

THE DIMENSIONS AND SENSITIVITIES OF SEMICIRCULAR CANALS

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INTRODUCTION

For any semicircular canal a sensitivity factor G depending on the dimensions of the semicircular canal can be derived theoretically (ten Kate, 1969). On this basis a study was undertaken to determine the relation between G and the size of the semicircular canals. The sensitivity is defined by

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

where

- A = area enclosed by the average canal (see Fig. 1),
- ρ = specific density of the endolymph,
- r_c = inner radius of the narrow duct,
- l_1 = length of the narrow duct,
- O_a = inner cross-section of the ampulla at the site of the crista.

With this definition it is possible to compare the mechanical sensitivities of all semicircular canals. For this purpose three different approaches seem feasible.

- (1) The effect of growth of one particular semicircular canal on G in one species.
- (2) Comparison of values of G for the three semicircular canals in one species.
- (3) Comparison of values of G of the horizontal canal in different species.

Measurements of the geometry of the labyrinth of the pike have therefore been made. At the same time we studied the increase of the geometrical parameters of semicircular canals of the growing pike in relation to the bodylength of the animal. For the comparison of different species values of G were deduced from the literature.

METHODS

Whole pike, or heads of pike, were preserved for about half a year in solutions of 10% formaline.

While submerged in boiled distilled water, sixty labyrinths were carefully extracted under the dissection microscope. The skulls of the larger animals were opened with the aid of a dental drill. To check the effect of the formaline fixative the labyrinths of fresh pike were prepared and subsequently compared with the preserved labyrinths (open triangles in the figures). No significant divergences between the two sets of values were observed.

Most measurements were made on the canalis lateralis and the canalis posterior, because the canalis anterior was sometimes deformed during the preparation. This membranous canal is suspended in tissue between the skull and the brain capsule and disconnecting the tissue on one side often causes deformation. Measurements on the canalis anterior had to be regarded with suspicion. The two other canals are better defined as they are attached by tissues in cartilage tubes. After preparation the whole labyrinth was brought into a square cuvette filled with glycerol. The lens effect of the round transparent walls is neutralized by the liquid with refractive index $n_r = 1.47$. This quality of glycerol gives us the possibility of determining all desired internal measures of the semicircular canals before dissecting the labyrinth. Measurements were made both by means of a microscope and by projecting an image of the cuvette containing the labyrinth on a screen with the aid of a slide projector. Microscopically determined values of the dimensions of the labyrinth do not deviate more than $\pm 2\%$ from the values obtained by the projection method.

The measurement of areas could be undertaken by carefully drawing the projected outline of the ampulla inner cross-section O_a , and of the average canal for the determination of A .

Subsequently the areas were measured with the aid of a compensation polar-planimeter of G. Coradi (Willers, 1948). Then the relations between the parameters A , $2r_c$, l_1 , O_a , h_c , $(l_1 + l_2)$ and the body length L were determined by plotting the measured values on double logarithmic paper. The allometric relations were obtained by the least-square method of linear regression curves to the measured values. The use of the body length L is preferred because the body mass B is affected by several factors which do not influence the body length L , viz. the skeleton, the filling of the intestines, the condition of nourishment and health, the sex, the development of the gonads, the loss of products from the gonads, etc. (Hegemann, 1964). Furthermore, the constant ratio between the skull measures and the body length L of pike of different sizes favours the use of L in the allometric expressions (Ohlmer, 1964; ten Kate, 1969).

RESULTS

Since formula (1) contains r_c^4 , small inaccuracies on the measurement of $2r_c$ have a large effect on G . Therefore the inner cross-sections of the narrow ducts were examined more precisely. First, we checked that the inner cross-sections approximate to circles. Secondly, the course of $2r_c$ along the length of the narrow ducts was studied for a number of labyrinths, filled with indian ink and submerged in glycerol. The values of $2r_c$ exhibit a slight increase along the duct from the ampulla towards the connexion with the common crus (see Fig. 2). This is true if the elliptic cross-sections of the connexions are excluded. Then the average value of r_c^4 along the duct is determined. Subsequently we chose that spot at the narrow duct corresponding to the average value of r_c^4 as the appropriate location for the determination of r_c for semicircular canals of different sizes.

At this best position all diameters $2r_c$ of the inner cross-section of the fifty-five narrow ducts were measured with a microscope. During these measurements the labyrinths were submerged in glycerol.

The resulting values of $2r_c$ for the canalis lateralis are plotted against the body

length L on double logarithmic scale (Fig. 3). The slope of the inner diameters (I) is somewhat smaller than the slope of the inner radii r_c (II) of the ray (Werner, 1960). Curve III is a rough estimation of the outer diameters of the horizontal semicircular canal (h.s.c.) of the pike. The outer shape of the cross-section of ducts in larger pike is irregular. The straight solid line in Fig. 3 represents $2r_c = cL^n$ for which n and c are computed from the 55 measured values of $2r_c$ by the least-square method. The slope of the line is the calculated n , and the point of intersection of the straight line with the ordinate (at $L = 1$ cm) represents the calculated value of c .

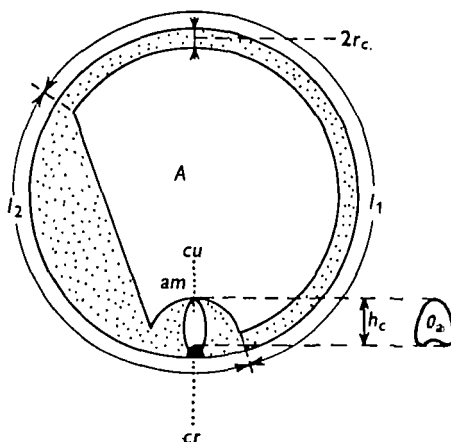


Fig. 1. Locations of the used symbols at the semicircular canal. A = enclosed area by the average canal, am = ampulla, cr = crista, cu = cupula, h_c = cupula height, l_1 = length of canicular duct, l_2 = length of the wide part, O_a = cross-section of the ampulla at the summit of the crista.

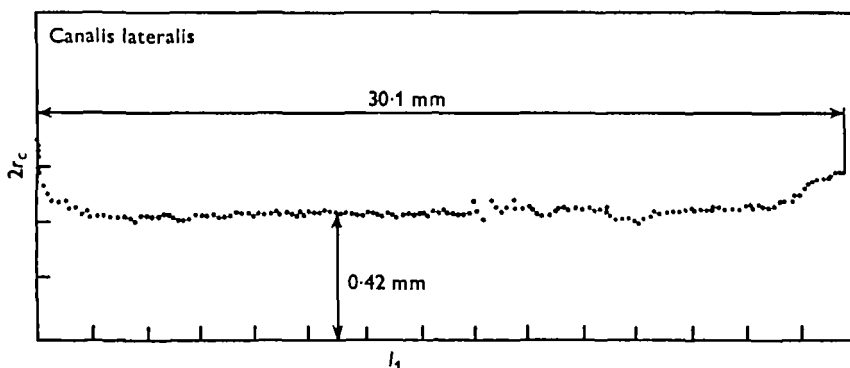


Fig. 2. The diameter of the narrow duct, $2r_c$, plotted against the length of the duct, l_1 .

Some parameters (A_h , l_1 and r_c) of the semicircular canals of the pike could be compared to those of the rays determined in other growth studies (Werner, 1927, 1960). From Fig. 4 one may conclude that the open circles agree very well with the data for the pike. The values for the average enclosed areas of the ray are determined from scaled pictures in the literature (Werner, 1927, 1960). Moreover, no divergence

between the values of preserved pike (black dots) and those of fresh pike (open triangles) could be observed.

At the moment some problems concerning the growing semicircular canals need to be considered more precisely. First, what values for c and n are obtained for para-

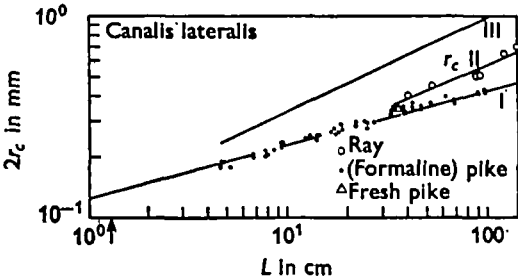


Fig. 3. Against the body length L is plotted curve I: the inner diameter of the duct of the pike; curve III: the outer diameter of the duct of the pike; curve II: the inner radii of the ray (Werner, 1960). The initial length of the pike at hatching is $L = 1.3$ cm. (Arrow at the abscissa in Figs. 3, 4.)

Table 1

I Parameter	II Canal	III c	IV n	V $M_e(\%)$	VI $E_e(\%)$
A_h	h.s.c.	$0.0704 \pm 0.0037 \text{ mm}^3$	1.730 ± 0.016	4	11.3
$2r_c$	h.s.c.	$0.122 \pm 0.003 \text{ mm}$	0.274 ± 0.007	1 to 2.8	4.6
l_1	h.s.c.	$0.0474 \pm 0.0013 \text{ cm}$	0.945 ± 0.008	1.5	5.6
O_a	h.s.c.	$0.0286 \pm 0.0014 \text{ mm}^3$	0.943 ± 0.015	3.75	14.2
h_o	h.s.c.	$0.165 \pm 0.003 \text{ mm}$	0.477 ± 0.005	1.5 to 0.3	3.7
$(l_1 + l_2)$	h.s.c.	$0.1031 \pm 0.0028 \text{ cm}$	0.865 ± 0.008	1	5.6
A_p	p.s.c.	$0.0570 \pm 0.0034 \text{ mm}^3$	1.692 ± 0.018	1	10.8
$2r_o$	p.s.c.	$0.142 \pm 0.004 \text{ mm}$	0.297 ± 0.008	1 to 2.3	5.9
l_1	p.s.c.	$0.0406 \pm 0.0018 \text{ cm}$	0.909 ± 0.013	1.75	9.2
O_a	p.s.c.	$0.0266 \pm 0.0013 \text{ mm}^3$	0.967 ± 0.014	3.75	10.0
h_o	p.s.c.	$0.164 \pm 0.003 \text{ mm}$	0.495 ± 0.005	1.4 to 0.3	3.4
$(l_1 + l_2)$	p.s.c.	$0.101 \pm 0.003 \text{ cm}$	0.823 ± 0.011	0.5	7.2
G	h.s.c.	$(4.44 \pm 0.95) \times 10^{-6} \text{ cm sec}$	0.94 ± 0.07	Obtained from <i>allometric expressions</i>	
G/h_o^3	h.s.c.	$(1.6 \pm 0.4) \times 10^{-8} \text{ cm}^{-1} \text{ sec}$	-0.02 ± 0.08		
G/h_o^3	h.s.c.	$(1.64 \pm 0.17) \times 10^{-8} \text{ cm}^{-1} \text{ sec}$	-0.02 ± 0.03		
G	p.s.c.	$(8.5 \pm 2.3) \times 10^{-6} \text{ cm sec}$	1.003 ± 0.049	Obtained from <i>allometric expressions</i>	
G/h_o^3	p.s.c.	$(3.1 \pm 0.9) \times 10^{-8} \text{ cm}^{-1} \text{ sec}$	0.01 ± 0.06		
G/h_o^3	p.s.c.	$(3.11 \pm 0.40) \times 10^{-8} \text{ cm}^{-1} \text{ sec}$	0.01 ± 0.04		
G/h_o^3	p.s.c.	$(1.9 \pm 0.5) \times 10^{-8} \text{ cm}^{-1} \text{ sec}$	0.01 ± 0.04	Obtained from <i>individual values</i> corrected for common crus	

meters A , r_c , l_1 , O_a , h_o and $(l_1 + l_2)$ of the h.s.c. and the p.s.c. (posterior semicircular canal). Secondly, how well the geometry of the semicircular canals is expressible in the allometric relations cL^n .

The coefficients c and the exponents n of all parameters are therefore listed with their corresponding standard deviations in the columns III and IV in Table 1.

The question can be raised whether these standard deviations are due to the measurement errors M_e or to the variability of the individual values of the parameters during growth. Comparing the values of M_e and the standard errors of estimate

E_s in columns V and VI in Table 1 reveals the correctness of the second possibility. The conclusion therefore seems to be justified that the variance in the values for the parameters of the semicircular canals for one particular body length L is greater than measurement errors.

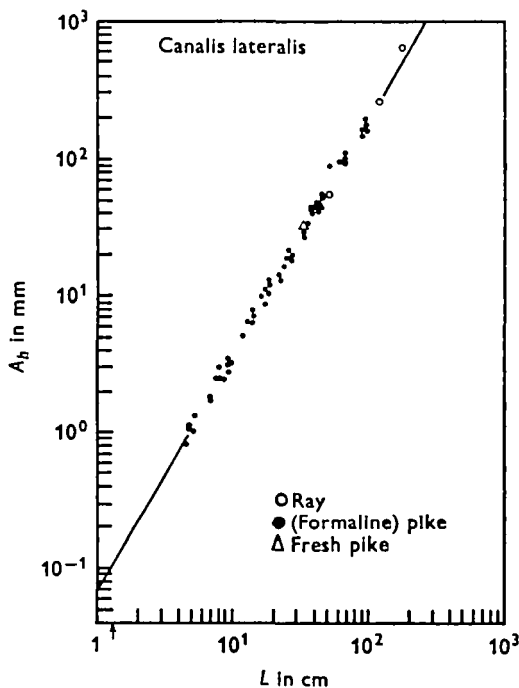


Fig. 4. Average enclosed areas of the h.s.c. versus body length L . Open circles are average enclosed areas of the h.s.c. of the ray (Werner, 1927, 1960).

Furthermore, we convinced ourselves of the correct fitting of the allometric function cL^n to the actual values of the semicircular canals by different procedures. First, all listed values of c and n are computed from 55 measured values of each one of the parameters A , $2r_c$, l , O_a , h_c and $(l_1 + l_2)$ by the least-square method. Then an impression of linearity was gained by the agreement of the straight regression curves with the measured values on the double logarithmic paper (see Figs. 3, 4). For the complete set of figures reference should be made to the literature (ten Kate, 1969). The straight lines could be drawn with the aid of the calculated slopes n and the calculated values of c as the points of intersection with the ordinates ($L = 1$ cm). Second, tests on linearity of $\log c + n/\log L$ were performed with two statistical analyses (description and results are given in the appendix). With the listed reliable set of data for A , r_c , l , and O_a we study the sensitivity G of the h.s.c. and the p.s.c. as a function of the body length L .

The measured absolute viscosity, $\eta = 1.25$ cP at 20° C, and $\rho = 1$ g/cm³ are used in formula (1) (ten Kate, 1969). In this way the listed values of c and n for G in Table 1 are obtained from the substitution of the allometric relations in formula (1). So the mechanical sensitivity G is dependent on the body length L .

This fact is in conflict with the preliminary experiments of post-rotatory stimulation, in which it was found that the minimum thresholds of the horizontal oculo-

vestibular reflex arc (h.o.v.r.a.) were independent of the size of the pike. The constant minimum thresholds might be explained by assuming a constant mechanical sensitivity of the h.s.c. during life (ten Kate, 1969). In this interpretation we suppose

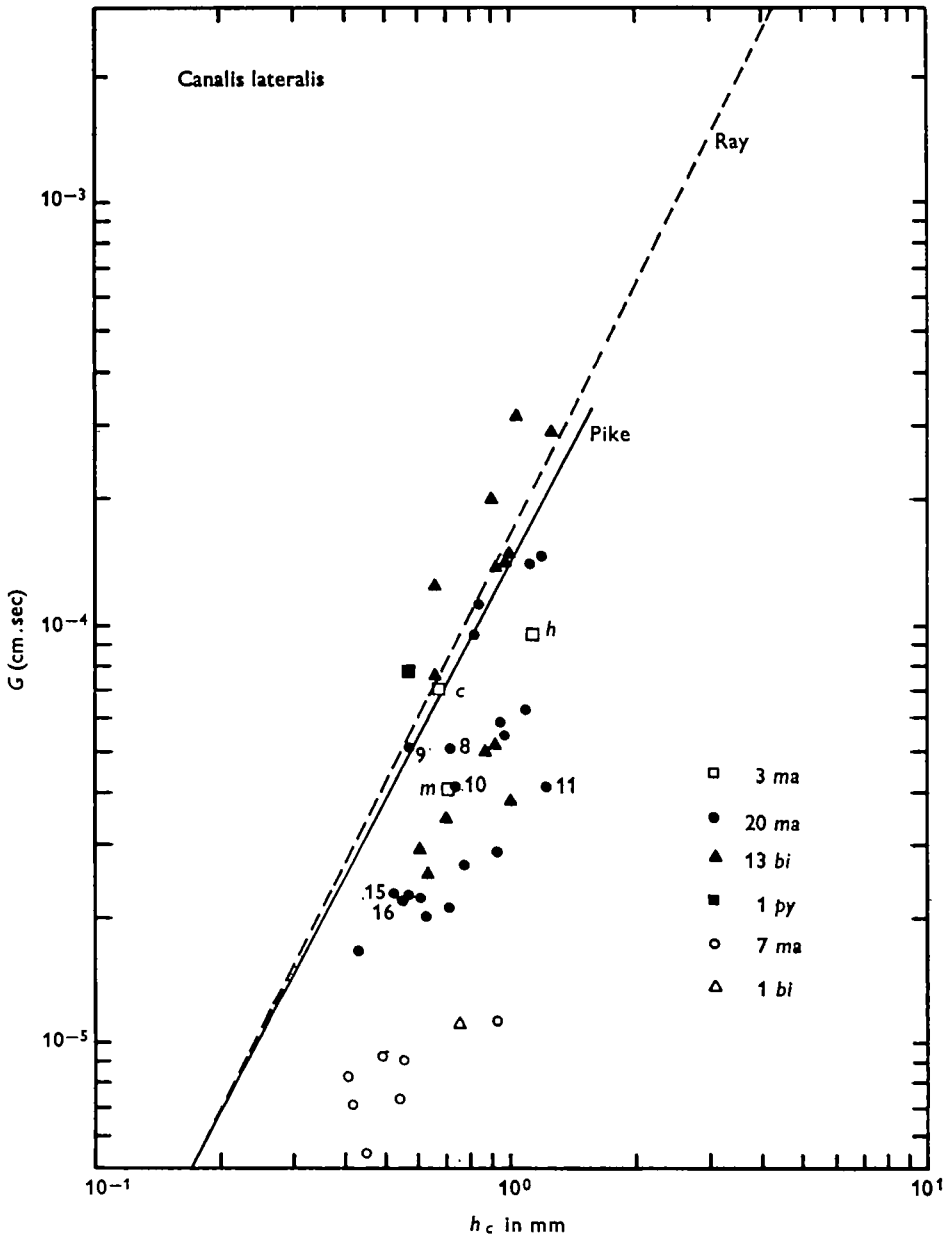


Fig. 5. The sensitivity factor G of h.s.c. versus cupula height h_c . *bi* = birds, *c* = cat, *h* = human, *ma* = mammal, *m* = squirrel monkey, *py* = python. For the numbers 8, 9, 10, 11, 15 and 16 see text.

that no change of sensory sensitivity and motor amplification in the h.o.v.r.a. take place during growth. From this point of view the value of G , for different values of L , can give information about the mechanical sensitivity of the semicircular canal. G

appeared to be dependent on the body length L . This dependence, however, may be due to the way in which the cupula is deformed. To study the deformation the sensitivity G of the horizontal semicircular canal was plotted against h_c in Fig. 5.

The slope of the straight regression curve is approximately 2, which indicates that G is proportional to the square of the cupula height h_c . The question can be raised how accurately the slope of G equals 2 in Fig. 5 and what limits exists for possible absolute values of G . From Table 1 we calculate

$$G = (1.6 \pm 0.4) \times 10^{-2} h_c^{1.98 \pm 0.17}. \quad (2)$$

Apparently the differences between sensitivities of several species and of the pike in Fig. 5 are by no means significant.

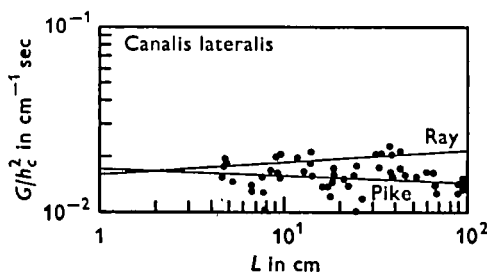


Fig. 6

Fig. 6. Theoretical sensitivity G/h_c^2 of the h.s.c. versus body length L .

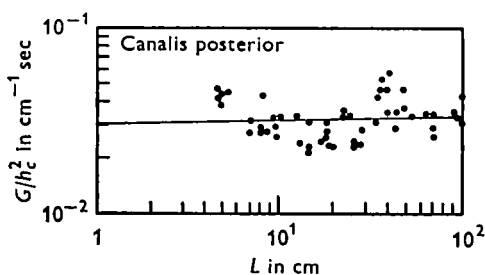


Fig. 7

Fig. 7. Theoretical sensitivity G/h_c^2 of the p.s.c. versus body length L .

The ratio of G to the square of h_c is given in Table 1 for both semicircular canals. G/h_c^2 is possibly an expression of constant sensitivity during the life of the pike, since the exponents n of G/h_c^2 for the h.s.c. and for the p.s.c. are about zero. Individual values of G/h_c^2 are subsequently computed from the values of A , l_1 , r_c , h_c and O_a for both semicircular canals (see Figs. 6 and 7). The corresponding values of c and n , found with the least-square method, are given in Table 1. The results for c and n from these individual values are in agreement with those obtained from the allometric functions. In Figs. 6 and 7 the straight lines represent the corresponding values c and n . Calculated values G/h_c^2 are spread about the straight lines. The maximum value of G/h_c^2 is about twice the minimum. In actual fact we encounter a spread in threshold values of the oculo-vestibular reflex for pike of different sizes after horizontal rotatory stimulation. The threshold angular velocity ranged between $2^\circ/\text{sec}$ and $9^\circ/\text{sec}$.

Comparison of the exponents n for both semicircular canals reveals that they are not significantly different from zero as is ascertained with a Student's t -test with a significance level of 5% ($t = 0.43$ and 0.53 respectively, to be compared to $t_{53;0.05} = 2.01$).

The coefficient c of G/h_c^2 for the p.s.c. needs a correction for the tacit neglect of the Poiseuille friction in the common crus, the correction factor being 1.65, so that c must be divided by 1.65. The resulting value of c is given in the last array of Table 1. Then the sensitivities G/h_c^2 are of the same order of magnitude. For an exact explanation of the differences between c of the factor G/h_c^2 for the h.s.c. and c of that factor for the p.s.c. dissections of the common crus are necessary. At the moment we conclude that

the sensitivities G/h_c^2 for both the vertical and the horizontal semicircular canals are the same.

THE SENSITIVITY G FOR DIFFERENT SPECIES

With the limited data given by Werner (1927, 1960) we expressed the parameters of the labyrinth of the ray in the allometric form cL^n . The exponents n of the various parameters of the horizontal semicircular canal in Table 2 are comparable with those of Table 1.

Table 2. (*Raja batis*)

	A_h	l_1	l_2	r_c	h_c	O_a	G	G/h_c^2
c	0.036 mm ³	0.48 mm	0.38 mm	0.11 mm	0.27 mm	0.0572 mm ³	12.07×10^{-4} cm s	1.65×10^{-8} cm ⁻¹ s
n	1.18	0.90	0.90	0.35	0.58	1.16	1.22	0.06

As shown in the eighth column of Table 2 and by the dashed line in Fig. 5 G increases with increasing L and h_c . The factor G/h_c (last column of Table 2) has a negligibly small value for the slope n (depicted in Fig. 6). This fact is in accordance with our findings for the pike. In Fig. 5 the open squares represent values of G for human (h), squirrel monkey (m), and cat (c), calculated from data given by Igarashi (1967), (see also ten Kate, 1969). For this (1) is changed to

$$G = R^2 \rho O_c (4\eta l_1 O_a)^{-1}, \quad (3)$$

which is an appropriate form for the mammalian 'circular' canal. Formula (1) could also be adapted to data of mammals, birds and one reptile, taken from the dimensional study of Jones & Spells (1963). Then

$$G = \pi \rho R_c^4 h_c (6\eta V_a)^{-1}, \quad (4)$$

where $\rho = 1.0$ g/cm³ and $\eta = 0.007$ P at 36 °C (for twenty-seven mammals and fifteen birds) and $\eta = 0.01$ P (for a reptile) are inserted.

Jones has determined r_c , R and V_a (volume of ampulla) from the stereoscopic photographs taken by Gray (1907). The cupula height h_c has been calculated from the volume V_a of the hemisphere (ampulla).

The sensitivities thus obtained for mammals are plotted in Fig. 5 as black dots. From the top downwards these black dots represent respectively the sensitivity G for the next sequence of twenty mammals: (1) horse (*Equus caballus*), (2) beisa-antelope (oryx) (*Oryx beisa*), (3) dugong (*Halicore australis*) (4) capybara (*Hydrochoerus capybara*), (5) hocheur monkey (*Cercopithecus nictitans*), (6) black ape (*Cynopithecus niger*), (7) pig (*Sus scrofa*), (8) black-faced kangaroo (*Marcropus melanops*), (9) slow loris (*Nycticebus tardigradus*), (10) common marmoset (*Hapale jacchus*) (11) Indian gazelle (*Gazella bennetti*), (12) green monkey (*Cercopithecus callitrichus*), (13) yellow baboon (*Cynocephalus papio*), (14) three-toed sloth (*Bradypus tridactylus*), (15) hairy-footed jerboa (*Dipus hirtipes*), (16) brush-tailed wallaby (*Petrogale penicillata*), (17) vulpine phalanger (*Trichosurus vulpecula*) (18) aardwolf (*Proteles cristatis*), (19) mongoose (*Herpestes griseus*), (20) common mole (*Talpa europaea*).

The sensitivity G of fourteen birds is indicated by black triangles in Fig. 5. From the top downwards these black triangles represent respectively: (1) common buzzard (*Buteo vulgaris*), (2) masai ostrich (*Struthio masai*), (3) cape gannet (*Sula capensis*),

(4) crowned crane (*Balearica pavanina*), (5) red-throated diver (*Clymbus septentrionalis*), (6) burrowing owl (*Speotyto cunicularia*), (7) crowned pigeon (*Goura coronata*), (8) common fowl (*Gallus domesticus*), (9) slender-billed cockatoo (*Licmetis nasica*), (10) carrion crow (*Corvus corone*), (11) cormorant (*Phalacrocorax carbo*), (12) great tinamou (*Rhynchotus rufescens*), (13) common duck (*Anas boschas*), (14) song thrush (*Turdus musicus*).

The value found for the only reptile (black rectangle in Fig. 5) the West-African python (*Pytho sebae*) agrees well with the sensitivity of the birds.

From top to bottom of Fig. 5 the open circles represent the sensitivities G for seven mammals viz.:

(1) common sheep (*Ovis aries*), (2) common squirrel (*Sciurus vulgaris*), (3) common otter (*Lutra vulgaris*), (4) jerboa mouse (*Antechinomys lanigera*), (5) fruitbat (*Pteropus medius*) (6) brush-tailed phascologale (*Phascologale peniciliati*) (7) short-nosed bandicoot (*Perameles obesula*).

The exceptional low value of G for the Mantell's kiwi (*Apteryx mantelli*) is shown as an open triangle in Fig. 5.

The reliability of the latter group (open circles and open triangle) for the sensitivities is rather questionable because of the improbable combinations of R , r_c and V_a observed. It should be remarked that the measurement of the semicircular canals (Jones & Spells, 1963; Gray, 1907) are subject to several errors: (a) the presence of irregular layers of celloidin disturbed an exact determination. (b) a possible shrinkage diminishes the values of the several parameters, (c) the approximation of the volume of the ampulla by a hemisphere is incorrect, since it appears to be approximately an ellipsoid, (d) the radius R is not realistic, since the shape of semicircular canal may not be truly circular.

Most calculated values of G are lower than those for pike. But we have also to take into account the effect of temperature on G . Our calculation for the pike (as for the ray) is based on the viscosity at 20 °C. The straight line for the pike (Fig. 5) will shift towards lower values of G if the average temperature, 12 °C, of the pike's biotope (Mook, 1968) is used. It seems justified to conclude that all semicircular canals possess mechanical sensitivities depending on cupula heights and having values of the same order of magnitude as for the pike.

DISCUSSION

Interpretation

Minimum thresholds to post-rotatory stimulation of the pike appear to be independent of size (15–50) cm (ten Kate, 1969). The horizontal oculo-vestibular reflex arc is, however, composed of several elements. Each one of these elements is subject to alterations during growth. If for simplicity no influence of the growth on the individual amplification factors of the components is assumed, only the increase of G with increasing L has to be explained. This is a restriction on the discussion of the question of how a constant mechanical sensitivity of the detector during life could be obtained. At the moment other possibilities cannot be excluded. For instance the increase of G with L may be counteracted by a regulation of the sensory sensitivity by the efferent vestibular system during growth. Further investigations are necessary to study the effect of growth on the components: the sense cells in the cristae, the efferent vestibular system, the trineuronic arc, and the extraocular muscles.

It is worthwhile to consider the ratio of G to the square of the cupula height h_c as a particular feature of the cupula deformation. On the ground of this assumption the following possibilities exist:

(a) the cupula bends as an elastic rod, which is fixed at its base (ten Kate, 1969); in this case the friction between the cupula and the wall of the ampulla need be of minor importance.

(b) the cupula is deformed in its centre, if the friction of the cupula with the walls is considerable; this idea corresponds very well with the parabolic flow in hydrodynamic models (Dittrich, 1963; Grohmann, 1968).

(c) the cupula glides over a subcupular layer; in this case the friction with the adjacent walls is neglected, and the cupula is supposed to turn like a door in the ampulla around the subcupular layer. (At the present time this is the most widely used model.)

It seems very likely that the kinocilia cause the excitation of the cell. In microscopical studies (Dohlman, 1964) the subcupular layer seems to be more rigid than the cupula. The stereocilia also contribute to its stiffness. The subcupular layer is therefore supposed to possess a thickness equal to the length of the stereocilia. When the stereocilia also elongate during the pike's growth the subcupular layer may increase in thickness too. 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 on flow at this boundary.

By its length, which is great with respect to the stereocilia, the kinocilium is very well anchored in the cupula. The displacement of the cupula with respect to the subcupular 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 assumed constant during growth. When the subcupular layer becomes thicker during growth the displacement of the boundary necessary to obtain 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 required 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 kinocilium, 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. If these properties are present, the non-linear features such as the non-linear superposition of the microphonic effect (Kuiper, 1956) may be clarified by the visco-elastic shearing in the boundary layer between the subcupular layer and the cupula.

Comparative anatomy of semicircular canals

In a dimensional study the semicircular canals of the pike can be compared to those the mammal by the allometric expression $c_b B^{n_1}$. For this purpose r_c and A_h are recalculated in relation to the body mass B (see Table 3) for pike.

Table 3 reveals that the growth rate n_1 for r_c is equally large for both species. The diameter (c_b) of the duct in the pike is 1.69 times that in the mammal for equal body mass. Concerning the area (A_h) enclosed by the semicircular canals, both the coefficient and the exponent are totally different. This aspect reflects the large size of the labyrinth in the fish as compared to the mammal. In case of a body mass of 1 kg for both species, A_h of the pike is about six times that of the mammal.

Table 3

	r_c (46 ma)	r_c (13 ma)	r_c (55 pikes)	A_h (46 ma)	A_h (55 pikes)
c_b	0.10 mm	0.11 mm	0.178 ± 0.011 mm	9.7 mm ²	65 ± 12 mm ²
n_1	0.07 ± 0.02	0.09 ± 0.02	0.091 ± 0.002	0.23 ± 0.06	0.577 ± 0.005

Another example is found in the comparison of a small mammal, the brush-tailed phaxologale (Jones & Spells, 1963) having a body mass of 25 g, to a pike of 11 cm body length with a corresponding body mass of 9.5 g. In that case enclosed areas A_h are equally large, viz. $A_h = 4.5$ mm². This pike of 11 cm is already large compared with one of 1.3 cm which has just hatched out. In such small pike the semicircular canal cannot enclose smaller areas than they actually have. Apparently the large fish labyrinth cannot be explained on the grounds that a large sensitivity is needed for the detection of the extraordinarily small accelerations occurring during the special propulsion of fish (Jones & Spells, 1963). Moreover, no significant differences between sensitivities of mammals, birds, and fish could be observed. Therefore the variance of A_h and r_c with increasing body mass for mammals seems to indicate a special combination of r_c , A_h , l_1 , O_a , h_c with a normal sensitivity of the canals in order to spare space in the mammalian skull. The large labyrinths can be seen as a logical consequence of the way fishes grow during their lifetime.

From Table 1 we calculated the volumes of different parts of the semicircular canals of the pike and related these to body length. We obtained the following values:

- (a) Duct of canalis lateralis $r^2 l_1 \propto L^{(1.48 \pm 0.002)}$,
- (b) Ampulla of canalis lateralis $h_c^3 \propto L^{(1.431 \pm 0.015)}$,
- (c) Duct of canalis posterior $r_c^3 l_1 \propto L^{(1.483 \pm 0.027)}$,
- (d) Ampulla of canalis posterior $h_c^3 \propto L^{(1.495 \pm 0.015)}$.

From these figures we concluded that the semicircular canals of pike increase as entities. The particular form of growth of the pike's semicircular canals may be the reflexion of a constant sensitivity during life.

SUMMARY

1. The dimensions of the semicircular canals of pike can be expressed as allometric functions of the body length L .

2. The equal sensitivity of pike of different sizes to rotatory stimulation can be explained as a quadratic bending of the cupula.

3. In the pike the sensitivity is of the same order of magnitude for the vertical and horizontal semicircular canals.

4. In the pike the growth rate of the volumes of duct and ampulla is the same for the horizontal semicircular canal and for the posterior semicircular canal.

5. The special growth rate of the dimensions of the horizontal semicircular canal of the ray can be explained by a quadratic bending of the cupula.

6. For equally large cupulae the sensitivity of the horizontal semicircular canal is of the same order of magnitude for twenty-three mammals, fourteen birds and one reptile as it is for the pike.

7. Within the limits of error the 'growth rate' of the diameter of the narrow duct is the same in mammals as in the pike.

8. At the same body mass the absolute value of the diameter of the narrow duct is smaller in mammals than in the pike by a factor of 1.69.

9. For a body mass of 1 kg the value of the enclosed area of the horizontal semicircular canal is 6 times smaller in mammals than in pike.

10. The model of the overcritically damped oscillator for the semicircular canal remains valid during growth if a quadratic bending of the cupula is assumed.

SYMBOLS

c	Coefficient of the allometric relation cL^n .
c_b	Coefficient of the allometric relation $c_b B^{n_1}$.
h_c	Cupula height.
l_1	Length of the narrow duct.
l_2	Length of the wide part.
n	Exponent of the allometric relation cL^n .
n_r	refractive index.
n_1	Exponent of the allometric relation $c_b B^{n_1}$.
r_c	Radius of the narrow duct.
A	Area enclosed by the average canal.
A_p, A_h, A_a	A for posterior, horizontal and anterior semicircular canal respectively.
B	Body mass.
E_s	Standard errors of estimate.
G	Sensitivity factor.
L	Body length of the pike.
M_1	Measurement error.
O_a	Area of the ampulla cross-section.
R	Radius of a circular area, representing A .
V_a	Volume of the ampulla.
η	Absolute viscosity of the endolymph.
ρ	Specific density of the endolymph.

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APPENDIX

Tests for linearity

As a test of linearity we performed the following statistical analyses: (A) The total number of measurements was split into three groups, viz. the measurements for the sixteen smallest pike, those for the sixteen largest and those for the intermediate sizes. Least-square fits were obtained in the first and second case for the logarithmic values of the parameters. With the variance-ratio (*F*) test we investigated the standard errors of the estimate. For all parameters, horizontal as well as posterior, the *F* values obtained did not exceed the 5 % significance level. This means that the standard error of estimate for each parameter may be taken as constant over the whole spectrum of pike length; and since logarithmic values were used, we may say that the variability of the parameters is a constant percentage of the length of the pike.

Furthermore, we tested for a possible difference between the slopes of the two parts of the total regression curve. This was done with Student's *t*-test. From the values found for *t* we conclude that for the h.s.c. there is no significant difference (5 % level) for the parameters (*l*₁ + *l*₂), *A*, *h*_c and *O*_a and a probable significant difference for *l*₁ and 2*r*_c.

In the posterior semicircular canal the difference is not significant for $(l_1 + l_2)$, $2r_c$, h_c and O_a , significant (1 % level) for A_h and highly significant (0.1 % level) for l_1 .

Least-square fits of logarithmic values with a second-order curve $c_0 + c_1 \log L + c_2 (\log L)^2$ were carried out. The confidence intervals for the coefficient c_2 of the quadratic term were obtained, using Student's t -test. For various significance levels the results are:

(1) *Horizontal semicircular canal*. The coefficient c_2 does not differ significantly (5 % level) from zero for the parameters A , h_c , O_a , G/h_c^2 ; probable significant difference from zero was found for $(l_1 + l_2)$, l_1 and $2r_c$.

(2) *Posterior semicircular canal*. The difference of c_2 from zero is non-significant for $(l_1 + l_2)$, $2r_c$ and h_c , significant (1 % level) for A and G/h_c^2 and highly significant (0.1 % level) for l_1 and O_a .

We feel justified in using the approximation of linear regression over the whole range of L .