

**THE MECHANICAL ANALYSIS OF THE RESPONSES
FROM THE END-ORGANS OF THE HORIZONTAL
SEMICIRCULAR CANAL IN THE ISOLATED
ELASMOBRANCH LABYRINTH**

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The hypothesis that the cupula-endolymph system of the semicircular canals of the vertebrate labyrinth may be considered to behave as a highly damped torsion pendulum has been the subject of previous investigations (Steinhausen, 1931; van Egmond, Jongkees & Groen, 1943; van Egmond, Groen & Jongkees, 1948, 1949).

If this hypothesis is correct, three quantities determine the behaviour of the system, as is the case with every pendulum. These are: the moment of inertia of the swinging mass Θ , the restoring couple† Δ and the damping Π . It is not necessary to know all three mentioned quantities, viz. Θ , Δ , Π for the prediction of the behaviour of this pendulum; it is sufficient to know two of their ratios, e.g. Δ/Θ , Π/Θ or Π/Δ .

Among the characteristic properties of a pendulum the following two will be useful in the determination of the unknown ratios:

(1) The natural frequency ω_0 . $\omega_0 = 2\pi/T$ (where T denotes the undamped period of the pendulum); also $\omega_0^2 = \Delta/\Theta \text{ sec}^{-2}$.

(2) The more or less damped movement of the pendulum on its return swing.

There are three possibilities:

(a) The pendulum returns, passes equilibrium and goes on to attain a deviation almost equal to the former one (oscillating type).

(b) The pendulum just returns to the equilibrium position without passing it. In that case it is critically damped, which means that the damping is just sufficient to keep the pendulum from oscillating.

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† Referred to as 'directional momentum' by van Egmond *et al.* (1949).

(c) The pendulum returns very slowly as if moving in treacle. It attains equilibrium in the end, but this takes a long time (over-critical damping).

It appears that the cupula-endolymph system belongs to case (c). It is over-critically damped (about ten times more than the critical case needs).

The deviation from zero-position of the returning cupula as a function of time represents an exponential decay. The power is $-\Delta/\Pi \text{ sec}^{-1}$. The larger the damping Π , the longer it takes the cupula to come back. For the determination of the differential equation which describes the behaviour of such a pendulum it is necessary to measure the natural frequency and the rate of decay. If this differential equation is found to predict the reaction of a structure, one is entitled to say that this structure behaves like a true pendulum.

van Egmond *et al.* (1949) carried out experiments on human subjects and succeeded in determining the two important ratios in man. They made use of the description and accurate timing of sensations by human subjects in response to various rotational stimuli. As was shown by the authors, their results are in striking agreement with the results of electrophysiological experiments on the nervus ampullaris of the ray (*Raja clavata*) in which Lowenstein & Sand (1940) measured the frequency of the nerve-impulse discharge in response to rotational stimulation. The experiments on the elasmobranch labyrinth did not, however, aim at the determination of the coefficients of the above-mentioned differential equation.

The experiments described in the present paper were designed to make use of the method of recording from the horizontal canal of the isolated labyrinth of the ray (*Raja clavata*) in order to analyse the responses to stimuli specially chosen to yield the desired coefficients.

METHODS

The method of isolation of the labyrinth and preparation of the nerve twigs for oscillographic recording has been fully described by Lowenstein & Sand (1940). The two types of stimulation used were (1) a sinusoidal oscillatory movement obtained with a torsion-swing, and (2) a sudden change in the velocity of turn-table rotation.

Torsion-swing and accessories. The torsion-swing used in our experiments consisted of a brass platform of 30 cm diameter suspended from a \cap -shaped brass strip and two parallel steel wires, the distance of which could be changed by means of a device incorporating left- and right-hand screws. In this way it was possible to vary the period of the swing between 2 and 16 sec. In the course of the work it appeared that this range of frequencies was not extensive enough. To obtain a longer period of oscillation a single steel strip was used for the suspension, whereas for very short periods the torsion-swing was suspended from a steel rod. Two heavy brass weights could be placed on horizontal bars, on opposite sides of the platform. By varying their distance from the axis of the swing it was possible to change the frequency by changing the moment of inertia. The total range of oscillation times thus obtained extended from 0.75 to 50 sec.

The preparation, mounted on a Perspex plate, was placed on the brass platform in a special clamping device. As will be seen from the theoretical considerations given below, accurate recording of the movement of the swing was essential. For this purpose a disk was fixed to the

torsion-swing, parallel to and below the platform. This disk was provided with slots round the edge at intervals of 1.5° . The filament of a small lamp above the disk was imaged on its edge. When a slot was in the light beam, the light fell on a photocell. The photocell current was used, via a simple electronic circuit, to light a small neon tube in front of the recording camera. This neon tube was imaged on one edge of the photographic paper in the camera. During the movement of the swing the neon lamp produced a dotted line on the paper film. When working at very small swing periods, smaller slots at 0.5° intervals were used. By means of the dotted line on the photographic paper the time of the turning points of the swing could be accurately measured. Furthermore, the number of dots between the turning points yields the amplitude A . Knowing the paper speed from a 50 c/s time marker trace, we could measure the time of a period, and thus the circle frequency ω . The product ωA is equal to the maximum angular velocity attained by the preparation.

The turn-table. The turn-table consisted of a horizontal circular disk resting on a vertical axis with a pivot bearing. The table was turned by means of a pulley and belt, driven by a motor through a 50:1 gear. By means of this gear the angular velocity of the turn-table could be varied within wide limits. The angular velocity generally used was between 10 and $60^\circ/\text{sec}$. The latter may be still considered a physiological velocity.

Electrical equipment. A conventional high-gain resistance-capacity coupled amplifier with oscillograph, monitor speaker, and bromide film camera was used. In addition, phonograms were sometimes taken to record the sound picture from the monitor speaker as well as protocol data. Finally, a counting-rate meter was used. This is a well-known electronic instrument used in nuclear physics. By means of this meter continuous readings could be made of the frequency of the impulse-discharge. As the meter had a significant integration time for the low frequencies we were dealing with, rapid changes of the frequency could not be followed by this instrument. It was therefore used to follow comparatively slow changes only.

THEORY

The theory covering the behaviour of the semicircular canal cupula in response to the motion of a torsion pendulum has been treated in a previous paper (van Egmond *et al.* 1949). For the sake of convenience a short survey of this theory may be given as follows:

The differential equation of a torsion pendulum without the action of an external force is

$$\Theta \ddot{\xi} + \Pi \dot{\xi} + \Delta \xi = 0 \quad \text{or} \quad \ddot{\xi} + \frac{\Pi}{\Theta} \dot{\xi} + \frac{\Delta}{\Theta} \xi = 0, \quad (1)$$

in which ξ , $\dot{\xi}$, $\ddot{\xi}$ are respectively the angular deviation, velocity, and acceleration of the endolymph relative to the skull; Θ is the moment of inertia of the endolymph; Π is the moment of friction at unit angular velocity; Δ is the moment of restoring couple due to the cupula at unit angular displacement. All these quantities refer to the endolymph ring in relation to the centre of the canal.

The approximate solution of this equation is

$$\xi = \gamma \frac{\Theta}{\Pi} (e^{-\Delta t/\Pi} - e^{-\Pi t/\Theta}), \quad (2)$$

if, when $t=0$, $\xi=0$ and $\dot{\xi}=\gamma$.

As the damping Π of the cupula-endolymph system is very large, the second term of the part within brackets of equation (2) can very rapidly (0.1 sec) be neglected in comparison with the first part.

When the endolymph is given a certain known initial angular velocity γ and the endolymph displacement ξ is measured as a function of time, the ratio Δ/Π can be determined. This can be done experimentally on the turn-table (see below). One can plot the logarithm of the increase or decrease of the frequency of the nerve discharges as a function of time. If this change in frequency is proportional to the deviation of the cupula, the curve of \log (frequency change) against time will be a straight line. The slope of this line is the same as that of the line: \log (deviation of the cupula) against time. This slope now represents Π/Δ .

The second relation between the coefficients of the differential equation (1) can be obtained by submitting the preparation to a harmonic oscillation by means of a torsion-swing. When the so-called circle-frequency of the torsion-swing is ω ,* the differential equation of the cupula-endolymph system is

$$\ddot{\xi} + \frac{\Pi}{\Theta}\dot{\xi} + \frac{\Delta}{\Theta}\xi = \alpha \sin \omega t, \quad (3)$$

in which α is the maximal angular acceleration of the torsion-swing. When we call the maximal amplitude of the swing A and the time of one period T , then

$$\alpha = \omega^2 A, \quad (4)$$

$$T = \frac{2\pi}{\omega}. \quad (5)$$

The solution (steady term) of (3) is

$$\xi = \frac{\omega^2 A \Theta}{\sqrt{[(\omega_0^2 - \omega^2) \Theta^2 + \omega^2 \Pi^2]}} \sin(\omega t - \phi), \quad (6)$$

with

$$\tan \phi = \frac{\omega}{\omega_0^2 - \omega^2} \frac{\Pi}{\Theta}. \quad (7)$$

ω_0 denotes the natural circle-frequency of the cupula-endolymph system, and ϕ the phase difference between the movement of the torsion-swing and the cupula.

As was pointed out in the introduction

$$\omega_0^2 = \frac{\Delta}{\Theta}. \quad (8)$$

In the case of resonance $\omega = \omega_0$; then $\tan \phi = \infty$; $\phi = 90^\circ$. This means that when the frequency of the torsion-swing is equal to the natural frequency of the cupula-endolymph system, a phase difference of 90° exists between it and the swing. When the swing has its maximal deviation (velocity zero) the cupula is in its equilibrium position and the sensation of a human test-subject would be that of zero velocity (rest). When the swing is in its equilibrium position (maximal velocity) the cupula has its maximal deviation, which causes the sensation of maximal velocity. Cupula movement and torsion-swing movement have a phase difference of 90° . But velocity sensation (or cupula deflexion, or impulse response of the sense organ) and velocity of the swing are in phase. This is not merely a coincidence, but it is an essential feature of the cupula-endolymph system. Its displacement during a physiological movement is always proportional to the velocity of the head, i.e. the cupula has at any given instant a deflexion proportional to the angular velocity of the head at that instant. The cupula deflexion gives rise to a sensation of angular velocity which appears to correspond accurately to the objective velocity. In this way a human test-subject has a quantitatively correct impression of what is happening. It is thus appropriate to introduce the angle $\psi = 90^\circ - \phi$, being the phase difference between the cupula deflexion (velocity sensation, or impulse response) and the velocity of the swing.

When $\omega \neq \omega_0$, $\phi \neq 90^\circ$ and $\psi \neq 0$. This means that the times of maximal and zero-velocity respectively as recorded by a test-subject are not the same as those of the torsion-swing. Now the cupula-endolymph system is highly damped; Π/Θ is a large factor. Therefore the factor $\omega/(\omega_0^2 - \omega^2)$ in (7) has to be fairly small, either negative or positive, in order that ϕ may differ considerably from 90° . Consequently ω has to be very much larger or smaller than ω_0 for finding a measurable phase difference.

When $\omega^2 \gg \omega_0^2$,

$$\tan \phi \approx \frac{\Pi}{\omega \Theta}. \quad (9)$$

Therefore, when we are able to measure ϕ and ω , Π/Θ can be calculated.

* The frequency of a vibration (ν), being the number of total vibrations per unit of time, is the reciprocal of the period T , $\nu = 1/T$. The circle-frequency ω is 2π times the frequency $\omega = 2\pi\nu$.

If, on the other hand, $\omega^2 \ll \omega_0^2$,

$$\tan \phi \approx \frac{\omega \Pi}{\omega_0^2 \Theta} \approx \frac{\omega \Pi}{\Delta} \quad (10)$$

from equation (8). Again after measurement of ϕ and ω , Π/Δ can now be calculated.

To summarize: three values of the ratios of the coefficients Θ , Π and Δ can be obtained by measuring the deviation of the cupula as a function of time after a sudden change in angular velocity and by measuring the phase differences between torsion-swing and canal at frequencies of the torsion-swing much greater or much smaller than the natural frequency of the canal. Only two are needed. Thus an additional control is available.

The maximum deviation of the cupula for a given maximal angular velocity of the torsion-swing is also dependent on the frequency.

From (6) follows

$$\xi_{\max.} = \frac{\omega^2 A \Theta}{\sqrt{[(\omega_0^2 - \omega^2) \Theta^2 + \omega^2 \Pi^2]}} \quad (11)$$

Making use of (7) one obtains after some calculation

$$\frac{\xi_{\max.}}{\omega A} = \frac{\Theta}{\Pi} \sin \phi. \quad (12)$$

This unfortunately is not a sharp criterion.

$\phi = 90^\circ$ in the case of resonance. For a phase difference ψ of, for example, 10° , $\sin \phi = 0.98$. For the highly damped cupula-endolymph system 10° phase difference is already considerable, and a 2% change in the ratio of $\xi_{\max.}$ and ωA is not measurable. Therefore relation (12) can hardly be checked by this method.

RESULTS

In the majority of the successful experiments we recorded from so-called single fibre preparations which are characterized by the appearance on the record of single impulses at certain frequencies, each spike potential being probably derived either from a single sensory cell or from a group of synchronously firing end-organs. The majority of such functional units are found to show a resting discharge in the absence of rotary stimulation. The frequency of this resting discharge will be referred to as the basic rate. It appears that the basic rate is remarkably constant for a sensory unit. Measurements of its fluctuation yielded a deviation of only about 4% from the average frequency. The mode of response from a semicircular canal is by now well known and consists, in the horizontal canal, of an increase of the discharge frequency in response to ipsilateral angular acceleration and a corresponding decrease on contralateral acceleration. The response from any given sensory unit is proportional to the magnitude of the stimulus. There is good reason to assume that there is no 'threshold' for such a response, representing, as it does, an upward or downward modulation of an already existing discharge activity (cf. de Vries, 1949). Of course, there must exist a threshold for *sensation*. The fact of the basic rate obviously sets a lower limit to the minimum perceptible angular acceleration. But even when we know the average fluctuation and derive the minimum perceptible angular acceleration from reflex tests or from tests with human subjects, we still do not know how many sense endings have to co-operate to evoke a sensation, and in what manner the central nervous system integrates the afferent signals.

Generally we found a different sensitivity of the sensory units for ipsilateral and contralateral angular acceleration. This difference was pronounced on stronger stimulation, and varied very much in different preparations. The reason for this differential sensitivity is obvious. The diminution in the impulse discharge on contralateral (inhibitory) acceleration cannot amount to more than the abolition of the basic rate, whereas there is much greater scope for an increase in the discharge frequency of ipsilateral (stimulatory) acceleration. This inequality between the responses to equal but opposite stimuli impairs the reliability of results under certain conditions. We therefore based our conclusions exclusively on the results gained from sense endings showing equal sensitivity over a considerable range both to ipsilateral and contralateral acceleration.

Experiments with the torsion-swing

Before recording the impulse response, the swing was kept in motion for some minutes to give the cupula in the semicircular canal the opportunity to acquire an induced periodic motion. The response to more than one complete swing was recorded even when oscillation periods of long duration were employed. The majority of responses recorded in this way were derived from single nerve fibre preparations. In this case two different ways of measuring the impulse frequency were used. When the period of the torsion-swing was short (e.g. 1 sec) we measured the distances between adjacent spike potentials on the photographic record. The frequency of the spikes was then calculated by taking the ratio of the film speed (in cm/sec) to the distance between the spikes (in cm). This procedure was necessary in the case of short torsion-swing periods because of the small number of spikes per period. When, on the other hand, the period was long (15–40 sec) we counted the number of spikes within constant time intervals (e.g. half a second or a second). Only rarely the records were derived from a massive discharge. In this case we always counted the number of spikes above an arbitrarily chosen amplitude. Such readings were not as accurate as those obtained from single fibre preparations.

The impulse frequencies so obtained were plotted as a function of time which was determined very accurately by means of the 50 c/s time marker on the record. The turning points of the swing were accurately determined by the photoelectric action signal.

The basic rate was always measured by making a record of the response before and/or after stimulation. The points of intersection between the sine-curve plotting frequency against time and the horizontal line drawn at the level of the basic rate indicate when the cupula was in its equilibrium position. The difference in time between these and the turning points of the swing represents the phase difference. This measured phase difference is not closely dependent on the value of the basic rate used, because the average of the phase differences was always measured at leading and trailing edges of the sine-curve.

Fig. 1 shows an example of the nerve impulse frequency plotted against time for a sinusoidal movement of the preparation. The phase differences are clearly visible.

Table 1 gives the results of a number of measurements and the calculated values of Π/Δ and Π/Θ . Not all measurements listed in this table have been used for the computation of Δ/Θ . Some results were not reliable, as the plot of impulse frequency against time, which ought to be a sine-curve, showed distortion; in others the phase differences were too small to yield accurate results.

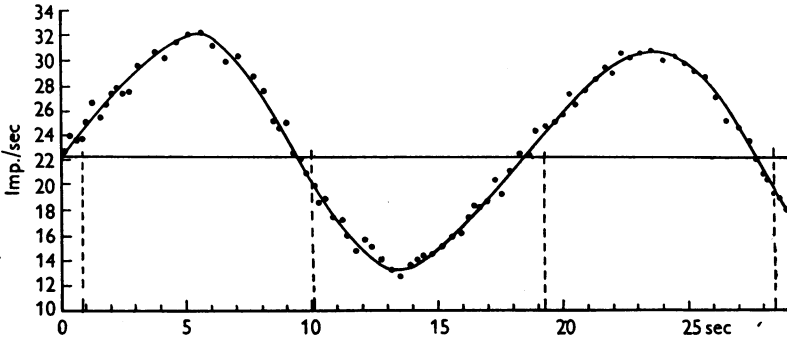


Fig. 1. The frequency of nerve impulses as a function of time during a sinusoidal movement. $T = 18.4$ sec; $\omega = 2\pi/T = 0.34$ sec⁻¹; $A = 54^\circ$; $\omega A = 18.5^\circ/\text{sec}$. Total response = 9.2 impulses/sec; sensitivity = 0.50 impulses/degree; phase lead = $13.5 \pm 2^\circ$. The turning points of the torsion swing are marked by the broken vertical lines.

For $T > 2\pi/\omega_0$, the cupula leads in respect to the torsion-swing, while for $T < 2\pi/\omega_0$, the cupula lags.

According to equation (7)

$$\tan \psi = \tan (90^\circ - \phi) = \cot \phi = \frac{\omega_0^2 - \omega^2 \Theta}{\omega \Pi}.$$

When $T \gg \frac{2\pi}{\omega_0}$ or $\omega \ll \omega_0$,

$$\tan \psi \approx \frac{\omega_0^2 \Theta}{\omega \Pi} = \frac{\Delta T}{\Pi 2\pi}. \tag{13}$$

When $T \ll \frac{2\pi}{\omega_0}$ or $\omega \gg \omega_0$,

$$\tan \psi \approx \omega \frac{\Theta}{\Pi} = \frac{2\pi \Theta}{T \Pi}. \tag{14}$$

In Fig. 2 the phase differences ψ have been plotted against the logarithm of the time of the period of the swing (T). It will be seen that the differences between the semicircular canals in various preparations are not large. The two branches of the curve for a cupula-leading or cupula-lagging phase difference against swing period have an asymptote. The slope of the asymptote

for $T \gg \frac{2\pi}{\omega_0}$ is $\frac{1}{2\pi} \frac{\Delta}{\Pi}$; for $T \ll \frac{2\pi}{\omega_0}$ it is $\frac{1}{2\pi} \frac{\Theta}{\Pi}$. The following values can thus be arrived at:

$$\frac{\Pi}{\Delta} = 22 \text{ sec}; \quad \frac{\Pi}{\Theta} = 36 \text{ sec}^{-1}; \quad \text{thus } \frac{\Delta}{\Theta} = 1.64 \text{ sec}^{-2}; \quad \text{hence } \omega_0 = 1.3 \text{ sec}^{-1}.$$

TABLE I

Ray	T sec	Basic rate impulses/sec	Sensitivity impulses/degree	ψ	Π/Δ sec	Π/Θ sec ⁻¹	Single unit (<i>s</i>) or massive (<i>m</i>)	
2	2.1	34	0.33	Lag 6°	—	—	<i>s</i>	
	3.9	32	0.33	Lag 3°.6	—	—	<i>s</i>	
	3.9	31.5	0.33	0	—	—	<i>s</i>	
	7.1	31	0.35	0	—	—	<i>s</i>	
3	8.0	55	0.67	0	—	—	Two units	
	2.1	38	+1.2	Lag 9°	—	—	<i>m</i> distorted	
	2.1	43	+1.1	Lag 5°	—	—	<i>m</i> distorted	
	2.1	43	+1.2	Lag 8°.5	—	—	<i>m</i> distorted	
4	22.0	23	0.25	Lead 6°.5	31	—	<i>s</i>	
	2.2	23	0.25	Lag 2°.5	—	—	<i>s</i>	
	2.2	22	+0.2	0	—	—	<i>s</i> distorted	
			-0.14					
5	0.86	100	1.7	Lag 12°	—	34	<i>m</i>	
	17.5	80	2.0	Lead 2°.5	64	—	<i>m</i>	
6	17.6	31	0.28	Lead 7°	23	—	<i>s</i>	
	2.1	6.1	+0.10	Lead 32°	—	—	<i>s</i> distorted	
			-0.05					
	2.1	8.0	+0.20	Lead 5°	—	—	<i>s</i> distorted	
			-0.10					
	2.1	6.1	+0.22	Lead 27°	—	—	<i>s</i> distorted	
			-0.09					
	2.1	7.5	+0.10	Lag 2°.5	—	—	<i>s</i>	
7	6.8	6.7	+0.08	Lead 18°	—	—	<i>s</i> distorted	
			-0.017					
	6.8	7.7	+0.20	Lead 3°.5	—	—	<i>s</i> distorted	
			-0.14					
	9	0.76	21	+0.37	Lag 14°.4	—	32	<i>s</i>
				-0.25				
0.76		6	+1.0	Lead 24°	—	—	<i>s</i> distorted	
			-0.25					
0.76		20	+0.37	Lag 13°	—	34	<i>s</i>	
			-0.33					
0.76		6	+0.71	Lead 20°	—	—	<i>s</i> distorted	
10	0.76	20	0.25	Lag 15°	—	31	<i>s</i>	
	44	20	1.2	Lead 18°	21	—	<i>s</i>	
	13.6	7	0.59	Lead 12°	10	—	<i>s</i> distorted	
	11	0.76	25	0.11	Lag 9°	—	52	<i>s</i>
		29.1	27	+0.17	Lead 12°	21	—	<i>s</i>
			-0.13					
18.4	21.3	+0.48	Lead 13°.5	12	—	<i>s</i>		
		-0.50						
19.1	20.5	+0.43	Lead 11°.6	15	—	<i>s</i>		

+ means 'at stimulation'; - means 'at inhibition'. Both are given separately when they are unequal.

Experiments with the turn-table

On the turn-table the preparation was given a constant angular velocity during a time large enough for the cupula to reach its equilibrium position. After that the rotation was suddenly stopped, the largest deceleration thus applied being from a velocity of $72^\circ/\text{sec}$ to rest. In such a case the sudden* cessation of a constant speed rotation will rapidly deflect the cupula from its resting position. Whether this deflexion will lead to an increase or decrease of the impulse discharge depends on the direction of rotation prior to deceleration.

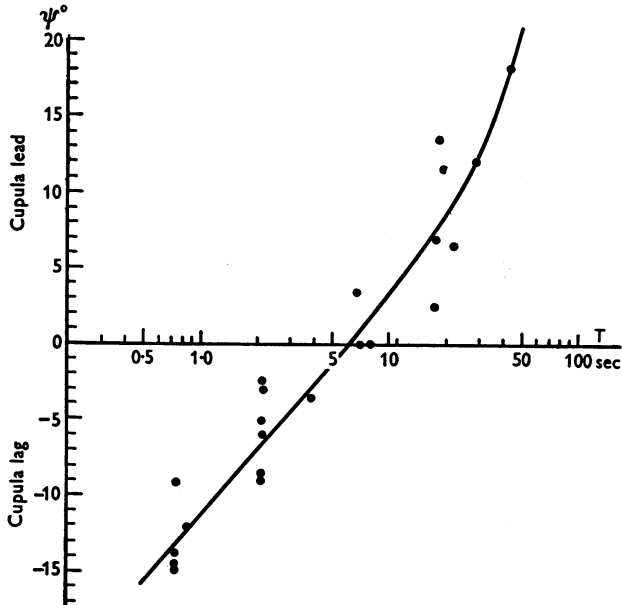


Fig. 2. Phase difference (ψ) of the impulse frequency (deviation of the cupula) in relation to the sinusoidal stimulus as a function of the logarithm of the 'swing' time (T).

In the case of the left horizontal semicircular canal sudden arrest of prolonged clockwise rotation at constant speed will result in an increase, and arrest of a similar counter-clockwise rotation will be followed by a decrease in discharge frequency. During the ensuing state of rest the discharge frequency will return towards the basic level, the time taken over this return (decay) depending on the various factors discussed under Theory (p. 331).

The frequency of the impulse response before and after the stimulus was usually measured by means of the counting-rate-meter. Sometimes, however, for the sake of greater accuracy, the changes of the impulse discharge were recorded on film. Owing to the relatively long 'decay' times involved,

* The change in velocity is called 'sudden' when the time during which the total change takes place is short with respect to the natural period of the cupula, the latter being of the order of 5 sec.

continuous recording on bromide film was impracticable and therefore only 2 out of every 10 sec were recorded. The number of impulses per second was computed and the logarithm of the difference from the basic rate was plotted against time. The resulting curve was called a decay curve. In these experiments the accurate assessment of the basic rate is very important. The basic discharge was therefore recorded not only before, but also after the experiment.

Fig. 3 shows an example of a decay curve. In general, the decay curves were satisfactorily straight when we restricted ourselves to such sensory units as showed good proportionality between response and stimulus. The slope of such a curve yields Π/Δ .

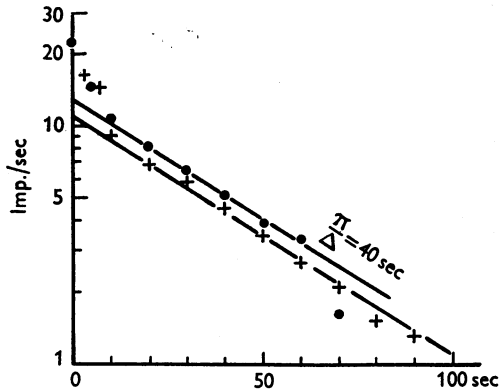


Fig. 3. A 'decay curve', i.e. the logarithm of the change (increase or decrease) of the impulse frequency plotted against time after a sudden change in velocity (γ). Data calculated from a single unit record. $\gamma = 36^\circ/\text{sec}$. Sensitivity: 0.31 impulses/degree for stimulation (+), 0.36 impulses/degree for inhibition (-).

Theoretical calculation of Π/Θ

The value of Π/Θ of the cupula-endolymph system of human beings was calculated by van Egmond *et al.* (1949). They showed that

$$\frac{\Pi}{\Theta} = \frac{4\eta}{\sigma r^2}, \quad (15)$$

in which η is the viscosity of the endolymph, σ the density (mass per unit of volume) and r the radius of the cross-section of the semicircular canal.

We made one measurement of the inner diameter of the cross-section of a horizontal canal of a ray and found it to be 0.68 mm. Substituting for $\eta = 0.010$ c.g.s. units, and for $\sigma = 1.0$ g/cm³ in equation (15),

$$\frac{\Pi}{\Theta} = \frac{4 \times 0.01}{1 \times 0.034^2} \approx 35 \text{ sec}^{-1}.$$

As the shape of the semicircular canal is not as simple as is assumed in the calculation and as the value of the viscosity is uncertain, it was very gratifying to find this value of the right order of magnitude (see p. 336).

Some general considerations

Before discussing the significance of these results we shall consider some peculiarities of the response of the neuromast end-organs in more detail, as they appear to be of importance for the proper evaluation of our findings.

Most of the sensory units have a basic discharge. There are, however, some that show no such resting activity and yet respond to an ipsilateral stimulus of sufficient magnitude. At the other extreme end of the range there are sensory units with a lively basic discharge which cannot be increased by ipsilateral, but only reduced by contralateral acceleration. Such end-organs constitute a type of receptor sensitive to one direction of rotation only; and they are definitely in the minority. Lastly, there are a considerable number of

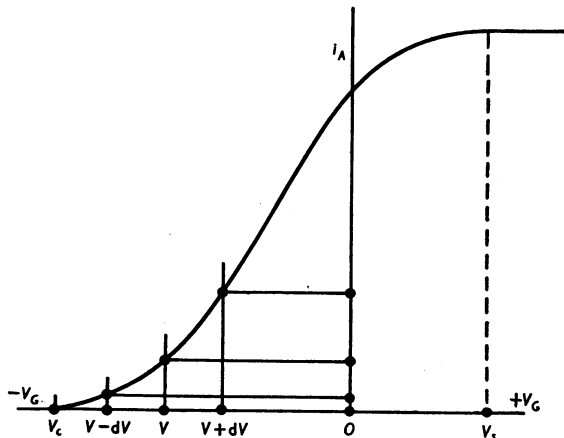


Fig. 4. Characteristic curve of a triode valve illustrating the behaviour of the sensory units. Explanation in text.

organs (see p. 334) which show a difference in sensitivity to the two opposite stimuli, i.e. whose response is not uniformly proportional to the strength of the stimulus. It would be possible to make a fairly accurate census of the distribution of these functional types of organs in the crista, but this has not been attempted. However, in this connexion, a comparison of the behaviour of the sense endings with that of a triode electronic valve quite obviously suggests itself. The well-known characteristic curve of such a triode valve is shown in Fig. 4. In the absence of a signal the grid-bias voltage determines the anode current. Any signal voltage applied to the grid produces either an increase or a decrease in the anode current. For our purposes we can compare the anode current with the frequency of the nerve discharge; the magnitude of the basic rate is then determined by a 'bias'. The 'bias' can be so large that the sense organ is in the 'cut off' position (V_c in Fig. 4). In that case there is no basic discharge and only a stimulus which reduces the negative bias can give rise to a response. On the other hand, a sense organ can be biased in such

a way that the 'working point' is in the horizontal upper part of the curve (V_s in Fig. 4). In this case there is a considerable spontaneous activity (corresponding to the anode current in our metaphor) and this can only be decreased by an appropriate stimulus which reduces the positive bias. As pointed out, these two types of sense organs have actually been found. They can be said to have a clear threshold. Of course, this analogy does not *explain* the mode of action of our sense organ. But we should like to emphasize that by using this metaphor one can consider the different types of sense organs found, from one and the same point of view. From our experiments it is thus possible to calculate the 'characteristic curve' of a particular sense organ. To use this terminology, we would say that we found that, for the purpose of our investigation, only such sense organs are suitable as have a reasonably linear part in their 'characteristic curve' and whose 'working point' is situated in this linear part.

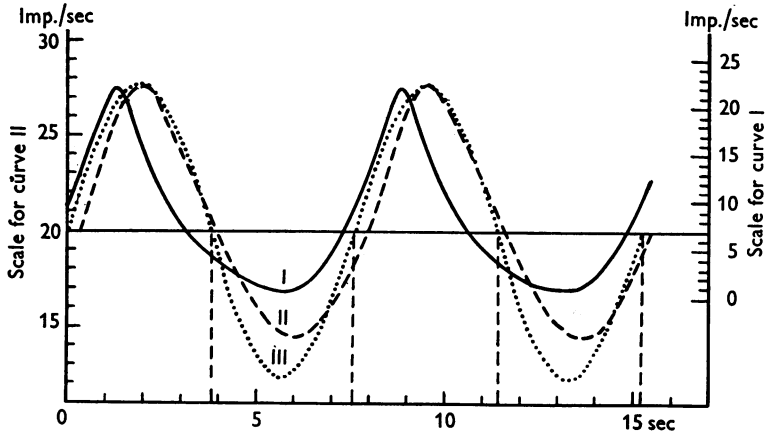


Fig. 5. Impulse frequency plotted against time, derived from two sensory units in one and the same preparation, recorded simultaneously during sinusoidal stimulation. I: distorted sine-curve, leading phase $+24^\circ$; II: less distorted sine-curve, lagging phase -13° ; III: pure sine-curve for comparison, in phase 0° . $T=0.76$ sec, $\omega A=18^\circ/\text{sec}$. The turning points of the torsion-swing are marked by broken vertical lines.

This comparison has, of course, its limits. The properties of the response of a sense organ are much more complicated. They can only be described in first approximation by such a characteristic curve. As is well known the response from a sense organ at a particular moment is not only a function of the stimulus at that moment, but also of the preceding stimuli. There is a kind of 'hysteresis'. The 'post inhibitory rebound' and the 'post excitatory inhibition', the so-called 'silent period', have often been described. In our experiments similar phenomena were observed.

The response of the sense organ to a sinusoidal movement (applied by the torsion-swing) gave sometimes a clearly distorted sine-curve. In Fig. 5 the

frequency of the response of two units of one preparation is shown. One unit (curve I) gives a much distorted sine-curve and there was a phase lead while a lag was expected on first principles. The response of the second unit (curve II) is less distorted; it is much nearer to the true sine (curve III), which is also given for comparison. The phase is in fact lagging. The kind of distortion demonstrated by curve I in Fig. 5 could be explained by some of the last mentioned physiological peculiarities of the sense organ.

The reliability of the turn-table method

Using a three-unit preparation, we tested to what extent the cupula-crista system is liable to be damaged by strong stimulation. In Fig. 6, the response in impulses/sec is plotted against stimulus ('impulse'). The

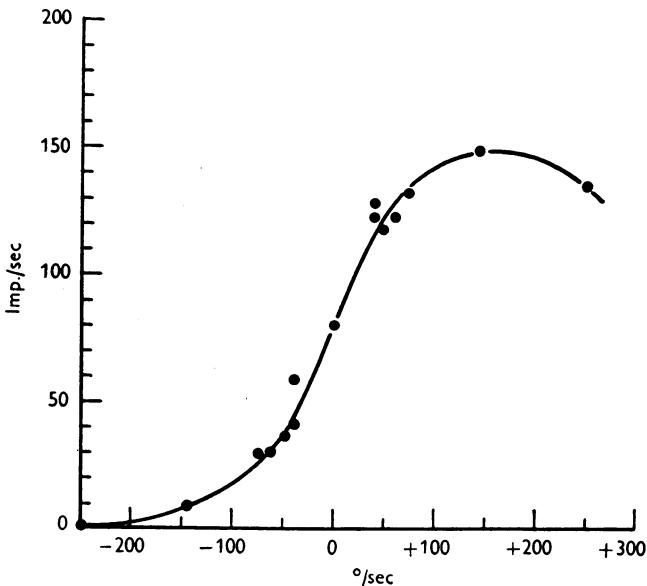


Fig. 6. Three-unit preparation. Characteristic curve of response frequency plotted against mechanical 'impulse'.

'triode' shape is clearly visible. The linear part is $\pm 40^\circ/\text{sec}$ wide on either side of zero-stimulation (80 imp./sec). As it happened, this preparation was very resistant to over-stimulation. Even after a stimulus of $250^\circ/\text{sec}$ on the turn-table, ipsi- and contralateral, its behaviour was not appreciably altered. In Table 2, the stimuli (in degrees/sec), the slopes of the decay curves (in seconds) and the sensitivities (in impulses/degree) are given, both for stimulation and for inhibition.

The first stimulus of $36^\circ/\text{sec}$ was repeated after a very strong 'impulse' of $252^\circ/\text{sec}$ and the data are given at the bottom of the table. The slope did not alter much; it is comparable to the average of the $36^\circ/\text{sec}$ and the $48^\circ/\text{sec}$

before the 252°/sec stimulus. The sensitivities to the inhibitory and the excitatory stimulus, i.e. 1.11 imp./degree are not very different from the initial value. From these data one would perhaps draw the conclusion that the cupula-crista system is not very vulnerable. However, most of our records show that secondary phenomena can, in fact, appear after only slight stimulation.

TABLE 2

Stimulus (degrees/sec)	Π/Δ in sec		Sensitivity (impulses/degree)	
	Inhibition	Stimulation	Inhibition	Stimulation
36	26	22	0.62	1.34
48	37	32	0.77	1.00
60	32	36	0.83	0.71
70	37	27	0.71	0.71
144	40	33	0.50	0.48
252	*	32	0.33	0.22
36	31	25	1.11	1.11

* Total inhibition of too long a duration.

Secondary after-sensation

During experiments on human subjects on the turning chair, a so-called secondary after-sensation (the 'post-post' of the clinicians) is sometimes observed. The human subject is placed on a turning chair and is submitted to rotation with a constant angular velocity. When the subject has no sensation of turning he is suddenly stopped. The subject has then the sensation of turning in a direction opposite to the direction of the initial rotation. This is called the after-sensation. Now, sometimes after the dying down of this sensation, the human observer reports an additional sensation, viz. of turning in the direction identical with the original direction of the mechanical rotation. This is the so-called secondary after-sensation. This phenomenon occurs especially after strong stimuli. We were able to observe a corresponding phenomenon after strong turn-table stimulation of the labyrinth preparation. During the 'decay', the frequency decreased in such a case, not only to the basic rate (return of cupula to resting position) but beyond it, after this gradually rising again to the value of the basic rate. This effect probably corresponds to the secondary after-sensation in human subjects.

A possible explanation is that the cupula, which is not only deflected but also deformed by the strong stimulus, returns slowly in its deformed state to the equilibrium position. After having reached this equilibrium the deformation is corrected. It is this restoration of the original shape of the cupula which may be responsible for the secondary after-sensation.

DISCUSSION

The agreement between the results obtained by the experiments on the torsion-swing and turn-table with the theoretical calculated values is fairly good. An analysis of the possible errors will show that it is even better than

it appears at first sight. There are some sources of systematic error which must be considered. We have mentioned the possibility of hysteresis of the sense organ and we have rejected all those experiments in which this effect was clearly apparent. But we must not forget that the phase differences obtained on the torsion-swing are rather small and that the distortion of the sine response due to hysteresis can affect the measured phase differences considerably. This will be clear from Fig. 5. Therefore it is possible that in most experiments hysteresis tends to enhance the leading phases and diminish the lagging ones. Consequently, according to equations 13 and 14, too small a value for the Π/Δ and too large a Π/Θ will result from the recorded responses.

The same phenomenon affects the results of the turn-table tests. However, its influence will be almost limited to the frequencies measured shortly after the cupula has reached its maximum deviation. We did not pay much attention to these particular frequencies in the determination of the slope and, therefore, it is not likely that this effect has had a serious influence on our results. But here a possible alinearity may be of great importance. As the majority of the sense organs appear to have their 'working point' in the lower part of their characteristic curve ('bias' in the neighbourhood of V_c in Fig. 4), the alinearity tends to make the slope (Δ/Π) of the decay curve, after an inhibitory stimulus, smaller than would have been the case with perfect proportionality. Thus the Π/Δ value of these inhibition decay curves may be somewhat too large. The influence of alinearity on the slope of the decay curve after an excitatory stimulus would be in the opposite direction, but is in general much smaller. This is in full agreement with our results, as can be seen from Table 3.

The results of the measurements from three preparations may be discussed in more detail, because those measurements were the most complete. When the average results are listed, weighted according to the probable systematic error, we obtain the figures given in Table 4.

The agreement between the results in rays nos. 5 and 9 is very good indeed. No. 11 gives less consistent results. However, in this case, the sine curves of impulse frequency against time were slightly distorted. The leading phase differences may therefore be too large, the lagging ones too small. This makes for a correction in the right direction. The average value of Δ/Θ for these three preparations is about unity.

Yet another phenomenon has to be considered. The Π/Δ determined by the turning test and measured by means of the counting-rate-meter gives a smaller value than the one measured by photographic record. In the latter the spikes from one single unit are counted, while the rate-meter counts the spikes of all fibres which make good enough electrical contact with the electrode. Now, we have pointed out that sometimes sense organs have been found which work as uni-directional units (see p. 339) 'biased' at V_s or V_c of Fig. 4. When such fibres are present in the strand which makes contact with

TABLE 3

Ray	Π/Δ in sec		γ in degrees/sec	Measured by counting-rate- meter (CR) or record (R)
	Inhibition	Stimulation		
3	28	—	27	CR
4	38	12	27	R
	—	12	27	R
5	—	90	27	CR
	50	—	27	CR
	—	40	27	CR
	—	50	60	CR
	63	—	60	CR
	—	54	60	CR
	65	65	60	CR
9	30	—	70	R
	—	20	70	CR
	—	21	70	R
	—	19	70	CR
	19	—	36	CR
	—	15	36	CR
	23	—	36	CR
10	—	19	36	CR
	50	—	36	CR
	—	45	36	CR
11	51	—	36	CR
	—	20	36	CR
	21	—	36	CR
	—	43	36	R
	48	—	36	R
	—	25	36	CR
	28	—	36	CR
	26	—	36	CR
	—	22	36	CR
	37	—	48	CR
	—	32	48	CR
	32	—	60	CR
	—	36	60	CR
	37	—	72	CR
	—	27	72	CR
31	—	36	CR	
—	25	36	CR	

TABLE 4

Ray	Turn-table Π/Δ in sec		Torsion-swing		ω_0 in sec ⁻¹
	Inhibition	Stimulation	Π/Δ in sec	Π/Θ in sec ⁻¹	
5	59	60	64	34	0.73
9	24	19	21	32	1.2
11	30*	28*	19	52	1.1
	48†	43†	—	—	—

* Measured by counting-rate-meter.

† Measured by record.

the electrode the counting-rate-meter will measure a decay which is more rapid than the decay shown by one single unit. It is not certain that this has happened. But whatever the explanation, the difference between results obtained by counting-rate-meter and by single unit record may be very important, as the sensation of an animal is likely to correspond to the over-all reading of the rate meter rather than to the afferent impulse stream of a single sensory unit. The experiments with human beings make it, in fact, very likely that the Π/Δ measured by the sensation is smaller than the true value of the Π/Δ of the canal.

The results obtained with ray no. 4 (Table 3) show disagreement not only between the values obtained on turn-table and torsion-swing, but also on repetition of the same reading. The explanation here may be that, owing to experimental difficulties, the preparation was 3 hr old before we started the measurements. As delay does not as a rule produce such effects, it is safer to say that we can assign no cause for the unreliability of this preparation.

After consideration of the various sources of error, it can be stated with confidence that the 'pendulum theory' of the cupula-endolymph system is fully confirmed by our experiments. There is no reason to assume that the system is more complicated. For the average ray's labyrinth the differential equation which describes the behaviour of this system will be about

$$\ddot{\xi} + 35\dot{\xi} + \xi = 0.$$

SUMMARY

1. The mechanical properties of the cupula-endolymph system were subjected to experimental tests by means of the oscillographic method of recording from the nerve supplying the horizontal semicircular canal of the isolated labyrinth of the ray (*Raja clavata*).

2. Tests on torsion-swing and turn-table furnished conclusive evidence that the cupula-endolymph system behaves like a true pendulum.

3. On the basis of the measurements made, the quotients:

$$\frac{\Pi}{\Delta} = \frac{\text{moment of friction at unit angular velocity}}{\text{cupula restoring couple at unit angle}},$$

and
$$\frac{\Pi}{\Theta} = \frac{\text{moment of friction at unit angular velocity}}{\text{moment of inertia of endolymph}},$$

were computed and the latter value compared with a theoretical value deduced from the dimensions of the system. The values were found to be in fairly good agreement.

4. A differential equation describing the behaviour of this system in an 'average' labyrinth is suggested thus:

$$\ddot{\xi} + 35\dot{\xi} + \xi = 0.$$

5. During the tests, sense organs deviating from the expected mode of behaviour were encountered, but a simple physical model (the characteristic curve of an electronic valve) renders possible a unified description of all behaviour types of semicircular canal organs.

6. Questions relating to the vulnerability of the cupula-crista system to excessive stimulation, and to the so-called secondary after-sensation in man, are discussed on the basis of the experimental results.

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