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THE MECHANICS OF THE GROWING
SEMICIRCULAR CANAL

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INTRODUCTION

The function of the three semicircular canals of the vertebrate labyrinth which are situated in three approximately perpendicular planes is the detection of angular accelerations. Because of the inertia of the liquid (endolymph) in the membranous canal a fluid current is set up in the endolymph by angular acceleration. This endolymph current displaces the cupula in the ampulla. The cupula–sensory system converts the mechanical signal into a train of action potentials travelling to the brain, simultaneously with the actual deformation of the cupula. However, during small physiological accelerations the displacements of the cupula are submicroscopical. So this actual deformation can only be studied with a mathematical model, which closely approaches the real geometry of the growing semicircular canal. The model of the semicircular canal is a tube in a closed loop of non-circular shape with a narrow duct and a wide part, the cross-section being circular along the whole length of the narrow duct. The tube has rigid walls without bifurcations (the interference with the endolymphatic current by the two other canals is neglected) and contains an incompressible liquid and an elastic cupula. Since the common semicircular canal (for birds and fish) does not conform to a torus in shape, the generally accepted overcritically damped torsion pendulum model (Egmond, 1952; Groen, 1952; Jones, 1963) is not valid for a precise dimensional study of the semicircular canal (see Fig. 1). The equation of motion for the endolymph in any semicircular canal, including a non-circular region, will be used. In this overcritically damped second-order model, linear displacement, linear velocity and linear acceleration of the endolymph are related to the angular acceleration (de Vries, 1956).

This equation will be solved for three different kinds of stimuli, namely step-velocity input, step in angular acceleration and sinusoidal angular oscillations. The endolymph displacements caused by these stimuli will depend on the dimensions of the semicircular canal. A mechanical sensitivity factor can be derived and expressed in geometrical parameters of any semicircular canal. This provides the theoretical basis of a previous study on dimensions and sensitivities of semicircular canals in fish (ten Kate, 1969, 1970). The sensitivity of the canal may also inform us about the actual deformation of the cupula during small physiological accelerations. In connexion with this it should be noticed that no sufficient evidence is available for

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the generally accepted model in which the cupula moves like a door. (See comments below, formula (26).) Furthermore, on the basis of data derived from the semicircular canals of pike, amplitude and phase diagrams for sinusoidal angular oscillations will be predicted. These theoretical consequences can be checked in the future by electrophysiological techniques and are already indicated by some eye characteristics of pike of different sizes.

THEORY

The equation of motion for the endolymph in the semicircular canal is derived from the requirement of equilibrium of forces. The acceleration pressure $P_a = 2A\rho a$ is opposed mainly by the friction pressure $W\dot{x}$ of the streaming fluid in the narrow duct of the semicircular canal but also by the inertial pressure $M\ddot{x}$ of the endolymph and the directive pressure Fx delivered by the 'elastic' cupula (denotation of the symbols is given in a list at the end of the article, see also Fig. 1). Accordingly the equation of motion is

$$M\ddot{x} + W\dot{x} + Fx = 2A\rho a, \tag{1}$$

where

$$M = \rho(l_1 + l_2) \text{ g/cm}^2, \tag{2}$$

$$W = 8\eta l_1 \, r_c^{-2} \text{ dyne sec/cm}^3, \tag{3}$$

F (dyne/cm^3) = directive pressure per cm displacement of the fluid in the narrow duct.

Note that in the equation of motion: (1) x, $\dot{x}$ and $\ddot{x}$ are linear endolymph parameters instead of the angular parameters ϕ, $\dot{\phi}$, $\ddot{\phi}$ in the torsion-pendulum theory; (2) the system constants M, W and F differ from the moments π, θ and Δ in the torsion-pendulum theory; (3) any area A enclosed by a tube of an arbitrary shape can be substituted in the equation of motion.

The torsion-pendulum theory is restricted to a torus with a radius R and $A = \pi R^2$. In the model the flow is assumed to be laminar in the narrow duct. This assumption is justifiable with the small value of the Reynolds number ($\simeq 10^{-4}$) for physiological stimuli and the negligibly small value of the average velocity of the secondary flow (caused by Coriolis' forces) with respect to the 'inertial' flow (see Grohmann, 1968).

In (1) different time-dependent angular accelerations can be substituted by step-velocity input, step in constant angular acceleration or sinusoidal angular oscillation.

(a) Step-velocity input

At the moment of abrupt stopping after a constant angular velocity (1) changes into

$$\ddot{x} + (W/M)\dot{x} + (F/M)x = 0 \tag{4}$$

with the initial conditions

$$t = 0, \ x = 0, \ \dot{x} = \gamma 2A(l_1 + l_2)^{-1} = \gamma C \tag{5}$$

This is justified by earlier work (ten Kate, 1969).

It follows from (4) and (5) that the relation between x and t is

$$x = C\gamma M/W \{\exp(-Ft/W) - \exp(-Wt/M)\}. \tag{6}$$

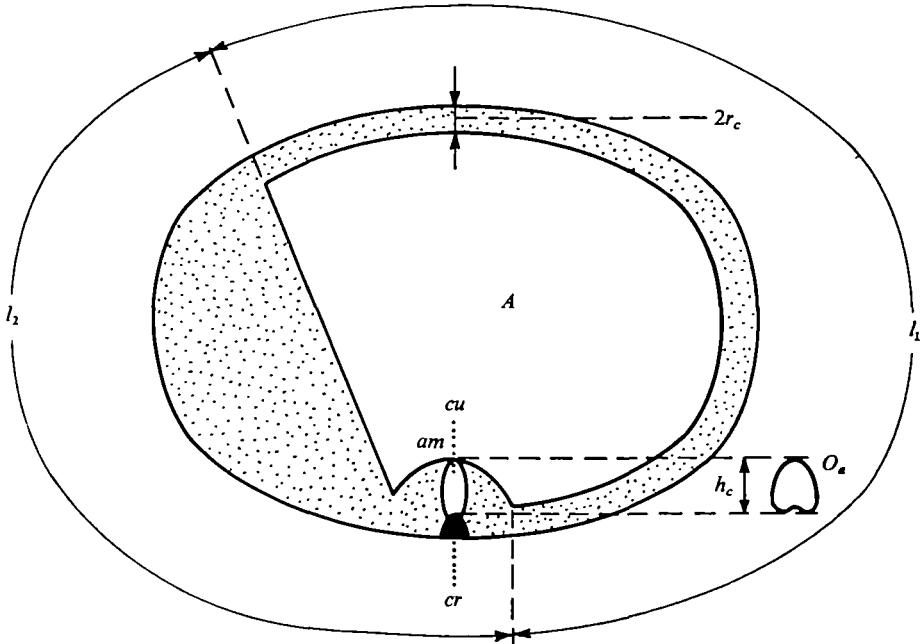* A list of symbols used is given on page 365.

Fig. 1. Locations of the symbols used in the study of the semicircular canal. A, Enclosed area by the average canal; *am*, ampulla; *cr*, crista; *cu*, cupula, h_c, cupula height; l_1, length of canal duct; l_2, length of the wide part; O_a, cross-section of the ampulla at the summit of the crista; $2r_c$, inner diameter of the duct.

This function has the maximum value

$$x_0 = C(M/W)B\gamma = (A\rho r_c^2\gamma)(4\eta l_1), \tag{7}$$

where $B \simeq 1$ (see ten Kate, 1969).

This expression can also be deduced from the Navier–Stokes equations of the fluid dynamics in a torus by integration of the average velocity. This integration results in

$$x_0 = \frac{a^2 b_1}{4\nu_1}(\psi_1 - \psi_1) \tag{8}$$

(derived formula (2) of the article of Grohmann, 1968).

Equation (8) is reduced to (7) by substituting in (8)

$$\nu_1 = \eta/\rho, \quad a_1 = r_c, \quad A = \pi b_1^2, \quad l_1 = \pi b_1, \quad \psi_1 = \gamma, \quad \psi_2 = 0.$$

The use of the simple second-order system is justified by this fact. (See Steer, 1967.)

(b) Constant acceleration input

Equation (1) is rewritten

$$\ddot{x} + (W/M)\dot{x} + (F/M)x = 2Aa(l_1 + l_2)^{-1} = Ca \tag{9}$$

with the initial conditions

$$t = 0, \quad x = 0, \quad \ddot{x} = 2A(l_1 + l_2)^{-1}a = Ca. \tag{10}$$

The general solution of (9) is simplified by first-order approximation to the displacement

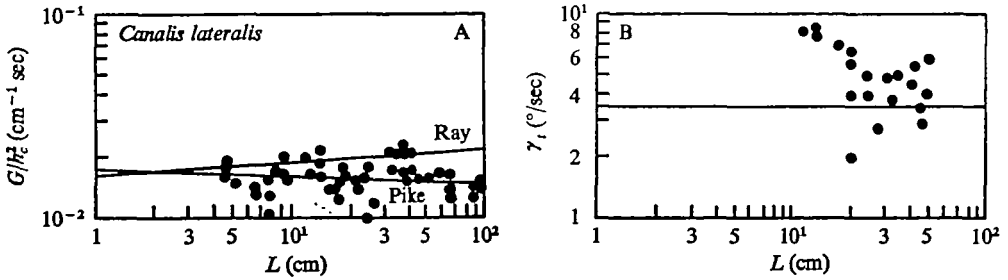$$x = (CaM/F)\,[1 - \exp(-Ft/W)]. \tag{11}$$

Fig. 2. (A) Individual values of G/h_c^2 of the horizontal semicircular canal plotted against body length L in cm. (B) The threshold values γ_t of pikes of different sizes plotted against body length L in cm.

The approximate formula for the velocity of the endolymph is

$$x = (CaM/W)[\exp(-Ft/W) - \exp(-Wt/M)]. \tag{12}$$

Relation (12) is of the same form as (6).

The first term of the Taylor series of (11) is

$$x = C(M/W)at = (Ar_c^2\rho at)/(4\eta l_1) \tag{13}$$

This is the well-known Mulder's law (see also Fernandez, 1968).

(c) *Sinusoidal angular oscillation*

(1) is rewritten as

$$\ddot{x} + (W/M)\dot{x} + (F/M)x = 2A(l_1 + l_2)^{-1}a_m \sin \omega t = Ca_m \sin \omega t. \tag{14}$$

The solution without transients is

$$x = Ca_m \{(\omega_0^2 - \omega^2) + (W/M)^2\omega^2\}^{-\frac{1}{2}}\sin(\omega t - Q), \tag{15}$$

where $\omega_0^2 = F/M$ and $\tan Q = \omega(W/M)(\omega_0^2 - \omega^2)^{-1}$. \hfill (16)

Substituting $a_m = -\omega^2 U$ in the amplitude factor of (15) yields

$$x_m = -C(\omega U)\{(\omega_0^2\omega^{-1} - \omega)^2 + (W/M)^2\}^{-\frac{1}{2}}. \tag{17}$$

If $\omega = \omega_0$ (17) becomes

$$x_m = -C(M/W)U\omega_0. \tag{18}$$

The values of x_m given in (17) are approximately constant over a relatively wide frequency range, if $U\omega$ is kept constant (ten Kate, 1969) (see also Fig. 4). It follows that

$$x_m \simeq -C(M/W)U\omega = -A\rho r_c^2 U\omega/(4\eta l_1). \tag{19}$$

This equation (19) is of the same form as (7) and (13). Multiplication of (7), (13) and (19) by the factor $(\pi r_c^2)/O_a$ yields the endolymph displacement $\bar{z}$ in the ampulla:

$$\bar{z} = A\rho\pi r^4\gamma_v/(4\eta l_1 O_a), \tag{20}$$

where γ_v is one of the terms γ, $U\omega$ or at.

It seems possible now to investigate the actual deformation of the cupula using equation (20). In actual fact the minimum values of individual thresholds to the applied angular velocities γ_v, measured in pike of different sizes, are observed to be the same (see Fig. 2B). Therefore a mechanical sensitivity G of the semicircular canal may be defined as

$$G = (A\rho\pi r_c^4)/(4\eta l_1 O_a). \tag{21}$$

This equation (21) will possibly reflect the real deformation of the cupula if a dimensional study of semicircular canals of different sizes within a single species, which grows considerably, is undertaken, assuming that the properties of the central nervous system do not change during growth.

RESULTS AND THEORETICAL CONSEQUENCES

The allometric relations cl^n between the dimensions of the horizontal semicircular canal (A, r_c, l_1 and O_a) and the body length L for 55 pike of different sizes have been determined (ten Kate, 1970). All values of c and n are computed from 55 measured values of each of the parameters A, $2r_c$, l_1, O_a, h_c and (l_1+l_2) by the least squares method.

The values of c and n of the parameters are listed in columns III and IV with the corresponding standard errors (see Table 1). In column V and VI the measurement errors M_e are compared to the standard errors of estimate E_g. It is concluded that variance in the values for the parameters of semicircular canals for one particular body-length L is paramount to measurements errors. The linearity of the regression curve $\log c + n \log L$ was statistically tested (ten Kate, 1970). Moreover $\rho \simeq 1$ g/cm³ and $n = 1\cdot25$ cP at 20 °C (ten Kate, 1970) have been measured.

Substituting all data in (21) yields

$$G = (4\cdot44 \pm 0\cdot95) \times 10^{-6} L^{(0\cdot94 \pm 0\cdot07)} \text{ cm sec.} \tag{22}$$

With the aid of the allometric relation between h_c and L we obtain:

$$G/h_c^2 = (1\cdot6 \pm 0\cdot4) \times 10^{-2} L^{(-0\cdot02 \pm 0\cdot08)} \text{ cm}^{-1} \text{ sec.} \tag{23}$$

This quotient is nearly independent of the body length L. Individual values of G/h_c^2 are also computed from the values of A, l, r_c and O_a for the horizontal canal (see Fig. 2A). Comparing these individual values of G/h_c^2 to the threshold values γ_t (step-velocity inputs) in Fig. 2B yields a corresponding relationship to L. The spreads of G/h_c^2 and γ_t are, however, of different magnitudes. For this and explanation can be sought in some stochastic process(es) in the neuronal tracts of the vestibulo-ocular reflex. G/h_c^2 appears to be practically independent of L. Therefore, G/h_c^2 may represent the actual sensitivity of the semicircular canal to angular velocity.

On this basis the two main concepts about the cupula deformation, mentioned in the literature, seem to be incorrect (Egmond, 1952; Groen, 1952; Jones, 1963; Kuiper, 1956). The cupula is neither turning like a door nor is it simply gliding over the crista. Three other possibilities can be visualized.

(*a*) The cupula bends as an elastic rod (elastic view) (see also Dijkgraaf, 1963).

(*b*) The cupula is deformed at its centre (cf. the book of Dittrich, 1963, and a report of Grohmann, 1971), (hydrodynamic view).

(*c*) The cupula top and a more dense subcupular layer are linearly sheared at the same time. Then the thickness of the layer depends on the supposed increasing length of the sensory hairs during growth of the animal (ten Kate, 1970; Dohlman, 1964). In this paper we will work out only hypotheses (*a*) and (*c*) in somewhat more detail.

Hypothesis (*a*). Theoretically it appears possible to explain the equation (23) by a cupula that bends in a circular way (Fig. 3A). Then the ampulla is approximated by an ellipsoid and the neutral surface of the deformed cupula is depicted as the
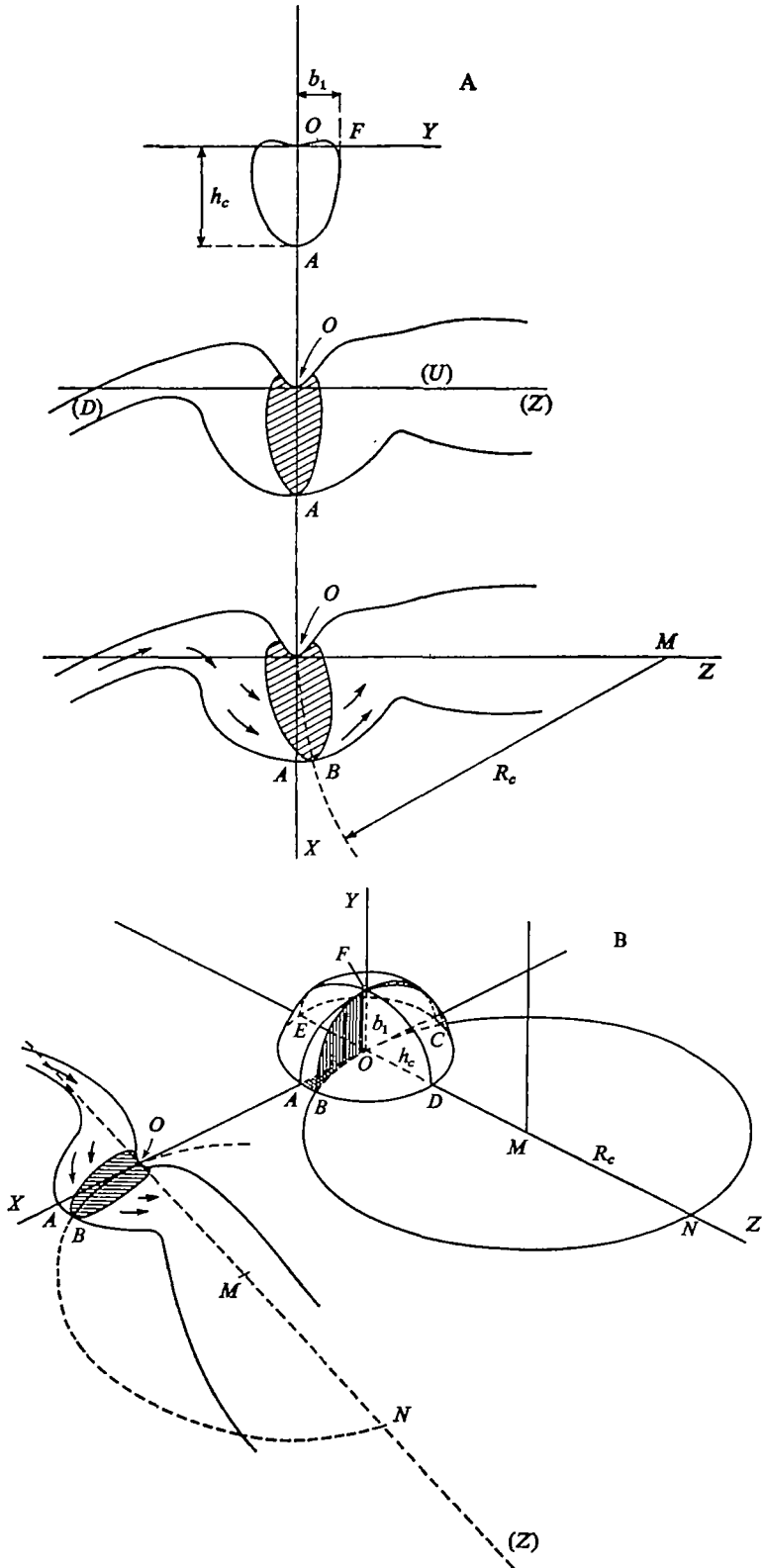
Fig. 3. For legend see facing page.

Table 1.

I Parameter	II Canal	III c	IV n	V $M_s(\%)$	VI $E_s(\%)$
A_λ	h.s.c.	$0 \cdot 0704 \pm 0 \cdot 0037$ mm²	$1 \cdot 730 \pm 0 \cdot 016$	4	$11 \cdot 3$
$2r$	h.s.c.	$0 \cdot 122 \pm 0 \cdot 003$ mm	$0 \cdot 274 \pm 0 \cdot 007$	$1 - 2 \cdot 8$	$4 \cdot 6$
l_1	h.s.c.	$0 \cdot 0474 \pm 0 \cdot 0013$ cm	$0 \cdot 945 \pm 0 \cdot 008$	$1 \cdot 5$	$5 \cdot 6$
O_s	h.s.c.	$0 \cdot 0286 \pm 0 \cdot 0014$ mm²	$0 \cdot 943 \pm 0 \cdot 015$	$3 \cdot 75$	$14 \cdot 2$
h_c	h.s.c.	$0 \cdot 165 \pm 0 \cdot 003$ mm	$0 \cdot 477 \pm 0 \cdot 005$	$1 \cdot 5 - 0 \cdot 3$	$3 \cdot 7$
$(l_1 + l_2)$	h.s.c.	$0 \cdot 1031 \pm 0 \cdot 0028$ cm	$0 \cdot 865 \pm 0 \cdot 008$	1	$5 \cdot 6$

surface of a cylinder (compare Fig. 3A and Fig. 3B). The radius of the cylinder corresponds to the radius of curvature R_c. The volume between the neutral plane of the cupula in the equilibrium position and the cylindrical surface in the ellipsoid is calculated with the aid of elliptic integrals. The average displacement is then theoretically

$$\bar{z} = h_c^2/(8R_c). \tag{24}$$

This equation (24) is an attractive explanation of (23). Combining (23) and (24) yields

$$R_c = (7 \cdot 8 \pm 1 \cdot 7)\gamma^{-1}L^{(0 \cdot 02 \pm 0 \cdot 08)} \text{ cm.} \tag{25}$$

Substituting the minimum threshold angular velocity $\gamma = 2°/\text{sec}$ for pike of different sizes

$$R_c = (220 \pm 48)L^{(0 \cdot 02 \pm 0 \cdot 08)} \text{ cm.} \tag{26}$$

On account of this large value it is no miracle that the small bending of the artificially evoked cupular motion is not taken as essential (Steinhausen, 1931; Dohlman, 1935; Vilstrup, 1950). During experiments with indian-ink injections, however, relatively large forces are applied, causing an inelastic deformation at the cupula basis, i.e. a sliding motion. Since the radii of curvature for $L = 5$ cm and 100 cm are large (see (26)) only small threshold values are found for the deviation of the sensory hair tops, namely of the order of those in the human cochlea. For sensory hairs of $5 \ \mu\text{m}$ long these deviations lie between $0 \cdot 06$ and 1 Å. This is a consequence of the fact that either the cupula is simply bending, or undergoes a combination of bending and a negligible gliding over the crista.

In any case, for this model, the displacement of the sensory hair at its base or at its top seems to be of an incredible small order of magnitude. Large effects caused by gliding of a whole cupula over the crista is more easily acceptable as a means of efficient stimulation. However, no experimental evidence is available as yet for the absence of a neuronal coincidence circuit in the vestibular tracts. Therefore the large number of ampullar nerve fibres (von Békésy, 1955) might be explained as necessary for the lowering of the threshold perception.

Fig. 3. (A) The upper figure is the cross-section of the ampulla. The middle figure is the ampulla with the cupula in rest position. The lower figure is the cupula during endolymph displacement. A, Top of the ampulla; B, summit of the deviated cupula; b_1, half-width of the cupula; D, canal duct; h_c, cupula height; O, summit of the crista; R_c, radius of curvature.

(B) Theoretical stereometric figure used for the derivation of $x \propto h_c^2$ (see text). An ellipsoid is intersected by a cylinder. $ABDCE$ is the intersection of the ellipsoid in the XOZ plane. The ellipsoid is an approximation of the ampulla. OBF is the cylindrical surface between the XOZ plane and the surface of the ellipsoid. $b_1 = b/2$. The line in point M perpendicular to the XOZ plane is the axis of a cylinder with radius P.
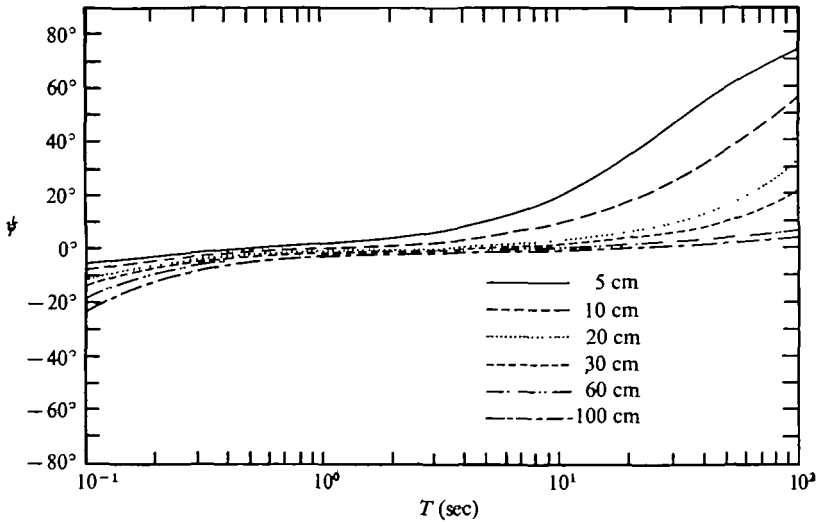
Fig. 4. The effect of growth on the relation between the period T and the phase differences between the maximum cupula deflexion and the maximum angular velocity in the case of low cupular stiffness. Curves are calculated for pike of 5, 10, 20, 30, 60 and 100 cm body length.

Another consequence is that the restoring pressure per cm displacement F in the narrow duct can also be expressed in the dimensions of the semicircular canal and in the physical constants of the corresponding cupula.

For this purpose the cupula is idealized as an elastic bar with elliptical cross-section along the axis. In this way the following relation is obtained

$$F = \pi b k^3 E O_c (4 h^3 O_a)^{-1}, \tag{27}$$

where b and k are respectively the major and minor axes of the perpendicular elliptic cross-section of the cupula. The Young's modulus of elasticity E can be estimated by substituting values for F and the corresponding dimensions. The values for F are deduced either indirectly from the slow return of the pike's eye or directly calculated from the cupula deflexion in the pike's semicircular canal (Steinhausen, 1931; de Vries, 1956). From substitutions in (27) we obtain $E = 0.35 \times 10^3$ dyne/cm^2 and 1.85×10^3 dyne/cm^2 respectively; these values are near to the lower limit of the Young's modulus for known gelatins.

The value for the Young's modulus of elasticity for the cupulae on the skin of the mud-puppy is found to be of the same order of magnitude, by measurement of the deflexions with calibrated glass fibres (C. M. Oman, personal communication). Furthermore, the value for cupulae in the human semicircular canals are calculated to be 2.8×10^3 dyne/cm^2 (Oman & Young, 1971).

The system constants of the differential equation (1) can be expressed in terms of the body length L:

$$(27) \to F = 224 L^{-0.91} \text{ dyne/cm}^3, \tag{28}$$

$$(2) \to M = 0.103 L^{0.87} \text{ g/cm}, \tag{29}$$

$$(3) \to W = 1.25 \times 10^2 L^{0.40} \text{ dyne sec/cm}^3. \tag{30}$$

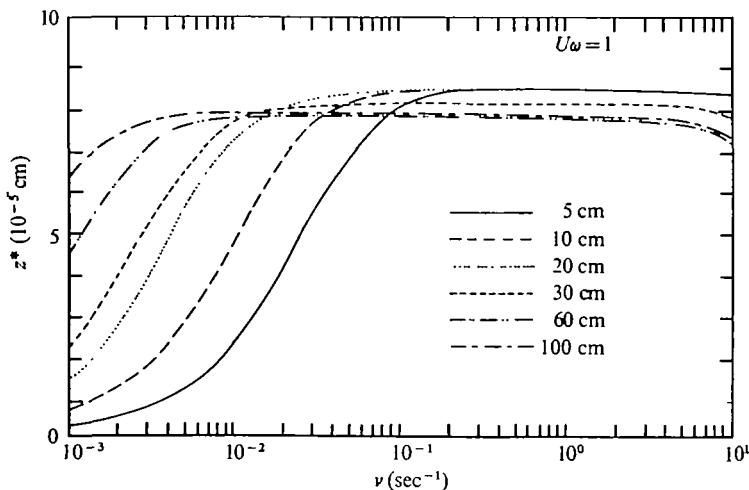Substitution of these values in the phase and amplitude relations will elucidate the

Fig. 5. Normalized deviations z^* of the cupulae plotted against the frequency ν in cyc/sec for constant maximum angular velocity for pike of different sizes in the case of low cupular stiffness.

effect of growth on the pike's semicircular canal. With $\psi = (\pi/2 - Q)$ and $\omega = 2\pi/T$ equation (16) is rewritten:

$$\tan \psi = FT(W2\pi)^{-1} - 2\pi M(TW)^{-1}. \tag{31}$$

The phase diagrams in Fig. 4 are obtained with (28), (29), (30) and (31). The phase differences ψ between the cupula deviation and the maximum angular velocity shift towards the large periods T for increasing body length L.

The effect of growth on the amplitude characteristics can be obtained by the substitution of (28), (29), (30) in (17). Since an equal bending of cupulae of different sizes is necessary for equal stimulation of the sense epithelia, the amplitude diagrams are normalized to the top deviations of the smallest one ($L = 5$ cm). z^* means the deviation of the cupula at the same height h_c as the smallest cupula height h_c. These deviations z^* are plotted against ν for pike of different sizes in Fig. 5 for the constant angular velocity of 1 radian/sec. It should be noticed that the frequency range for equal amplitudes increases for pike of larger sizes. This signifies that larger pike are capable of detecting angular velocities at lower frequencies than small pike.

The ratio z^*/a_m, an amplification factor, is also plotted in log decibel units against the frequency ω (see Fig. 6). In a relatively wide frequency range the amplification factor z^*/a_m for pike of different sizes is approximately constant.

These calculated diagrams of the cupula deviation can be compared to the dynamical characteristics of the vestibulo-ocular reflex (see below). In several pike we have already observed shifting of phases to larger periods T and shifting of amplitude characteristics as predicted by the theory (ten Kate, 1969).

Returning to hypothesis c the following problem arises: Is it also possible to develop such a model based on hypothesis (c)? To do this it has to be proved that the average endolymph displacement is proportional to h_c^2.

Hypothesis (c). It seems very likely that the kinocilia cause the excitation of the cell. The stereocilia are much shorter and may serve another purpose. These sensory hairs are embedded in the so-called subcupular layer. In microscopical studies
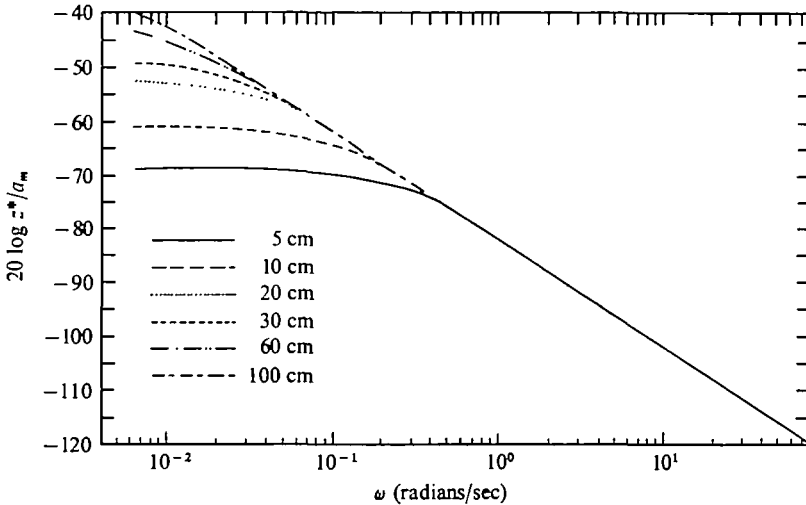
Fig. 6. Log–decibel plot of x^*/a_m against the frequency ω in radians/sec for pike
of different sizes in the case of low cupular stiffness.

(Dohlman, 1964) the subcupular layer seems to be more rigid than the cupula. The
stereocilia also contribute to its stiffness. Therefore the subcupular layer is supposed
to possess a thickness equal to the length of the stereocilia. When the stereocilia
elongate during the pike's growth the subcupular layer may also increase in thickness.
Indeed some evidence is available for the growth of the sense cell (Proebsting, 1924).
The growth rate of the sense cells is in accordance with that of the cupula height h_c.
It is very likely that the thickness of the subcupular layer increases proportionally
to h_c. The shearing of the cupula mass will occur just at the boundary between
the subcupular layer and the cupula. The visco-elastic material of the cupula will
shear off or flow at this boundary.

By its length, which is great with respect to the stereocilia, the kinocilium is very
well coupled in the cupula. The displacement of the cupula with respect to the sub-
cupular layer deflects the kinocilium over a certain angle. For threshold excitation
of the sense cell a minimum angle of the kinocilium is necessary. This angle is
constant during growth. When the subcupular layer becomes thicker during growth
the displacement at the boundary for obtaining the minimum angle of deviation
increases proportionally. Hence this displacement is proportional to h_c during
growth.

Suppose, however, that the cupula glides over the subcupular layer and turns
like a door in the ampulla. Then, to obtain the same angle of cupula deflexion in the
case of a large cupula, more fluid has to be displaced than in the case of a small
cupula. The average endolymph displacement is then proportional to h_c. However,
at threshold the deflexion of the cupula has to increase with h_c, because at threshold
the minimum deviation of the kinocilium increases proportionally to h_c. Hence,
during growth the average displacement of the endolymph (in the ampulla) necessary
for threshold responses has to be proportional to h_c^2.

The properties of the cupula substance, in particular at the location of the kino-
cilium, are important for this latter model. When the cupula substance is a visco-

elastic material, the shearing at the boundary is determined by the time course of the acceleration pressure.

The problem then arises: is the decrease of F with L specific for hypothesis (a)? (see formula (28)). According to hypothesis (c) the cupula only glides over the sub-cupular layer. If the cupula is deflected through an angle β it will shear over the the subcupular layer. This will counteract the force acting on the cupula. Therefore the restoring force per unit of angle is proportional to the surface of the crista O_{ac} under the cupula. The pressure μ per unit of angle of cupular deflexion should remain constant during growth since O_{ac}/O_a does not depend on L (equal growth rates). In the case where the cupula is deflected over an angle β (in radians) the displaced volume of endolymph is $4\beta h_c\,O_a(3\pi)^{-1}$. (The ampulla is approximated by an ellipsoid.) (The calculation is made by multiplying the volume of the ellipsoid by $\beta/2\pi$, which yields $\frac{2}{3}h_c b\beta$. In the latter form $O_a = \pi/2h_c b$ is substituted.)

The average displacement $\bar{z} = 4\beta h_c(3\pi)^{-1}$. Hence the average pressure/cm F_a in the ampulla is proportional to $\mu\ 3\pi(4h_c\beta)^{-1}$. For the pike, the restoring pressure F per cm displacement in the narrow duct is

$$F \propto 3\pi O_c\mu(4h_c O_a\beta)^{-1} \propto L^{-0.90} \tag{32}$$

The exponent of the relation between F and L in (32) is only slightly different from that of the relation between F and L in (28). Therefore no conclusion can be drawn from the shift of the resonance frequencies and the change of phase and amplitude characteristics during growth about the correctness of either hypothesis (a) or hypothesis (c).

THE EFFECT OF GROWTH ON THE VESTIBULO-OCULAR REFLEX AND DISCUSSION

On being turned around the vertical axis vertebrates react by turning their eyes in the opposite direction. This phenomenon is called the horizontal vestibulo-ocular reflex because the horizontal semicircular canal is the sense organ which detects the angular acceleration. The three main subdivisions of this reflex arc are: the semi-circular canal, the brain and the eye system. In fact the whole arc can be considered as a set of filters, an array of seven elements, namely the semicircular canal, the hair cells, the vestibular nerve fibres, the central nervous system, the motor nerve fibres, the eye muscles and the eye-ball in its socket.

Now, as a first attempt at verification of the growth effect on the course of phase and amplitude diagrams of the semicircular canal, the horizontal vestibulo-ocular reflex arcs of pike of different sizes will be studied. For pikes of one size (20–25 cm body length) some properties of this reflex arc have already been obtained: (a) the reflex arc behaves like a linear system; (b) the reflex arc can be described with a set of filters (ten Kate, 1969). On this basis it seems reasonable to expect some influence of the change in the filter characteristics of one component, the semicircular canal, on the overall transfer function. The effect of growth necessarily has to be reflected in the diagrams of the vestibulo-ocular reflex arc.

The eye responses of pike of different sizes are recorded in the following way. On the turntable pike from 4 to 87 cm in length are mounted in special Lucite fish-holders. Small mirrors are attached to the eyes. These mirrors are illuminated
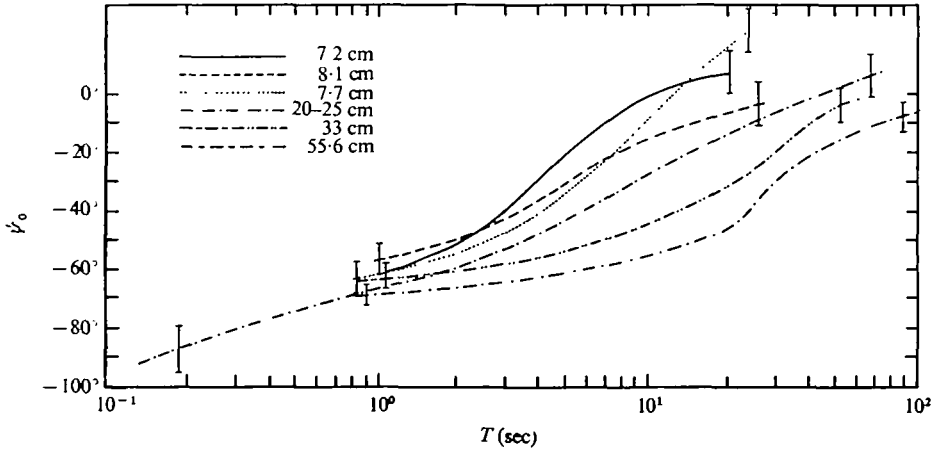
Fig. 7. Phase differences ψ_0 between the maximum eye deviation and the maximum angular velocity plotted against the period of oscillation T for pike of different sizes. Solid bars indicate the spread in measured values.

by a spot of light. The light source, a slit, is focused by a lens and an image of the slit is obtained on a screen. The horizontal position of this vertical line is then recorded on a continuously running film in a camera provided with a horizontal slit. Sinusoidal eye movements and the sinusoidal oscillation of the turntable are recorded on the same film. (Non-linear phenomena like the quick jerks of nystagmus are absent for low angular acceleration.)

After the experiment the phase differences between the maximal eye deviation α_m and the maximal angular velocity γ_m are determined. Then for the pike of different sizes phase and amplitude diagrams are plotted. The phase relation with the frequency do indeed shift towards the larger periods of T for increasing body length L (see Fig. 7). This observation agrees with the theoretical predictions. The numerous measured values of phases in Fig. 7 are omitted in order to prevent confusion; only average curves are drawn. The spread in the measured values is indicated by solid bars at the beginning and at the end of the curves.

A phase shift during growth appears to be present. This fact can be seen as a confirmation of the growing semicircular canal model. However, one may also interpret this in the model of the vestibulo-ocular reflex arc as due to growth effects of one or more filters other than the semicircular canal. Data are lacking about these influences on biological filters like neuronal networks.

It should be noticed that at the moment no evidence is available for such a dynamical change of these filters. No methods are possible to separate these different growth effects. Some reasoning, however, may indicate the correct solution of this growth problem. The uncertainty in the exact value for the modulus of elasticity of the cupular substance is a chief obstacle to the drawing of definite conclusions. For that reason an attempt was made to explain Fig. 7 with the use of the upper limit ($1 \cdot 85 \times 10^3$ dyne/cm^2) for this modulus. In that case a constant phase delay of 55–$65°$ for all frequencies is obtained for all periods of T. Such a constant phase difference is incompatible with the model of the vestibulo-ocular reflex (since no dynamics of the eye system seem to be present). If, on the other hand, the small value of $0 \cdot 35 \times 10^3$
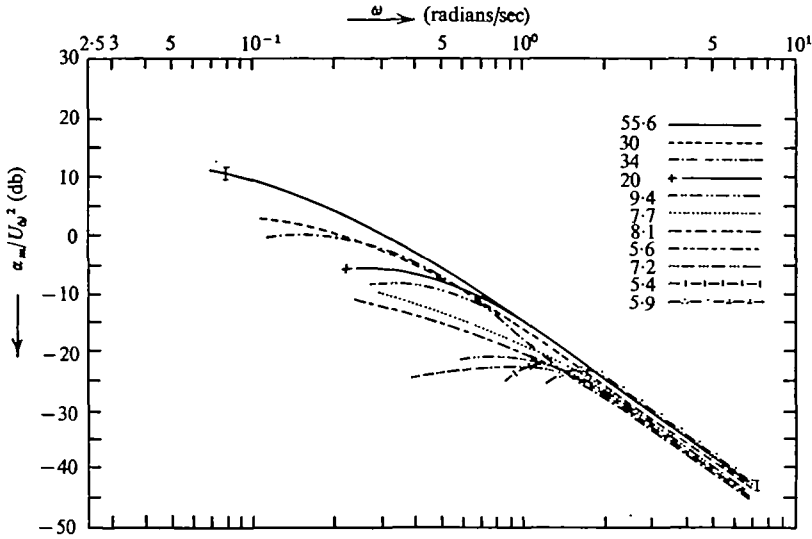
Fig. 8. Log–decibel plots for the amplification $\alpha_m/U\omega^2$ against the frequency in radians per sec for pike of different sizes.

dyne/cm² is chosen (formula 18), growth effects on other filter characteristics need to be present. The only justifiable conclusion is that the phase diagrams of the reflex arc are not in conflict with the predicted diagrams of the semicircular canals.

Additionally, the amplification factors $\alpha_m/U\omega^2$ are plotted against the frequency ω (see Fig. 8) (α_m = maximal eye deviation and U = amplitude of the turntable movement.) For convenience the various measured values of $\alpha_m/U\omega^2$ are omitted. Also in this figure the spread of the measured values is indicated by the solid bars located at the beginning and the end of the curve of $L = 55\cdot6$ cm. These amplification factors under study do not differ much in the range of 2 radians/sec $\leqslant \omega \leqslant 7$ radians/ sec. For these frequencies the amplification factors do not spread more than for pike of one particular size (20–25 cm). Apparently this result implies that during the pike's whole life the vestibulo-ocular reflex arc has the same degree of compensation in the high-frequency range.

Comparison of Figs. 8 and 6 reveals that the region of equal amplification in Fig. 8 is smaller than in Fig. 6. This fact suggests a greater cupular stiffness, or a larger value for the modulus of elasticity than that of formula (18).

Another conspicuous fact is the difference in the slopes of the curves in Figs. 8 and 6. The last figure has a maximal value of -6 dB per octave at the higher frequencies. In Fig. 8 several curves have slopes with values between $-9\cdot5$ and $-10\cdot3$ dB per octave in the high-frequency range.

The difference in slopes between the calculated and experimental curves shows the effect of growth on both filters (the brain and the eye system). From these values one may only conclude that this reflex arc is a complicated system, because the slope is not a simple multiple of -6 dB per octave; on the other hand, differences between the slopes at the high-frequency side are small for pike of different sizes.

Another evidence for linearity of the whole reflex arc is obtained in the comparison of Figs. 8 and 7. As the slope of the curves in Fig. 8 is about 10 dB per octave, the

phase lag of the eye response with respect to the angular acceleration is approximately $\frac{10}{12} \times 180° = 150°$. This corresponds to the actual value of ψ_0 at $T = 1$ sec, since ψ_0 is defined as the phase difference between the eye amplitude and the maximum angular velocity. For comparison of these diagrams the standard approximation with asymptotes is not useful, since the low-frequency ends of the curves are determined by the thresholds of the vestibulo-ocular reflex. In other words, the plotted amplification factors $\alpha_m/U\omega^2$ are too small in the low-frequency region. This is easily understood from the fact that the relation between α_m and U is linear above threshold at one particular frequency. But at threshold, $\alpha_m = 0$ with $U \neq 0$.

It seems reasonable to conclude on the basis of the growth effects on the phase and amplitude diagrams of the horizontal vestibulo-ocular reflex of the growing pike that the proposed mechanical model (hypothesis (a)) of the growing semicircular canal is possible. For further study on the growing horizontal semicircular canal this model seems to be a useful working hypothesis.

SUMMARY

1. The motion of the endolymph in the semicircular canal is described with the aid of a linear second-order system, comprising the applied angular acceleration and the linear displacement, the linear velocity and the linear acceleration of the endolymph.

2. A sensitivity factor G for angular velocity is derived and expressed in the dimensions of the semicircular canal.

3. The sensitivity factor G of the semicircular canal proves to be consistent with the equivalent sensitivity factor of a more sophisticated hydrodynamic model of these canals.

4. The sensitivity of the growing semicircular canal is defined to be G/h_c^2, independent of the pike's size. Threshold angular velocities for the vestibulo-ocular reflex of 27 pike between 4 and 50 cm bodylength are in agreement with this assumption.

5. At threshold stimulation with an angular velocity of 2°/sec the radius of curvature R_c of the cupula is calculated to be 220 ± 48 cm.

6. At the threshold angular velocity $\gamma = 2°$/sec the deviation of sensory hairs 5 μm long is assessed to be between 0·06 Å and 1 Å.

7. Young's modulus of elasticity for the cupular substance is found to be between $0·35 \times 10^3$ dyne/cm² and $1·85 \times 10^3$ dyne/cm² (on the basis of a circular bending for the cupula).

8. Characteristics of the model of the growing semicircular canal are calculated for pike with body length between 5 and 100 cm.

9. Observed growth effects of the pike's vestibulo-ocular reflex arc are correlated to the growth effects calculated on basis of the model for the growing semicircular canal.

10. The pike possesses the same degree of vestibulo-ocular compensation in the high-frequency range (2 radians/sec $\leqslant \omega < 7$ radians/sec) of angular oscillations during its whole life (11 observations of pike of body length 4–56 cm).

LIST OF ABBREVIATIONS

a	Angular acceleration.
$a_m(=-U\omega^2)$	Maximum angular acceleration during sinusoidal oscillation.
b	Width of the ampulla cross-section at the summit of the crista.
c	Coefficient of allometric relation.
h_o	Cupula height.
k	Thickness of the cupula at the summit of the crista.
l_1	Length of the narrow duct.
l_2	Length of the wide part of the semicircular canal.
n	Exponent of allometric relation.
r_o	Radius of the inner cross-section of the narrow duct.
t	Time.
x	Average endolymph displacement in the narrow duct.
x_m	Average maximum displacement during sinusoidal oscillation.
x_0	Average maximum displacement caused by post-rotatory stimulation.
$\dot{x}$	Average linear velocity of the endolymph in the duct (cm/sec).
$\ddot{x}$	Average linear acceleration of the endolymph in the duct.
$\bar{z}$	Average endolymph displacement in the ampulla.
z	Endolymph displacement in the ampulla.
z^*	Normalized deviations of cupulae with respect to the cupula of a pike with body length $L = 5$ cm.
A	Area enclosed by the average semicircular canal.
C	$= 2A(l_1+l_2)^{-1}$.
E	Young's modulus of elasticity.
F	Restoring pressure per cm in the duct (dyne/cm).
G	Sensitivity factor of the semicircular canal.
L	Body length of the pike.
M	Inertial pressure coefficient of the endolymph (g/cm).
O_a, O_o	Areas of the cross-sections of the ampulla and of the duct respectively.
O_{ao}	Surface of the crista.
Q	Phase difference between a_m and x_m.
R	Radius of a circular area, equal to the area enclosed by the average canal.
R_o	Radius of curvature of the deflected cupula.
T	Period of the sinusoidal oscillation.
U	Amplitude of the applied angular oscillation.
W	Coefficient for the Poisseuille friction in the duct (dyne sec/cm).
α_m	Eye amplitude of the sinusoidal eye response.
β	Angle of linear cupula deflexion (like a door).
γ	Applied constant angular velocity.
γ_t	Threshold angular velocity for the transient eye response.
γ_m	Maximum angular velocity during sinusoidal angular oscillation.
η	Absolute viscosity of the endolymph.
μ	Pressure per unit of angular deflexion.
v	Frequency of sinusoidal angular oscillation.
ρ	Specific density of the endolymph.
ϕ	The angle of the endolymph deviation in the torsion pendulum.
ψ	Phase difference between x_m and γ_m.
ψ_0	Phase difference between α_m and γ_m.
ω	$= 2\pi v$
θ	The moment of Poisseuille friction in the torsion pendulum model.
π	The moment of inertia in the torsion pendulum model.
Δ	Restoring moment, with respect to the centre of the semicircular canal, exerted by the cupula.

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