beta)\rho R\alpha. \tag{19}$$

Again, of course, we have ignored the pressure gradient associated with $\mathbf{a}_c$ (see (12) *et seq.*). Combining this result with the pressure gradient due to the cupula we have

$$\frac{\partial p}{\partial z} = \frac{\gamma}{\beta}\rho R\alpha + \frac{K\Delta V}{\beta R}. \tag{20}$$

Introducing (16) into (20) and substituting the resulting expression into (14), we obtain the governing equation for the fluid flow in the semicircular canals:

$$\frac{\partial u}{\partial t} + \left(1 + \frac{\gamma}{\beta}\right) R\alpha = -\frac{2\pi K}{\rho \beta R}\int_0^t \int_0^a u(r,t)\, r\, dr\, dt + \frac{\nu}{r}\frac{\partial u}{\partial r}\left(r\frac{\partial u}{\partial r}\right). \tag{21}$$

Equation (21) is non-dimensionalized by substituting the following variables:

$$r' = r/a, \quad t' = t\nu/a^2, \quad u' = u/R\Omega,$$

where $\Omega$ is some characteristic angular velocity of the canal. In terms of these variables (21) becomes

$$\frac{\partial u'}{\partial t'} + \frac{1+\gamma/\beta}{\Omega}\alpha(t') = -\epsilon \int_0^{t'} \int_0^1 u' r' dr'\, dt' + \frac{1}{r'}\left(r'\frac{\partial u'}{\partial r'}\right), \tag{22}$$

where $\epsilon = 2K\pi a^6/\rho\beta R\nu^2$. This equation contains only one non-dimensional parameter, $\epsilon$.

## 5. Solution

We now wish to study the response of the canals to two specific kinds of angular acceleration. We shall first obtain an approximate solution for the case of a step input in angular velocity, corresponding to an abrupt angular motion of the head. Since the problem is a linear one, the frequency response to sinusoidal motion of the head can be readily obtained from this first solution.

A step in angular velocity corresponds to an impulse in angular acceleration. Thus, in dimensionless form,

$$\alpha(t) = \Omega\delta(t), \tag{23}$$

where $\delta(t)$ corresponds to a unit impulse or Dirac delta function applied at $t = 0$. Substituting (23) into (22), we obtain the governing equation for the particular flow we are considering:

$$\frac{\partial u}{\partial t} + \left(1 + \frac{\gamma}{\beta}\right)\delta(t) = \frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial u}{\partial r}\right) - \epsilon\int_0^t\int_0^1 ur\,dr\,dt. \tag{24}$$

Note that in (24) we have dropped the primes. From this point on we shall work with the non-dimensionalized form of the governing equation only.

The boundary and initial conditions for this problem are

$$u(1,t) = 0, \quad \partial u(0,t)/\partial r = 0, \quad u(r,0) = 0. \tag{25}$$

Before solving (24), we examine the order of magnitude of the constant $\epsilon$. The dimensions of the human semicircular canal are $a = 0{\cdot}15$ mm and $R = 3{\cdot}2$ mm (Igarashi 1966). Studies of the physical properties of endolymph (e.g. Steer 1967) suggest that it has a viscosity and density close to those of water, i.e. $\mu = 1{\cdot}0$ mPa s and $\rho = 10^3\,\mathrm{kg/m^3}$. Detailed geometrical studies of the labyrinth of the cat (Fernandez & Valentinuzzi 1968) indicate that $\beta = 1{\cdot}4\pi$ and $\gamma = 0{\cdot}42\pi$. We accept these values for humans. No data are available in the literature for the cupula stiffness $K$ of humans. For the purpose of this discussion we adopt the value $K = 3{\cdot}4\times10^9\,\mathrm{Pa/m^3}$. (This is not entirely arbitrary, as it yields results consistent with experiment, as will be seen below.) Using these values,

$$\epsilon = 2K\pi a^6/\rho\beta R\nu^2 = 0{\cdot}017.$$

Thus $\epsilon$ is very small, while the normalized velocity $u$ is of order unity. Thus the last term on the right side of (24) is very small when $t$ is of order unity or less. However, since the term is an integral over $t$, it can in fact dominate when $t$ is large. This gives the problem a *singular* character. We shall obtain a first approximation using a singular perturbation method.

### 5.1. *Small values of t*

The solution is assumed to take the form of a perturbation series

$$u = u^{(1)} + \epsilon u^{(2)} + \epsilon^2 u^{(3)} + \dots. \tag{26}$$

Substituting this series into (24) and equating terms of like order gives the first approximate equation:

$$\frac{\partial u^{(1)}}{\partial t} + \left(1 + \frac{\gamma}{\beta}\right)\delta(t) = \frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial u^{(1)}}{\partial r}\right). \tag{27}$$

The solution satisfying the initial and boundary conditions (25) has been obtained by Van Buskirk & Grant (1973), and is

$$u^{(1)} = -2\left(1+\frac{\gamma}{\beta}\right)\sum_{n=1}^{\infty}\frac{\exp(-\lambda_n^2 t)\,J_0(\lambda_n r)}{\lambda_n J_1(\lambda_n)}, \tag{28}$$

where $J_0$ is the zeroth-order Bessel function of the first kind, $\lambda_n$ is its $n$th root and $J_1$ is the first-order Bessel function of the first kind. We are interested in the displacement of the cupula. An appropriate non-dimensional measure of that displacement is the volume-flow-rate integral $\phi$, given by

$$\phi = \int_0^t\int_0^1 ur\,dr\,dt \tag{29}$$

(note that $\Delta V = 2R\Omega\pi a^4\phi/\nu$). The first approximation to $\phi$ (for small $t$) is

$$\phi^{(1)} = \int_0^t\int_0^1 u^{(1)}r\,dr\,dt = -2\left(1+\frac{\gamma}{\beta}\right)\sum_{n=1}^{\infty}\frac{1-\exp(-\lambda_n^2 t)}{\lambda_n^4}. \tag{30}$$

### 5.2. *Large times, small* $\epsilon$

Let $\bar{t} = \epsilon t$ be the stretched independent variable. When this is substituted into (24) we find that

$$\epsilon\frac{\partial u}{\partial \bar{t}} + \left(1+\frac{\gamma}{\beta}\right)\delta(t/\epsilon) = \frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial u}{\partial r}\right) - \int_0^{\bar{t}}\int_0^1 ur\,dr\,d\bar{t}. \tag{31}$$

The integral on the right-hand side of (31) can be written as

$$\int_0^{\tau(\epsilon)}\int_0^1 ur\,dr\,d\bar{t} + \int_{\tau(\epsilon)}^{\bar{t}}\int_0^1 ur\,dr\,d\bar{t}, \tag{32}$$

where we assume $\epsilon/\lambda_1^2 \ll \tau(\epsilon) \ll 1$. If $\epsilon$ is sufficiently small, then, according to (30), for all practical purposes

$$\int_0^{\tau(\epsilon)}\int_0^1 ur\,dr\,d\bar{t} \simeq -2\left(1+\frac{\gamma}{\beta}\right)\epsilon\sum_{n=1}^{\infty}\frac{1}{\lambda_n^4} \tag{33}$$

and the first approximation to (31) for $t \gg \tau(\epsilon)$ is

$$\frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial u^{(1)}}{\partial r}\right) = \int_{\tau(\epsilon)}^{\bar{t}}\int_0^1 u^{(1)}r\,dr\,d\bar{t} - 2\left(1+\frac{\gamma}{\beta}\right)\epsilon\sum_{n=1}^{\infty}\frac{1}{\lambda_n^4}. \tag{34}$$

Equation (34) is easily solved by using the Laplace-transform method, the result being

$$u^{(1)} = \left(\frac{\epsilon}{4}\right)\sum_{n=1}^{\infty}\frac{2(1+\gamma/\beta)}{\lambda_n^4}(1-r^2)\,e^{-\frac{1}{16}t\epsilon}. \tag{35}$$

Then

$$\phi^{(1)} = \int_0^t\int_0^1 u^{(1)}r\,dr\,dt = (e^{-\tau(\epsilon)} - e^{-\frac{1}{16}t\epsilon})\sum_{n=1}^{\infty}\frac{2(1+\gamma/\beta)}{\lambda_n^4}, \tag{36}$$

and since $\tau(\epsilon) \ll 1$, we have

$$\phi^{(1)} \simeq (1-e^{-\frac{1}{16}t\epsilon})\sum_{n=1}^{\infty}\frac{2(1+\gamma/\beta)}{\lambda_n^4}. \tag{37}$$

Equations (30) and (37) can now be combined to yield the following *uniformly valid* first approximate solution for $\phi$:

$$\phi = \sum_{n=1}^{\infty} \frac{2(1+\gamma/\beta)}{\lambda_n^4}[\exp(-\lambda_n^2 t) - \exp(-\tfrac{1}{16}t\epsilon)]. \tag{38}$$

### 5.3. *Transfer function*

The transfer function relating the non-dimensional volumetric displacement $\phi$ to the angular acceleration $\alpha$ is obtained by finding the Laplace transform of $\phi$ and dividing by the Laplace transform of $\alpha$. The first approximation is

$$\frac{\phi}{\alpha}(s) \simeq \sum_{n=1}^{\infty} \frac{2(1+\gamma/\beta)}{\lambda_n^4}\left(\frac{\frac{1}{16}\epsilon - \lambda_n^2}{(s+\frac{1}{16}\epsilon)(s+\lambda_n^2)}\right), \tag{39}$$

which may in turn be approximated to very high accuracy by the simpler expression

$$\frac{\phi}{\alpha}(s) \simeq \frac{-2(1+\gamma/\beta)/\lambda_1^2}{(s+\frac{1}{16}\epsilon)(s+\lambda_1^2)}. \tag{40}$$

This may be put into a form analogous to (3), i.e.

$$\frac{\phi}{\alpha}(s) \simeq \frac{-2(1+\gamma/\beta)/\lambda_1^2}{(s+\tau_1^{-1})(s+\tau_2^{-1})}, \tag{41}$$

where $\tau_1 = 16/\epsilon$, the non-dimensional long time constant, and $\tau_2 = 1/\lambda_1^2$, the non-dimensional short time constant. Transforming back to the physical time domain and expressing the transfer function in terms of $\theta$ and $\omega$, we obtain

$$\frac{\theta}{\omega}(s) = \frac{-4(1+\gamma/\beta)s/\lambda_1^2}{(s+T_1^{-1})(s+T_2^{-1})}, \tag{42}$$

where $T_1 = 8\mu\beta R/K\pi a^4$ and $T_2 = a^2/\lambda_1^2\nu$.

### 5.4. *Frequency response*

The frequency response of the system is illustrated in figure 2. The important points on this figure are the gain $G = 4(1+\gamma/\beta)a^2/\lambda_1^4\nu$, the lower cut-off frequency $T_1^{-1}$, the upper cut-off frequency $T_2^{-1}$ and the natural frequency $f_n = (T_1T_2)^{-\frac{1}{2}}$. In the physical domain

$$G = 3{\cdot}5\,\text{ms}, \quad T_1^{-1} = 0{\cdot}048\,\text{rad/s} = 7{\cdot}6\,\text{mHz}, \quad T_2^{-1} = 260\,\text{rad/s} = 41\,\text{Hz},$$
$$f_n = 3{\cdot}5\,\text{rad/s} = 0{\cdot}56\,\text{Hz}.$$

### 5.5. *Impulse response*

The impulse response of the system given by (42) is

$$\theta \simeq \frac{4(1+\gamma/\beta)\Omega a^2}{\lambda_1^4\nu}[\exp(-t/T_2) - \exp(-t/T_1)], \tag{43}$$

where $\Omega$ is the magnitude of the step in angular velocity. The initial displacement of the cupula is governed by the 'short' time constant $T_2 = 3{\cdot}9$ ms and is shown in figure 4. The maximum displacement of the endolymph is

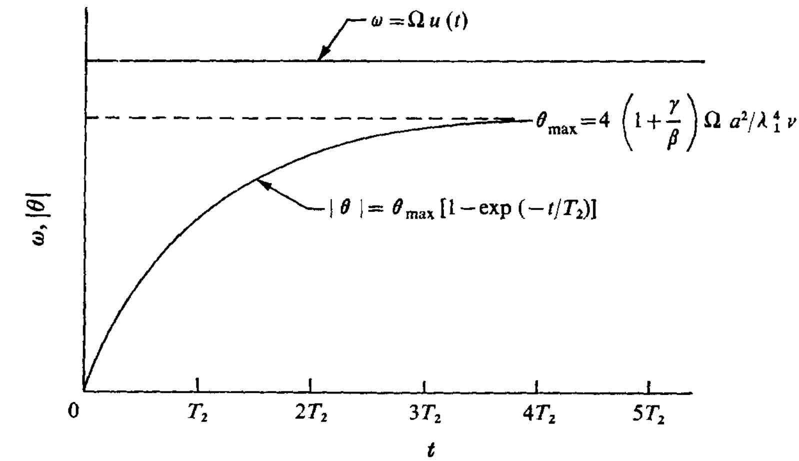


FIGURE 4. The short-term response of the endolymph to a step input in angular velocity of magnitude $\Omega$.

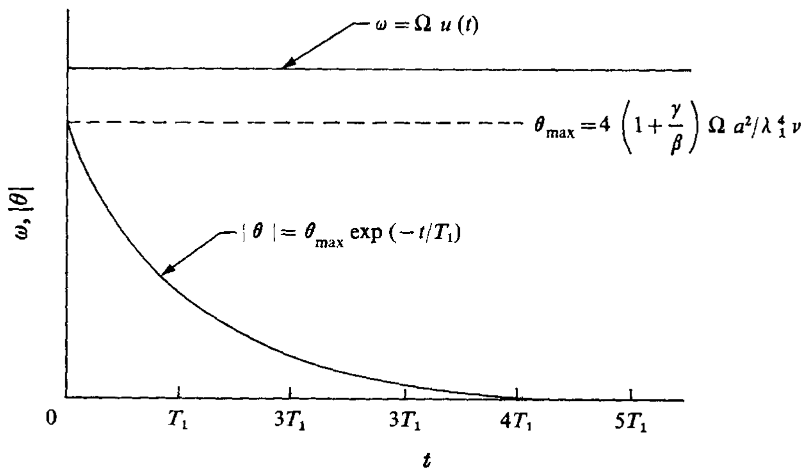


FIGURE 5. The long-term response of the endolymph to a step input in angular velocity of magnitude $\Omega$. The time scale in this figure is much longer than that in figure 4.

$3{\cdot}5 \times 10^{-3}\Omega$ rad, where $\Omega$ is given in rad/s. The return phase of the cupula is governed by the 'long' time constant $T_1$ and is shown in figure 5. $T_1 = 21$ s, which is approximately what has been observed in experimental studies.

It is interesting to note the sensation associated with such stimulation. The time constant $T_2$ is too short to be 'felt' and the sensation is of an instantaneous onset of angular velocity. But then, even though the angular velocity remains at a constant level, the sensation of angular velocity decays exponentially. Obviously, one's sensation of angular velocity is linked to the displacement of the cupula.

## 6. Experimental observations

Several researchers have attempted to ascertain experimentally the mechanics of the semicircular canals. The first of these were probably van Egmond *et al.* (1949). Using subjective sensation as an indicator of canal response they measured the long time constant $T_1$ and the natural frequency $f_n$ for humans. They found $T_1 \simeq 10$ s and $f_n = 0{\cdot}16$ Hz. Later researchers used a more objective measure of semicircular-canal response, namely nystagmus, a characteristic movement of the eyes associated with semicircular-canal stimulation. Malcolm (1968), using nystagmus and accounting for adaptation of the central nervous system, found a mean value of $T_1 = 21$ s for eight subjects. Niven & Hixson (1961), using sinusoidal oscillation as a stimulus and nystagmus as a measure of canal response, found a mean value of $f_n = 0{\cdot}21$ Hz for six subjects.

By choosing an appropriate value for $K$, we have matched our theoretical time constant $T_1$ to that observed by Malcolm (1968). We should note in all candor, however, that our predicted value of $f_n$ is more than twice that observed experimentally. Of course, neural processing could account for that difference, but a definitive answer will have to await further study.

## 7. Summary and conclusions

In this paper we have examined the fluid dynamics of a single semicircular canal. We have shown that it responds, as earlier studies had suggested, like a heavily damped, second-order system. An examination of the frequency response shows that its function is that of an angular-velocity meter. While the canals work quite well as $\omega$-meters for ordinary motions, we see from an examination of the impulse response that an unphysiological motion can lead to the generation of erroneous signals. It has been suggested in the literature that erroneous signals to the central nervous system are the cause of spatial disorientation and motion sickness (Johnson & Jongkees 1974).

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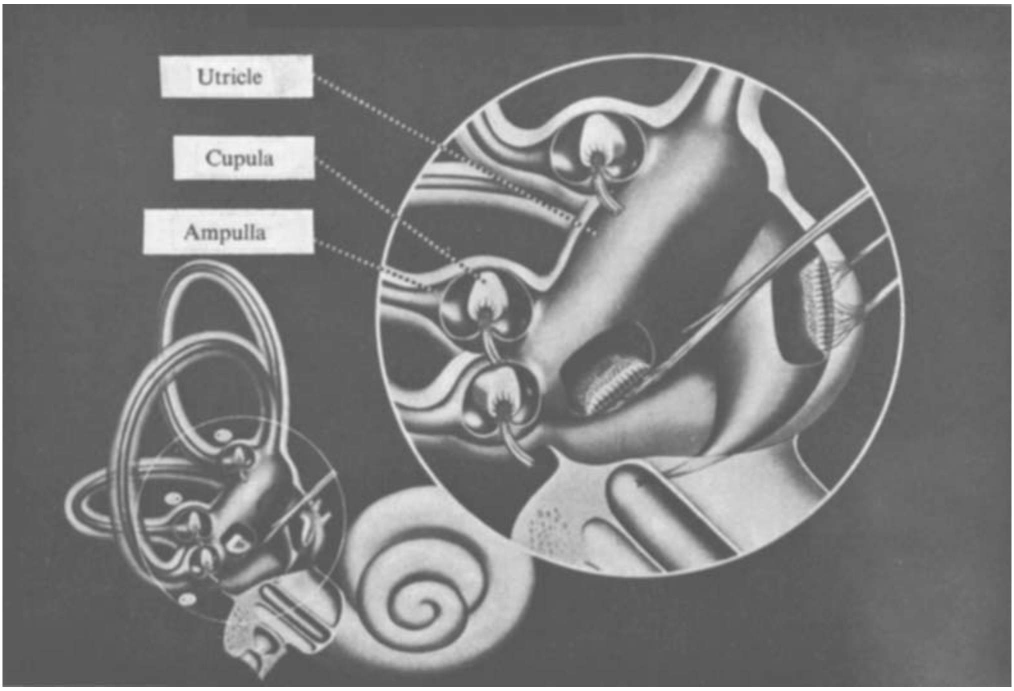


FIGURE 1. The vestibular apparatus of man.