THE VISCOSITY OF THE PIKE'S ENDOLYMPH

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INTRODUCTION

The mechanical sensitivity of the semicircular canals of the vertebrates is determined by the dimensions and the absolute viscosity η of the fluid inside the vestibular organ (ten Kate, 1969). As Table 1 shows, η diverges widely in different species and measurements. These different values reveal the necessity of viscosity determination for comparative labyrinthology. According to Table 1 the viscosity values of the endolymph and of the perilymph are not the same. This is due to the different concentrations of the organic and inorganic compounds (Rauch, 1964; Silverstein, 1966; Fernandèz, 1967).

Evidence exists that there are certain cells that regulate the chemical composition of the endolymph (Bélanger, 1953; Dohlman *et al.* 1959, 1964). On account of the uncertainty of η and the need felt for an accurate value of η, the viscosity of the endolymph of the pike was studied in detail. The development of a microviscometer, based on Stoke's law, has been undertaken. The effect that coagulation of proteins and globulins of the endolymph has on the measurement of η will be reduced compared with most capillary viscometers.

METHODS

A sphere is allowed to fall in a tube filled with endolymph (method A). The amount of endolymph which can be extracted from one pike is limited (about 30 μl for a pike of 50 cm body length). Therefore the dimensions of the tube and the sphere have to be small. The capillaries used had a length of 6–10 cm and a (circular) inner diameter of 500 μ. The amount of liquid needed to fill one capillary was maximally 19 μl.

The absolute viscosity η of the endolymph is determined with a modified and corrected form of Stoke's law, viz.;

$$\eta = (\rho_k - \rho_L) 2 r_k^2 g t \{ 9 s_t (1 + 2 \cdot 1 \, r_k / d) \}^{-1} \tag{1}$$

(see ten Kate, 1969, and Ladenburg *et al.* 1932). (Denotation of symbols at the end of the article.)

In Fig. 1 the specially shaped capillary is depicted.

The dimensions s_t and d of the capillary and the radius r_k of the metal alloy sphere (1 % deviations from a perfect sphere) can be measured accurately. The densities ρ_k and ρ_L are found by determination of mass and volume.

Thus in our experiments we have measured the time t which the sphere takes to fall in a capillary filled with liquid over a distance s_t marked by two slits S_1 and S_2.

When the sphere passes the first slit S_0 a photomultiplier produces an electric pulse, which triggers an oscilloscope. The second and third slits S_1 and S_2 subsequently cause vertical deflexions on the oscilloscope screen. In this way the time t could be measured (see Fig. 2).

Table 1

Authors	Method	Species	Liquid	η in cP	Tempera-ture (°C)	Remarks
Bekesy (60)	C	Human	p (co)	1·97	37	
Doesschate (14)	C	Plaice	e	$1·95 \times \eta_w$	0	$V_1 = 2$–5 cm³
		Haddock	e	$1·220 \times \eta_w$	0	Hirudine added
		Cod	e	$1·279 \times \eta_w$	0	
Money (66)	R	Pigeon (Columbia livia)	e	1·15	40	Preliminary results
			p	0·78	40	$V_1 = 2$–3 cm³
Rauch (59)		Human	e	1·03–1·05	27	
			p	1·02–1·03	27	
Rossi (14)	C	Pigeon	e	3·20	20	
			p	1·70	18–20	
Schnieder (64) & Schindler	{ B	Guinea pig	{ e	1·00 (1 ×)	20	f, $V_1 = 1·6 \times 10^{-4}$ l
			p	0·90 ± 0·11 (2 ×)	20	f su/li = 1/25 $\Delta r_s/r_s = 0·08$ 0·10
	C		p	1·15 ± 0·09 (1 ×)	20	wf
	B }		p }	1·12 ± 0·07 (1 ×)	20	wf
Vilstrup (54)	C	Shark (Acanthias vulgaris)	e	24·0	20	1 % solution of an extract

B = Brownian motion, C = capillary viscometer, co = cochlea, e = endolymph, η_w = viscosity of water, f = freezing preparation method, Δr_s = error in radius r_s of the spherical particles, R = rolling sphere viscosity meter (Flowers, Höppler), su/li = ratio between the suspension and the liquid, V_1 = volume needed for method, wf = without freezing.

In the actual experiment the capillary tube $(H_1 H_2)$ could be turned through 180°, its position deviating maximally 0·12 degrees from vertical (ten Kate, 1969).

A sphere is produced by pushing a melt metal alloy through a glass pipette with a tip diameter of 1–2 μ. Then to overcome the surface tension this sphere, still attached to the tip of the pipette, is brought into the liquid of the capillary and is then dislodged (Fig. 1). At the end of the experiment with a microscope the exact diameter $2r_k$ is determined. In order to get the endolymph out of the semicircular canal, the sharp tip T of the capillary (Fig. 1) has been run through the thin wall of the ostium tubulare into the anterior ampulla with the aid of a micromanipulator (sometimes also into the ampulla lateralis). After sucking up the endolymph (with or without a seal of paraffin oil) T is removed from the nearly deflated labyrinth. Then each end of the capillary is closed with a rubber cover. Subsequently the above described procedure of viscosity determination begins.

Though we have carried out preliminary experiments with distilled water to confirm the correctness of the correction factor for Stoke's law in the case $r_k/d \geqslant \frac{1}{4}$ and $R_e \leqslant 3$, we have preferred also to check the effect of the adjacent walls on the absolute viscosity of the endolymph. Another method (method B) resembling the rolling sphere viscometer of Flowers (1914) was used in order to test method A and to avoid the effect of surface tension on the sphere. A 'large' sphere of 450 μ diameter falls in a straight tube of 500 μ width.
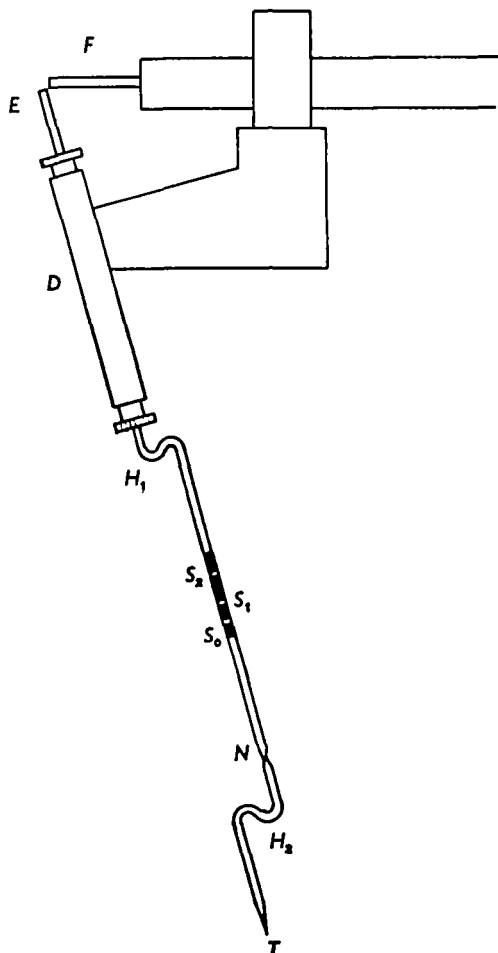
Fig. 1. Capillary used for the determination of the absolute viscosity of the endolymph. The capillary is clamped in a part of the manipulator (D). E and T are the two ends of the capillary. To prevent attachment of the sphere to the surface of the liquid, the capillary is bent in H_1 and H_2. S_0, S_1 and S_2 represent three slits in an aluminium coating of the capillary (width of slits 10–20 μ). In N the capillary is narrowed to assure that the sphere falls along the axis. Through F an air stream can be blown as a result of which the endolymph is sucked up in the capillary.

In all cases the endolymph has been taken from preparations of decapitated pike 20 min after death.

RESULTS

Method A

The successive peaks on the oscilloscope screen due to the passage of the sphere along the two slits S_1 and S_2 (Fig. 1) are represented in Fig. 2. In this case $t = 84 \pm 2$ msec. The vertical fall of the sphere is repeated 10 times and t is averaged. ρ_k of the metal alloy is $9 \cdot 82 \pm 0 \cdot 01$ g/cm³. We measured the specific density of the endolymph $\rho = 1 \cdot 01 \pm 0 \cdot 005$ g/cm³,

$$(\rho_k - \rho) = 9 \cdot 82 - 1 \cdot 01 = 8 \cdot 81 \text{ g/cm}^3, g = 98 \cdot 5 \text{ cm/sec}^2.$$

The radius r_k of the sphere, the radius d of the capillary and the distance s_t between the two successive slits S_1 and S_2 are determined under the microscope. All data are collected in Table 2 for the determination of the viscosity η of the endolymph for five pike. The Reynolds number R_e is also calculated. The value of η of pike 5 does not change more than 0·02 cP for larger spheres with $R_e = 2·5$.

The calculated values of η in Table 2 contain absolute errors calculated from estimated errors in the measurements. The errors in r_k and s_t are one-fifth of a scale
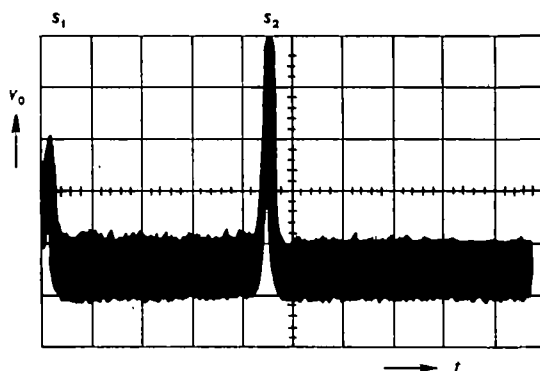

Fig. 2. Time interval between S_1 and S_2 (Fig. 1). Vertical axis: voltage of the photomultiplier, V_0. Horizontal axis: t = time scale (20 msec per division).

Table 2

Pike	r_k (μ)	t (msec)	s_t (cm)	d (μ)	η (cP)	R_e	Temperature (°C)
1	47·6	88	0·223	250	1·21 ± 0·09	1·99	23·0
2	46·5	114	0·281	250	1·21 ± 0·08	1·92	22·3
3	54·0	84	0·264	250	1·24 ± 0·08	2·74	23·1
4	39·5	138	0·259	250	1·20 ± 0·08	1·24	23·9
5	28·0	245	0·244	250	1·23 ± 0·10	0·46	23·4

Table 3

Pike	η_r	Temperature (°C)	η in cP	Remarks
1	1·20	22·3	1·14 ± 0·06	—
7	1·19	23·4	1·16 ± 0·06	—
8	1·37	22·6	1·30 ± 0·08	60 h after death
9	1·27	22·7	1·21 ± 0·08	—
10	1·28	22·7	1·21 ± 0·08	—

division in the microscopical measurements. Δt is one-tenth of the time scale on the screen of the oscilloscope. The relative error $\Delta\eta/\eta$ can be calculated easily from the individual relative errors (see ten Kate, 1969).

The resulting values of the viscosity of the endolymph obtained by method B are similar to the values of method A. This conclusion can be drawn from Table 3.

This conclusion appears to be also in agreement with simultaneous measurement of the endolymph viscosity by methods A and B, using endolymph from both labyrinths of one pike; with method A $\eta = 1·24 \pm 0·08$ cP and with method B $\eta = 1·20 \pm 0·07$ cP. The measured values are within the range of possible errors of both methods.

The example of pike 8 demonstrates the change in viscosity after death. The pike's

head was thawed after 60 h in the refrigerator. The increase in viscosity of the post-mortem endolymph was also observed by ten Doesschate (1914). All measurements of the pike's endolymph are performed 20–60 min after death and in this period no change of viscosity was noticed.

DISCUSSION

From the measurements we conclude that the average viscosity of the pike's endolymph at 23 °C is $\eta = 1\cdot20 \pm 0\cdot08$ cP. The values obtained can be compared to data on the endolymph viscosity mentioned in other reports. This is done on the assumption that temperature has the same effect on the viscosity of the endolymph as it has on the viscosity of water, according to Tietjens (1960). Then

$$\eta = (2\cdot31 \pm 0\cdot16)(1 + 0\cdot36\,t_e + 0\cdot000185\,t_e)^{-1}\text{ cP}, \tag{2}$$

where t_e = temperature in °C.

The data for the endolymph viscosity of the plaice, of the haddock, of the cod (Doesschate, 1914) at 0 °C, and that of the human endolymph (Rauch, 1959) at 27 °C agree with formula (2). In a recent report Steer (1966) mentioned $0\cdot852 \pm 0\cdot0017$ cP at 35 °C for the human endolymph and this also remains very well within the expected values of (2). However, the less reliable data for the pigeon's endolymph (Rossi, 1914; Money, 1966), that for the shark (Vilstrup, 1954), and that for the guinea-pig (Schnieder & Schindler, 1964) are in conflict with (2). At the moment more adequate and accurate determinations of the endolymph viscosity for different species are needed. As stated in the introduction, the sensitivity of the semicircular canals is affected by their dimensions and by the absolute viscosity. The sensitivity factor can be expressed in the following way

$$G = A\rho\pi r_c^4(4\,\eta l_1 O_a)^{-1}. \tag{3}$$

The substitution of η from (2) into (3) elucidates the dependence of the sensitivity upon temperature. The effect of temperature on the viscosity cannot be neglected.

When the temperature is raised from 8 to 37 °C. the sensitivity of the pike's semicircular canal would be doubled at a result of the change in the viscosity of the endolymph. If we compare the size of the semicircular canals of a pike and a mammal with the same body mass, the mammalian semicircular canal appears to be much smaller. Despite this difference in magnitude the semicircular canals of mammals and pike do have nearly the same sensitivity (ten Kate, 1969), if all parameters of the semicircular canal (including its dimensions) and the temperature are taken into account. In actual fact this aspect is related to the question of how the sensitivity and the dimensions of the pike's semicircular canal change during growth. This is described in a second paper.

SUMMARY

1. A micro method, based on Stoke's law corrected for the influence of adjacent walls, if used for the determination of the absolute viscosity of the pike's endolymph. Samples of maximally 19 μl were used.

2. The absolute viscosity has an average value of $1\cdot20 \pm 0\cdot08$ cP at 23 °C for ten individual pike labyrinths.

3. The values obtained are compared to those measured by a micro-rolling-sphere

viscometer. The absolute values determined by both methods agree within the limits of error.

4. The values obtained for the pike's endolymph agree with those obtained for other species, if the temperature-dependence of the viscosity of water is taken into account.

5. Though the semicircular canals in mammals are smaller than those in pike of equal body mass, they appear equally sensitive, if the temperature effect on the endolymph viscosity is taken into account.

SYMBOLS

d	inner radius of the capillary.
g	acceleration of gravity.
h_o	height of the cupula.
l_1	length of the narrow duct of the semicircular canal.
r_c	radius of the narrow duct.
r_k	radius of sphere.
s_t	distance in a capillary between S_1 and S_2.
t	time.
t_e	temperature in °C.
A	area enclosed by the average semicircular canal.
O_a	area of cross-section of ampulla.
R_c	radius of curvature of the deflected cupula.
R_e	Reynolds number.
η, η_r	absolute and relative viscosity of the endolymph, respectively.
η_w	absolute viscosity of water.
ρ, ρ_k	specific density of endolymph and of the sphere, respectively.

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