QUANTITATIVE STUDIES
OF THE REACTIONS TO HORIZONTAL ANGULAR
ACCELERATIONS IN AXOLOTLS

I. THE HEAD-TURNING REFLEXES OF NORMAL ANIMALS

KURT BRÄNDLE

*Arbeitsgruppe Neuro- und Rezeptorphysiologie Fachbereich Biologie d.
J. W. Goethe-Universität, Frankfurt/Main*

SUMMARY

1. Artificially metamorphosed axolotls were exposed to both brief (impulse) and long-lasting horizontal angular accelerations on a turn-table. The animals responded with a head-turning reaction.

2. The general course of the reaction to impulse acceleration was independent of stimulus intensity. The velocity of the head movement first increased to a maximum exponentially and then decreased in a negative exponential manner. Stimulus intensity had a linear relationship to the mean maximum velocity and mean total angle covered by head-turning. The average velocity–time curves at various stimulus intensities differed only by a velocity factor.

3. During long-lasting constant accelerations the velocity of the head-turning increased to a maximum velocity in a sigmoid time-course and then decreased, first to a constant velocity, and then further. Mean values of the maximum velocity were correlated linearly with the stimulus intensity.

4. It was concluded that the head-turning reflexes in axolotls do not agree with the accepted movements of the vertebrate cupula and therefore are not a simple 'copy' of the afferent input. It is also suggested that the reaction threshold differs from that for the labyrinthine input.

INTRODUCTION

In this paper a quantitative analysis is made of horizontal semicircular canal reflexes in axolotls. The study was undertaken to provide the necessary background for a companion study (Brändle, 1977) which investigates: (*a*) whether a supernumerary pair of labyrinths, implanted in axolotls, are functionally connected; (*b*) how this artificial doubling of the labyrinth influences the reaction of the experimental animals to horizontal accelerations.

Many vertebrates respond to angular acceleration with eye nystagmus. However, this has never been observed in axolotls. Instead, a head-turning reaction occurs which is similar to that described for lizards by Trendelenburg & Kühn (1908).

In numerous investigations on a variety of vertebrates, it has been found that the time course of the excitation in different parts of the vestibular system seems to be

similar to the time course of the mechanical process in the cupula–endolymph system (Goldberg & Fernandez, 1971; Honrubia et al. 1971; Llinàs et al. 1971; Precht et al. 1971; Shimazu & Precht, 1965; and previous studies cited by Trincker, 1965). It is widely accepted that the cupula acts like a torsion pendulum with overcritical damping (v. Egmond et al. 1949; Mayne, 1974; Steinhausen, 1931). Its movements can be described by the following differential equation:

$$X'' + LX' + PX = 0, \tag{1}$$

where L is the ratio between moment of friction at unit angular velocity and moment of inertia of the endolymph, P the ratio between the directional moment at unit angle of the cupula and moment of inertia of the endolymph.

For impulse acceleration, i.e. sudden arrest from constant angular velocity, equation (1) has the approximate solution:

$$X = V_0 \tau_2 (\exp\{-t/\tau_1\} - \exp\{-t/\tau_2\}), \tag{2}$$

where X is the angular deviation of the cupula, V_0 the angular velocity, $\tau_1 = L/P$ (long-time constant) and $\tau_2 = 1/L$ (short-time constant).

For long-lasting constant accelerations, equation (1) has the approximate solution:

$$X = b_0 \tau_1 . \tau_2 (1 - \exp\{-t/\tau_1\}), \tag{3}$$

where b_0 is the acceleration factor.

The following investigation tested whether the time course of the head-turning reaction in axolotls is in accord with the time course of the movement of the cupula.

MATERIALS AND METHODS

Animals for the experiments were eight adult axolotls (*Ambystoma mexicanum*) which had been induced to undergo metamorphosis by the injection of thyroxine. Study was made of the head movements resulting from brief (impulse) acceleration and from long-lasting horizontal angular acceleration.

Experimental procedure

To produce horizontal angular acceleration, a turn-table powered by a d.c. motor was employed. The animal was bandaged on to a pedestal, fixed to the turn-table, its front legs tied down to the body and the head projecting freely into the centre of the turn-table. (The bandage did not affect the head-turning reflexes.) A black cylinder enclosing the turn-table prevented optic orientation of the animal during the test. A pulse of angular acceleration was produced by suddenly stopping the turn-table, after rotation at constant speed for 10 s. The approximate speed of rotation was regulated by gears and a potentiometer was used for the fine adjustment. The velocity of the turn-table was increased in steps from 18°/s, which is only slightly above the stimulus threshold for normal animals (Brändle, 1977), through 24°/s and 30°/s up to 36°/s. The response of the animals at each speed was tested ten times. Because the time required to stop the turn-table remained approximately constant independent of the velocity, the negative acceleration at the time of stopping was proportional to the previous turn-table velocity, and followed the same stepwise increase.
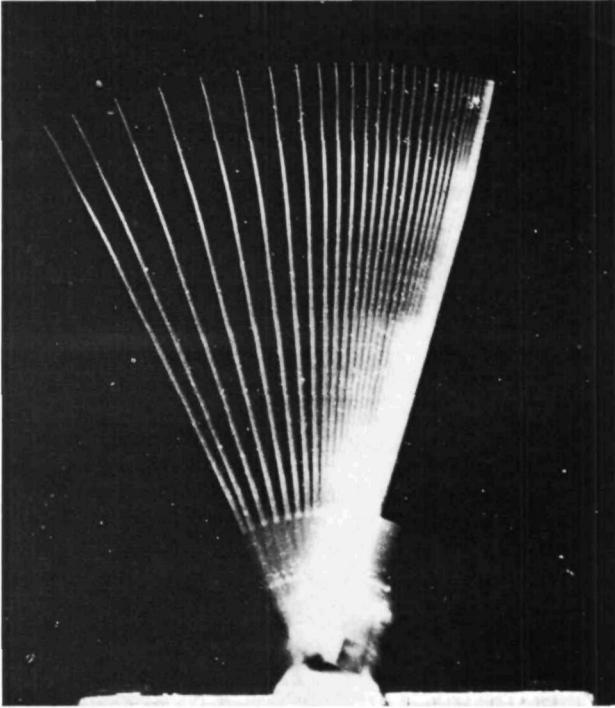
Fig. 1. Photographic recording, during an axolotl's head-turning reaction, of a pointer fixed to the head. From left to right, each position recorded in intervals of 0·2 s.
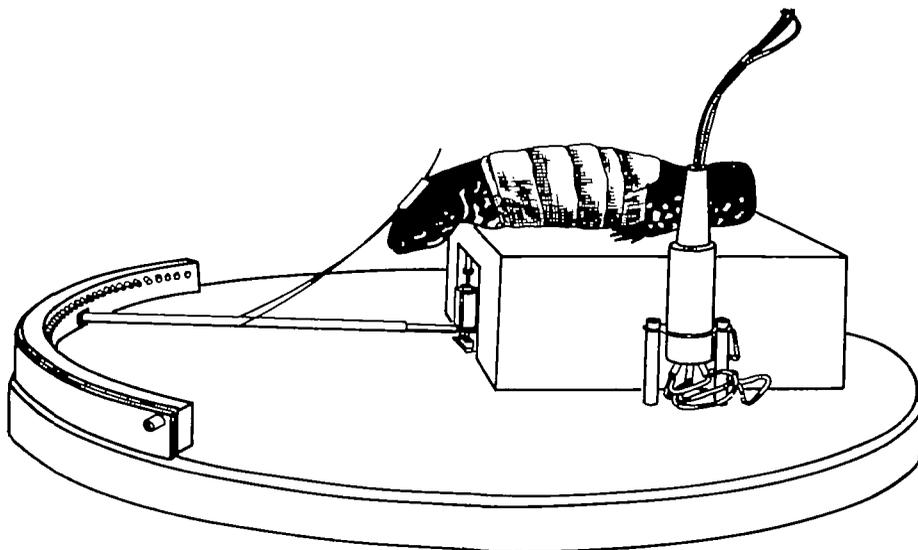
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Fig. 2. Electronic equipment for recording head movements. See text.

To produce a long-lasting constant angular acceleration, the motor was driven by a power amplifier coupled with a saw-tooth generator. Each saw-tooth pulse produced a single stimulation, and lasted for 10 s. Pulse amplitude determined the acceleration factor. Accelerations were 12·5°/s, 18·75°/s and 25°/s.

Recording methods

The head movements were registered either photographically or electronically.

The photographic method was applicable only for the tests of impulse-acceleration. Attached to the head of the animal was a black cardboard pointer bearing a thin strip of highly reflective paper. A camera was set up on a tripod directly above the middle of the turn-table. With the apparatus in darkness, the camera shutter was opened. As soon as the turn-table was stopped, the apparatus was illuminated by a stroboscope with a pulse frequency of 5 Hz. In this way, the pointer positions were recorded on the same frame of a negative at intervals of 0·2 s (Fig. 1).

The electronic method for measuring head movements was developed especially for the purpose and was employed during long-lasting angular acceleration as well as during impulse acceleration. The main element of the apparatus (Fig. 2) was a Hall generator which gives a voltage output proportional to magnetic field strength. The polarity of the voltage depends on the polarity of the magnetic field. The Hall generator was fixed on top of an indicator needle, the fulcrum of which was in the centre of the turn-table. A pointer, affixed to the animal's head, was attached to the indicator needle. At the edge of the turn-table, small magnets were arranged in an arc at intervals of 2° with alternating north and south poles. As the indicator needle moved in front of the magnets, the Hall voltage appeared as a periodic oscillation whose frequency corresponded to the angular velocity. A change in voltage from a positive maximum to a negative maximum indicated a head movement of 2°. The Hall voltage was recorded using a high-frequency pen recorder (Hellige, Helcoscriptor HE 16).

A comparison of measurements of the head-turning reflexes during impulse accelerations, performed with both the above methods, did not show any differences of the measured values. With both the above methods, the accuracy of angle measurement was limited to 0·2°. The consequences were:

(1) Measurements of the velocity as a function of time were unreliable at the lowest stimulus intensity (18°/s). However, the total angle ϕ and the maximum velocity V_{max} of the head movement (see below) were measurable in all cases.

(2) Near the end of the head-turning reaction the speed of the head movements was too slow to be measured any longer, so a speed of zero was assigned to these movements. Such speeds are therefore underestimated.

(3) The head-turning velocity could not be measured continuously but only in intervals of 0·2 s. For calculating the velocity time functions, each velocity value, estimated within 0·2 s, was assigned to the time point at the end of the corresponding interval.

Statistics

The reactions of the experimental animals varied in time course as well as in intensity. It was necessary to determine whether the variation in the measurements among individuals was statistically significant. Since the stimulus intensities tested were near threshold, there was often no reaction. Thus the distribution of values was skewed and it was necessary to use the non-parametric Kruskal–Wallis test for homogeneity. It was shown that the variation in the values for one individual was much higher than that among different individuals, so the values for all individuals could be considered together. The mean values in Figs. 3–7 were always calculated from measurements of all eight animals.

Curve fitting and determining the constants was performed by non-linear regression analyses according to the Gauss–Newton method (Adam *et al.* 1971).

RESULTS

(1) *Reaction to impulse angular accelerations*

(a) *General reaction time course*

When an axolotl was exposed to an impulse of horizontal angular acceleration, by stopping the turn-table, the animal reacted by turning its head in the direction of the preceding rotation. Throughout this paper this will be termed 'impulse reaction'. The velocity–time course of this reaction was quantitatively analysed. The velocity of the head increased quickly and reached a maximum (V_{max}). This part of the velocity–time function will be referred to as the ascending part. The velocity of the head then decreased, initially at a fast rate and then more slowly until the movement ceased (the head then remaining stationary). This part of the velocity–time function will be referred to as the descending part. The entire distance (in angular degrees) covered by the head movement is called the 'total angle'.

When rotation of the turn-table was commenced, there was also an impulse of horizontal angular acceleration. The axolotl reacted by turning its head in the opposite direction to the direction of the rotation. This movement is termed compensatory movement. It ceased after 2–3 s and therefore did not interfere with the impulse reaction.
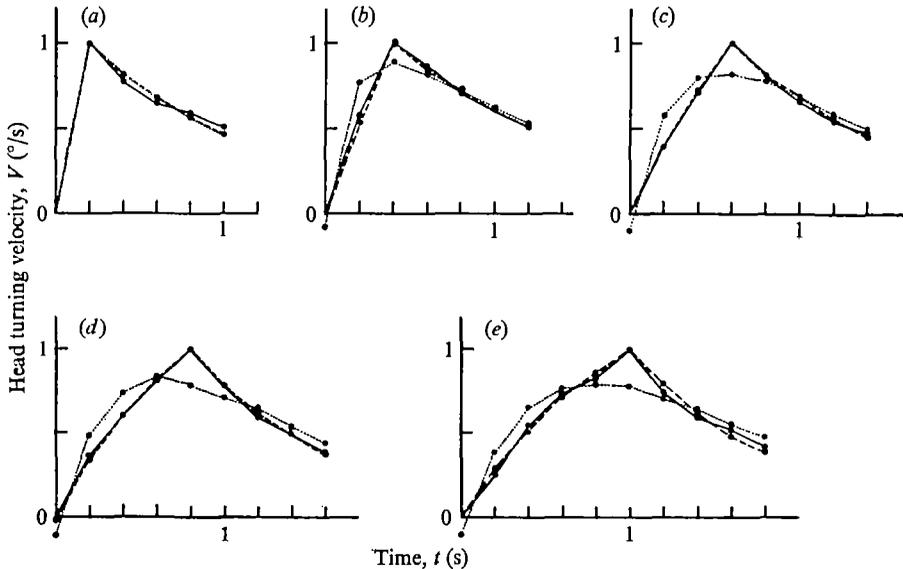
Fig. 3. Time-course of the impulse reaction. ———, averages of individual curves, independent of stimulus intensity, with the same time-span t_a, and following normalization to $V_{max} = 1$. – – –, fit curves for $V = p(1 - \exp\{-\alpha t\})$ (ascending part) and $V = V_{max} \cdot \exp\{-\beta(t - t_{max})\}$ (descending part) ...., fit curves for $V = c(\exp\{-t/\tau_1\} - \exp\{-t/\tau_2\})$. (a) $t_a = 0.2$ s; (b) $t_a = 0.4$ s; (c) $t_a = 0.6$ s; (d) $t_a = 0.8$ s; (e) $t_a = 1$ s.

(b) Quantitative analysis

For the ascending part of the reaction, the distribution of values for the time (t_a) between the beginning of the reaction and the attainment of V_{max} was not significantly affected by stimulus intensity. The mean t_a for all measurements was 0.46 s (S.D., 0.18) (see Table 3). For individual reactions, considerable variability of t_a could be observed with the same stimulus conditions, e.g. t_a could range from 0.2 s to 1.6 s.

In order to determine the time course of the reaction, curves with the same t_a were grouped, for each stimulus intensity, and the values of head-turning velocity were averaged in intervals of 0.2 s. For the various acceleration intensities the curves differed only by a velocity factor. When V_{max} was normalized to a value of 1, the resultant curves were almost identical.

At first sight the form of the curves seemed to be similar to the form of the velocity–time curves of the vertebrate cupula following impulse acceleration. If this were the case, the results should have been described by equation (2). Accordingly, fit curves for the head-turning velocity (v) were calculated for the function:

$$v = c(\exp\{-t/\tau_1\} - \exp\{-t/\tau_2\}). \qquad (4)$$

As can be seen in Fig. 3 and Table 1 the fit-curves did not match the measured curves very well. Moreover, the values for τ_2 varied remarkably with different values of t_a, instead of remaining constant, and the factor, c, did not correspond to the product $v_0 \cdot \tau_2$, which is demanded by equation (2).

Fit-curves for several other non-linear functions were tested by comparison of their correlation coefficients. The ascending part of the reaction $(t_a \geqslant 0.4$ s$)$ could be best described by the formula

$$v = p(1 - \exp\{-\alpha t\}); \ 0 \leqslant t \leqslant t_{max}, \qquad (5)$$

Table 1. *Time constants for different fit curves of the impulse reaction*

				Ascending part		Descending part	
	$v = c(\exp\{-t/\tau_1\} - \exp\{-t/\tau_2\})$			$v = p(1 - \exp\{-\alpha t\})$		$v = V_{max}.\exp(-\beta\{t - t_{max}\})$	
t_a* (s)	τ_1 (per s)	τ_2 (per s)	r^2†	α (per s)	r^2†	β (per s)	r^2†
0·2	−1·05	−0·013	0·97	—	—	−0·94	0·97
0·4	−1·20	−0·16	0·90	−0·95	0·99	−0·83	0·99
0·6	−1·03	−0·30	0·88	−0·90	0·99	−0·97	0·99
0·8	−0·82	−0·46	0·85	−1·07	0·99	−1·22	0·99
1	−0·82	−0·69	0·86	−0·98	0·99	−1·22	0·98

* Time spans of the ascending part.
† Squares of the correlation coefficients.

Table 2. *Mean values for V_{max} with different time spans (t_a) for the ascending part at three different stimulus intensities*

	24°/s*		30°/s*		36°/s*	
t_a (s)	V_{max}†	n‡	V_{max}†	n‡	V_{max}†	n‡
0·2	6·8°/s	7	11·9°/s	8	15·2°/s	7
0·4	6·2°/s	29	10·5°/s	11	17·6°/s	34
0·6	5·3°/s	23	9·3°/s	28	15·2°/s	39
0·8	5·7°/s	13	9·2°/s	10	13·3°/s	13
1	4·0°/s	5	8·8°/s	6	10·6°/s	3

* Constant speed of the turn-table before sudden arrest.
† Mean values of maximum velocity.
‡ Number of measurements.

which corresponds to equation (3) for the deviation of the cupula during long-lasting constant angular accelerations (Fig. 3). For the various values of t_a in the ascending part, α remained almost constant (Table 1). With increasing t_a, the velocity factor, p, decreased. So both p and t_a almost compensate for each other and hence the values for unnormalized V_{max} are only slightly decreased with increasing t_a (Table 2).

The descending part of the reaction fitted best to the formula

$$v = V_{max}.\exp\{-\beta(t - t_{max})\}; \; t \geqslant t_{max}, \tag{6}$$

which is similar to the descending part in equation (4), when the second term $(\exp\{-t/\tau_3\})$ is almost zero (Fig. 3). The constant β was almost identical with the constant α in equation (5) (Table 1). At the end of the reaction the velocity values measured were too low compared with equation (6), but these were underestimated (as mentioned in Materials and Methods). For individual curves, the velocity during the descending portion was not strictly monotone but was interrupted by short periods in which the velocity did not change or even increased. In a series of successive measurements it was, in many cases, observed that these points of inflexion occurred at the same time.

The original values for the velocity factor, p, and the maximum velocity, V_{max}, were strongly correlated with the stimulus intensity. In Fig. 4 the mean values of V_{max} are plotted against the rotation speed of the turn-table before arrest. Within the
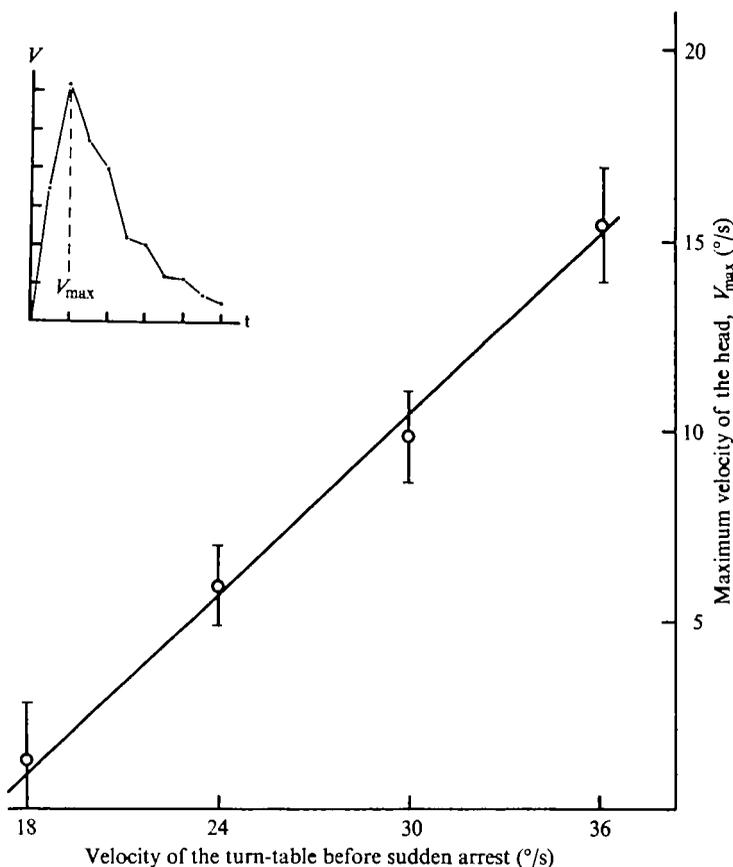
Fig. 4. Mean values and standard error for V_{max} of impulse reactions at different stimulus intensities. ——, regression line calculated from all values. Insert: schematic representation of the velocity curve of an individual reaction. t = time; v = velocity of the head; V_{max} = maximum velocity. All values in arbitrary units.

range investigated, a linear relationship was obtained. By regression analysis it was found that an increase in the rotation speed of 6°/s caused an increase in V_{max} of 4·76°/s.

(c) Total angle

Measurement was also made of the total angle of head-turning during the reaction, i.e. the distance covered, measured in angular degrees. Fig. 5 shows that the mean values of total angle, ϕ, have a linear relationship to stimulus intensity. According to the regression coefficient calculated from all individual measurements, an increase of 5·70° occurs when the rotation speed of the turn-table is increased by 6°/s.

If the assumed e-functions for the ascending and descending part of the time–velocity-function (equations 5 and 6) are correct, the measured values for ϕ should agree with the theoretical value, which is given by the sum of the integrated e-functions, the integrals being denoted by ϕ_1 and ϕ_2:
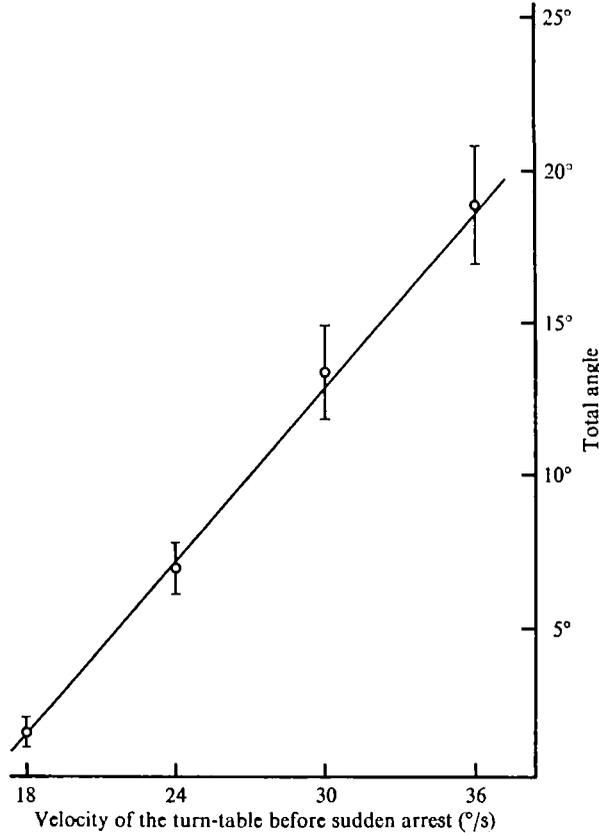
$$\phi = \phi_1 + \phi_2. \tag{7}$$

Fig. 5. Mean values and standard error of the total angle ϕ of impulse reactions at different stimulus intensities. ———, regression line calculated from all values.

The integral of the ascending part is

$$\phi_1 = \int_0^{t_{max}} p(1 - \exp\{-\alpha t\})\, dt$$

$$= p\left(t + \frac{1}{\alpha}\cdot\exp\{-\alpha t\}\right)\Big|_0^{t_{max}}. \tag{8}$$

For the integral of the descending part it follows that

$$\phi_2 = \int_{t_{max}}^{t_n} V_{max}\cdot\exp\{-\beta(t-t_{max})\}\, dt$$

$$= -\frac{V_{max}}{\beta}\cdot\exp\{-\beta(t-t_{max})\}\Big|_{t_{max}}^{t_n}. \tag{9}$$

At the time t_{max} it follows that $\exp\{-\beta(t-t_{max})\} = 1$.
At t_n, which corresponds to the end of the head movement, the term $-V_{max}/\beta\cdot\exp\{-\beta(t-t_{max})\}$ is almost zero.
So we get an approximate solution

$$\phi_2 \approx \frac{V_{max}}{\beta}. \tag{10}$$

Table 3 shows that at each stimulus intensity the mean value of the total angle was in good agreement with its calculated value.

Table 3. *Comparison of the measured total angle φ with its calculated values*

No. of measure-ments	Turn-table speed before sudden arrest (°/s)	Mean values and standard deviation for			φ calculated[*] (deg)
		V_{max} (°/s)	t_a (s)	φ measured (deg)	
29	18	1·30±0·5	0·44±0·22	1·54±0·16	1·64
74	24	5·95±0·35	0·42±0·17	7·01±0·28	7·44
64	30	9·85±0·4	0·48±0·24	13·39±0·52	12·65
98	36	15·45±0·5	0·44±0·20	18·90±0·65	19·48

[*] Calculated by integration of the *e*-functions (equations 5 and 6), using the mean values for V_{max} and the time-span t_a for the ascending part.
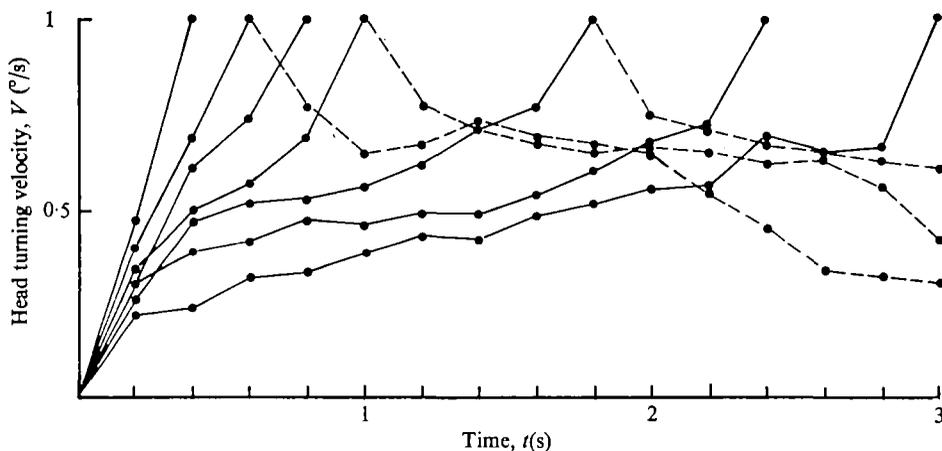

Fig. 6. Time-course of the head-turning reaction during long-lasting constant accelerations. ———, averages of the ascending part for individual curves with the same time-span t_a, independent of stimulus intensity. V_{max} normalized to a value of 1. – – –, averages of the corresponding descending part for t_a = 0·6 s, t_a = 1 s, and t_a = 1·8 s.

(2) *Reaction to long-lasting constant accelerations*

When an axolotl was exposed to long-lasting constant acceleration, the animal started to turn its head in the opposite direction to the direction of acceleration, immediately after the beginning of the acceleration. In spite of variations in the velocity curves of individual reactions there was conformity in the general course of the time–velocity curves.

In the following respects, the reactions were similar to the reactions following impulse accelerations. (1) The reaction could be divided into an ascending and descending part. (2) For various stimulus intensities the curves differed only by a velocity factor. (3) At the same stimulus intensity the maximum velocity (V_{max}) was attained after various time-spans (t_a), ranging from 0·2 to 3·8 s.

In three other respects, the reactions clearly differed from the reactions to impulse accelerations, as follows. (1) In Fig. 6 the maximum velocities were normalized to a value of 1 and the velocity values of curves with the same t_a were averaged. If the reaction were to be in accord with the cupula movement, it should follow the time course according to equation (3) and be similar to the ascending part of the impulse
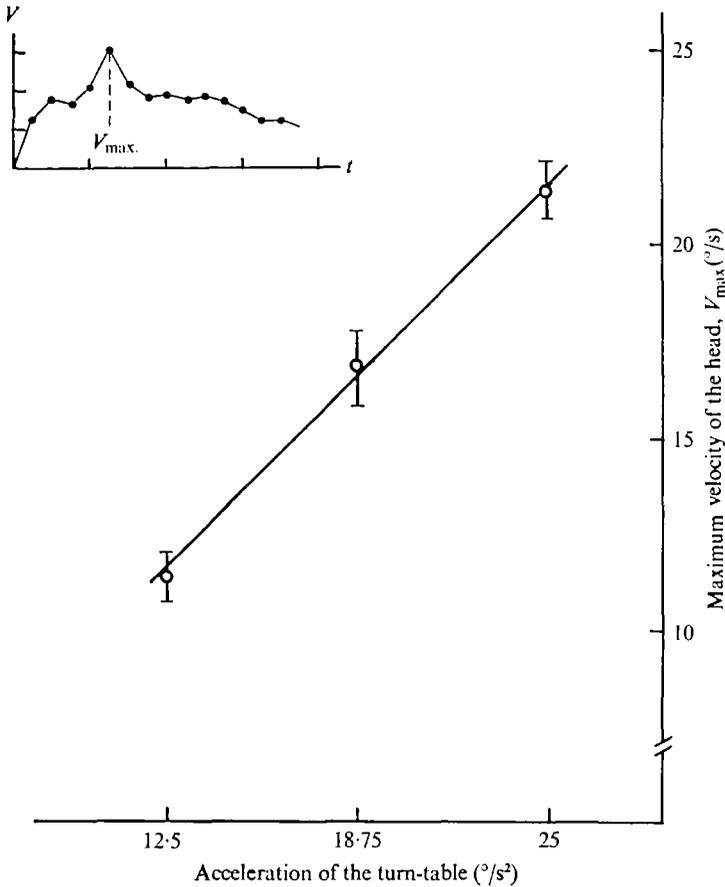
Fig. 7. Mean values and standard error for V_{max} of the head-turning reaction during long-lasting constant accelerations. For further explanations see Fig. 4.

reaction, but this was not the case. On the contrary, the form of the ascending part was sigmoid, even for relatively short time spans ($t_a = 0.4$ to 1 s). (2) When, for the first part of the ascending part of the reaction, up to the inflexion point of the sigmoid curve, the exponent α was calculated (deduced from equation 5), values between -2.0 s^{-1} and -5.0 s^{-1} were obtained, differing remarkably from those measured for the impulse reactions. (3) Having reached V_{max}, the velocity of the head-turning decreased rapidly to an almost constant level, which was maintained for at least 1–1.5 s. Then the velocity decreased further, probably due to adaptation, and the reaction ceased after 5–6 s. A parallel may be drawn between this decrease and the decrease, following a transient maximum, in the firing frequency of vestibular neurones of various vertebrates during long-lasting accelerations (Precht, 1974).

The mean values of V_{max} were plotted against stimulus intensity, revealing a linear relationship (Fig. 7). Changing the acceleration by $6.25°$/s caused an increase in the maximum velocity of $4.90°$/s.

DISCUSSION

It was shown that axolotls respond to horizontal angular accelerations by head-turning reactions which are correlated in strength and time course to the form and intensity of the stimulus.

Before attempting to interpret the experimental results one must first take into consideration the possibility that the head is passively turned due to its mass alone. If this were the case, the velocity of the head following, for example, a sudden arrest of the turn-table should initially be the same as the previous turn-table velocity and then decrease continuously. It was observed, however, that the velocity of the head when stopped was initially zero and increased to a maximum exponentially. Yet another argument against the passive head-movement assumption is the behaviour of animals following unilateral labyrinthectomy (Brändle, 1977). Acceleration in the direction of the operated side produced no reaction, even at the highest stimulus intensities. It therefore seems that all the reactions observed in the present study were due to active head movements.

After impulse accelerations, and during long-lasting constant accelerations, in many vertebrates there is a similar time-course to that of the accepted cupula movements for the following: potential changes in receptor cells (Trincker, 1957), frequency changes in peripheral afferent neurones (Goldberg & Fernandez, 1971; Löwenstein & Sand, 1940; Precht *et al.* 1971) and vestibular neurones (Shimazu & Precht, 1965 and the slow phase of the eye nystagmus (v. Egmond *et al.* 1949; Honrubia *et al.* 1971). Unfortunately, at present, direct observations of cupula movements and electrophysiological investigations in the vestibular system of axolotls are not available. Nevertheless, it can be assumed that they do not differ considerably from those in other vertebrates.

The present results raise doubts that the head-turning reactions bear a simple relationship to the cupula movements. A strong argument against such a correspondence is the time-course of the reactions for impulse and long-lasting acceleration. Although the descending parts of the reaction curves showed a certain similarity with the accepted cupula movements, this was not the case for the ascending parts. Beside this, there was a high degree of variability for the time span to reach the maximum velocity in individual reactions. It is hard to believe that at the same stimulus duration and intensity, the time required for the cupula to move could differ to such an extent. Finally, it is unlikely that the time constants obtained, α and β, correspond to those of the cupula–endolymph system, because (1) for impulse accelerations the short-time constant α is almost equal to the long-time constant, rather than larger, as demanded for the model of Steinhausen (1931), and (2) the long-time constant for long-lasting accelerations differed from that for impulse accelerations. Considerably variations of the time constants in different parts of the vestibular system are also described by other authors (Groen, 1960; Precht *et al.* 1971; Shimazu & Precht, 1965). Since, for the above reasons, the head-turning reflexes in axolotls do not appear to result from a simple 'copy' of the afferent input, we must assume that they are the result of some degree of information processing. Each form of stimulus, i.e. impulse and long-lasting accelerations, causes characteristic motor responses, which differ from each other.

With both impulse and long-lasting accelerations, a linear relationship was found

between stimulus intensity and reaction strength, within the stimulus range investi-
gated, In contrast, a logarithmic stimulus–response relationship has often been found
in other vertebrates (van Egmond *et al.* 1949; Goldberg & Fernandez, 1971; Shimazu
& Precht, 1965).

Do reaction thresholds correspond to sensory thresholds? The stimulus intensities
applied in the present study ranged down to close to threshold for impulse acceleration
(threshold is found with arrest of rotation at 16–18°/s; Brändle, 1977), and for constant
acceleration (threshold with acceleration of 6°/s; unpublished observation). Löwen-
stein (1956) has suggested that a threshold theoretically hardly exists for neurones, at
least for spontaneously active ones. In practice, however, the stimulus intensity must
exceed a minimum value before statistically significant changes in impulse frequency
can be observed. The thresholds for primary afferents, vestibular neurones and nyst-
agmus, measured in various vertebrates, are considerably lower than those obtained
for the head-turning reactions in axolotls (for summary see Precht, 1974). For the
following reasons, however, it must be concluded that neither the reaction threshold
for impulse acceleration, nor that for constant acceleration corresponds to threshold
for the labyrinthine input.

As mentioned above, and according to van Egmond *et al.* (1949), the deviation of the
cupula and the associated changes in the impulse frequency of the vestibular neurones
must attain a minimum value before they can elicit a response. Correspondingly, the
reaction ceases when the cupula returns below that critical deviation. If we assume
that the head-turning reactions are proportional in duration and reaction strength to
the cupula movement above threshold, for impulse reactions the following conditions
should be satisfied (Fig. 8 a):

(1) Since the time required for the cupula to attain maximum deviation (t_{max}) is
constant (see equation iii in van Egmond *et al.* 1949), the cupula reaches the threshold
deviation (*s*) earlier with higher stimulus intensities. So the duration (t_a) of the ascend-
ing part of the reaction (thick solid parts of the curves), between the beginning of the
head-turning reaction (corresponding to minimum deviation of the cupula at level *s*)
and the attainment of maximum velocity of the head-turning (vertical broken line),
should increase with increasing stimulus intensities. Also the duration (t_d) of the
descending part of the reaction should increase with higher stimulus intensities,
because it takes a longer time for the cupula to return to the threshold deviation,
where the reaction ceases.

(2) Because of this increase in the duration of the reaction with increasing stimulus
intensities, the total angle ϕ should increase nonlinearly with a linear increase of the
maximum velocity of the head-turning. ϕ corresponds to the integral of the reaction
time-course above threshold, represented in Fig. 8 a by the areas between level *s* and
the thick solid parts of the curves.

The obtained results, however, do not agree with the above threshold model. For
impulse accelerations the stimulus intensity is not only linearly related to the maxi-
mum velocity, but also to the total angle. In addition, the averages for the total angle
fit the values calculated by integration of the theoretical *e*-functions (equations 5 and 6).
Finally, the mean values for t_a remained constant at different stimulus intensities.

Provided that the threshold model of van Egmond *et al.* (1949) holds true also for the
vestibular afferents in axolotls, it is improbable that the observed threshold for the
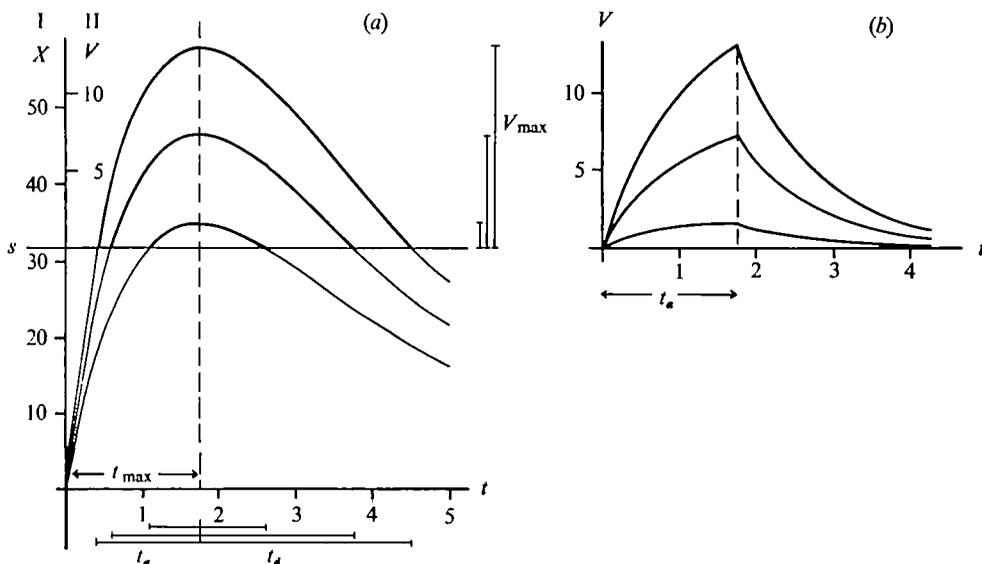
Fig. 8. Schematic representation of the time-course of the impulse reaction at three different stimulus intensities. (*a*) Time-courses of the cupula movements (solid curves; ordinate I) and of the corresponding reaction time-courses (thick solid parts of the curves above threshold *s*; ordinate II). (*b*) Reaction curves, which differ only in a velocity factor at different stimulus intensities. *s* = threshold; *t* = time in arbitrary units; t_a = duration of the ascending part of the reaction curves; t_d = duration of the descending part of the reaction curves; t_{max} = time required for the attainment of the maximum deviation of the cupula; *v* = head-turning velocity (in °/s) in arbitrary units; V_{max} = maximum head-turning velocity; *X* = cupula deviation (in deg.) in arbitrary units.

head-turning reflexes corresponds to the vestibular threshold. It seems more likely that the labyrinthine input, exceeding a threshold level, starts a fixed motor programme of the head-turning reaction; a programme which gives a time-course independent of stimulus intensity. As shown in Fig. 8*b*, only the velocity factor changes linearly with the stimulus intensity above threshold.

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