J. Physiol. (1974), **238**, *pp.* 603-625
With 8 *text-figures*
Printed in Great Britain

VESTIBULO-OCULAR AND OPTOKINETIC REACTIONS TO ROTATION AND THEIR INTERACTION IN THE RABBIT

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(*Received 12 November 1973*)

SUMMARY

1. Compensatory eye movements due to sinusoidal yaw movements on a torsion swing were measured in alert rabbits. A range of combinations of frequencies (0·048–1·8 Hz) and amplitudes (1–25°) were used. Gain (cumulative slow phase eye movement amplitude/swing amplitude) and phase (eye position *vs.* swing position – 180°) were calculated from averaged records.

2. Eyes were either closed (canal-ocular reactions only), open in earth-fixed visual surroundings (natural interaction of vestibular and optokinetic reactions), or looking at platform-fixed surroundings, which rotated with the animal (conflict situation). In some rabbits, the same stimulus programme was applied a month after bilateral destruction of the labyrinths (optokinetic reactions only).

3. For canal-ocular reactions, no true threshold was found. Yet the system showed a small but systematic non-linearity which is tentatively explained by an acceleration-dependence of gain. For the higher frequencies (0·40–1·8 Hz) used, gain was 0·55–0·75, with a decrease at the lower frequencies, down to 0·16–0·33 at 0·048 Hz. The response showed a phase-lead of about 45° at 0·048 Hz and was nearly in phase at 1–1·8 Hz. The long time constant of the cupula-endolymph system was estimated at about 3·3 sec.

4. With earth-fixed visual surroundings a frequency-independent gain (range 0·55–0·82) with negligible phase error was found for the entire stimulus range tested. This natural combination of canal-ocular and optokinetic systems appears to function very efficiently, with mutual correction of the defects of the systems apart.

5. With platform-fixed visual surroundings the canal-ocular system was severely inhibited and its non-linearities were markedly enhanced by the optokinetic system, especially when the torsion swing moved slowly.

6. The general shape of input–output relations of optokinetic reactions after labyrinthectomy were similar to those found earlier in normal animals, but gain was subnormal for the entire stimulus range tested.

INTRODUCTION

At least four sensory systems contribute to the stabilization of the mammalian eye: (1) visual motion detection (optokinetic reflexes), (2) semicircular canals (canal-ocular reflexes), (3) the statolith organs of the utriculus and sacculus (maculo-ocular reflexes), and (4) proprioceptive endings in the neck joints (spino-ocular reflexes). These reflexes (within certain limits) stabilize the eye position relative to gravity and to the visual surroundings. Maculo-ocular and neck-proprioceptive reflexes tend to keep the retinal image normally oriented with respect to gravity. Canal-ocular and optokinetic reflexes prevent too fast displacements of the projection on the retina.

Among mammals, the rabbit is eminently suited for an investigation of these stabilizing systems. The presence of the different stabilizing systems is well known since the classical studies of Magnus (1924) and Ter Braak (1936). Since voluntary eye movements are scarce in the rabbit, these systems can be studied without the complications of a superimposed fixation behaviour such as found in cat, monkey and man.

The dynamic properties of the rabbit's optokinetic system have been recently studied by Collewijn (1969, 1972*a*, *b*). In those experiments a striped drum was rotated around a stationary animal. Briefly, the results indicated that the optokinetic system is a velocity feed-back system with an optimal working range for angular speeds below and up to 1°/sec. Velocity-saturation effects occurring at higher stimulus speeds are a source of rather complex non-linearities.

Although the literature on canal-ocular reactions is prolific, most studies deal with eye movements only in terms of the fast components of nystagmus (usually frequency only). Few systematic measurements of the genuine compensatory part of canal-ocular eye movements (e.g. the slow component of nystagmus) are available.

The data of Niven & Hixson (1961) and Hixson & Niven (1962) for man are restricted to phase relations. Meiry's (1966) study in man, which gives data both for gain and phase relations, is the most complete one so far. Additional, and partially conflicting information has been gathered by Benson (1970, 1971).

For animals, data are even more scarce. For canal-ocular reactions in fish, we have the results of Ten Kate (1969) on the growing pike. Sugie & Jones (1971) studied similar reactions in cats under ether anaesthesia.

Carpenter (1972) studied the decerebrate cat, and recently Skavenski & Robinson (1973) published some findings in the alert monkey.

With these references, systematic input–output studies of compensatory canal-ocular reactions for a variety of frequencies and amplitudes appear to be practically exhausted. Experiments on animals using combined stimulation of canal-ocular and optokinetic system have not been reported at all.

Therefore, we decided to undertake a systematic investigation of canal-ocular reactions in the rabbit, elicited by sinusoidal rotatory oscillation of the animal as a whole in the horizontal plane within a rather wide range of frequencies (0·048–1·8 Hz) and amplitudes (1–25°).

First of all, canal-ocular reactions were studied in isolation, with the eyes of the animal covered. Then, the same stimuli were given while the animals had normal vision of the earth-fixed surroundings ('harmonious stimulation'). In this situation, optokinetic and canal-ocular reactions will cooperate as they do in normal life. After this, the stimulus programme was repeated with the eyes opened in a visual environment which was moving with the animal. In this situation of conflict, like that of a traveller inside a moving vehicle, any canal-ocular reactions will give rise to opposite optokinetic reactions and thus tend to be nullified. Finally, as a complement to the earlier studies of the rabbit's optokinetic system, some rabbits without labyrinths were subjected to the same stimulus programme.

METHODS

Animal preparation

Dutch rabbits, about 6 months old and weighing about 2 kg were used. Preparatory surgery, performed under halothane (Fluothane I.C.I.) anaesthesia, included: (1) cannulation of the trachea, (2) fixation of a bite board to the upper molars and incisors with acrylic, (3) suturing a scleral induction coil (diameter 15 mm, 10 windings of 0·05 mm isolated copper wire) upon the right eye (four sutures of 3–0 atraumatic silk). After this, the animal was fixed on an experimental board. By connecting the bite board to a stand, the head was rigidly immobilized (inclination of the bite board 45° forward). Trunk and legs were firmly tied down in a hammock, which contained a heating element. Body temperature was kept at 38 ± 0·5° C. The animal was immobilized firmly, but as comfortably as possible. At this point, anaesthesia was terminated. Measurements were started at least 2 hr later. Since there were no open wounds or pressure points, local anaesthetics were not required. The animals remained calm, without symptoms of severe distress and in good condition throughout the measurements, which lasted up to 12 hr. The eye with the coil attached showed no signs of irritation and was kept open spontaneously. At the end of the experiment, the animal was killed by an overdose of barbiturate. In five animals we destroyed both labyrinths surgically, one month before the measurements, using a lateral approach as described by Winkler (1907).

Movement generation

The animal on its board was secured to the platform of a torsion swing, which would execute a rotatory sinusoidal oscillation in the horizontal plane at its natural frequency after being bent from the mid-position and then released. The oscillation was damped by about 1 % per period, which was acceptable for the current experiments.

The torsion swing was essentially a mass-spring system which could be tuned to different natural oscillation frequencies by adding springs (elasticity) or weight (mass) to the system. The excursion of the swing was measured by a potentiometer with high precision and infinite resolution. An analysis of harmonic distortion (fast Fourier transform) of the steady-state oscillation was carried out for the different frequencies used. Higher harmonics could not be demonstrated at a level 44 dB below that of the fundamental frequency.

The animal was placed with the centre of its interaural axis in the vertical axis of rotation. Three different visual conditions were used:

(1) eyes covered (canal-ocular reflexes only),

(2) eyes open, swing surrounded by contrast-rich pattern (alternating white and black vertical bars, each 10° wide, at 140 cm distance from the eye) (this we call the 'harmonious' situation),

(3) eyes open, animal surrounded by a similar pattern on a drum of 45 cm diameter, mounted on the moving platform.

In each of these conditions, all combinations of seven frequencies (0·048, 0·068, 0·11, 0·18, 0·40, 0·76 and 1·8 Hz) and eight amplitudes (1, 2·5, 5, 7·5, 10, 15, 20 and 25°) were used, except that at 0·76 and 1·8 Hz the highest practical amplitudes were 20 and 7·5°, respectively.

Measurements

Eye position was measured by Robinson's (1963) method, which is based on angular position – dependent induction by stationary a.c. magnetic fields in a scleral coil, and has been applied by one of us before (Collewijn, 1969, 1972*a*). The coils used for generating the field were mounted on the animal board; they were rotated through a known angle to calibrate the system in each experiment. The performance of this system in terms of resolution, drift and noise is superior to most other methods for the recording of eye movements, especially electronystagmography.

Eye position and swing position were recorded on a pen-writer (Grass Polygraph Model 7). Five cycles of every amplitude-frequency combination were averaged on a DIDAC 800 computer. The averager was started during the second period of swing oscillation, to avoid transient effects. Immediately after computation of the average, the swing motion was arrested, to minimize any possible habituation effects.

Amplitude of swing and eye movement and their phase relation were measured directly from the averaged record.

Any fast eye movements that occurred were eliminated for the calculation of the amplitude by constructing the cumulative slow phase movement (Meiry, 1966, 1971), which consists of the successive slow phase segments put end to end.

From these measurements we derived

(1) peak angular velocity and acceleration of the swing,

(2) gain, defined as $\dfrac{\text{amplitude eye movement}}{\text{amplitude swing movement}}$,

(3) phase shift, defined as 0° when the eye movement is shifted 180° with respect to the swing movement and in phase with the visual movement of earth-fixed surroundings (exactly compensatory eye movement),

(4) directional asymmetry, defined as $(R-L)/(R+L)$.

R is the peak-to-peak amplitude of the sinusoidal eye movement measured while the eye moves from maximal left to maximal right deviation, *L* is the maximum eye movement amplitude when moving from right to left.

RESULTS

Canal-ocular reflexes, eyes covered

The eye movements elicited on the torsion swing with the eyes of the rabbit covered consisted of an approximately sinusoidal smooth horizontal tracking movement, with occasional fast eye movements superimposed upon it, especially when the large amplitudes were used. Some examples, written on the penrecorder, can be seen in Fig. 1*A*. (The apparent non-linear distortion in these examples is caused by the curvilinear writing of the recorder, it is absent in the rectilinear $X-Y$ plots of the averaged results, used for measurements.)

A complete series of measurements for all practical frequency-amplitude combinations was made in seventeen rabbits. For each of them, gain and phase were plotted as a function of frequency and of amplitude. Although the absolute values varied considerably between different animals, the general shapes of the relations were quite similar. In all animals, a systematic effect of amplitude on gain and phase was seen; thus the system appeared not to be perfectly linear. Analysis of variance showed that this amplitude effect was statistically highly significant ($P \leq 0.001$) for both gain and phase. Therefore, in calculating average values for the seventeen animals, the results for the different amplitudes have been kept separate. They are shown in Fig. 2. Some idea about the variability of these values in different rabbits can be obtained from Table 1, where overall averages (all amplitudes pooled) for gain and phase with their standard deviations are given.

The graphs for all individual amplitudes show the lowest gain (around 0·25) and the highest phase lead (around 45°) for the lowest frequencies used. With the increase of frequency, phase lead is decreasing to practically 0° at 1·8 Hz. A phase-lag was never observed. Gain is increasing with frequency to a level between 0·55 and 0·75, although at the highest frequency-amplitude combinations gain seems to decline somewhat again. The latter might be explained by the more frequent occurrence (often more than one per period) of fast eye movements with these stimuli. During the occurrence of a fast movement (duration in the rabbit 100–200 msec) there is no smooth compensatory movement and the reconstructed cumulative smooth eye movement (the slow tracking segments put end to end) will have a smaller amplitude for this reason.

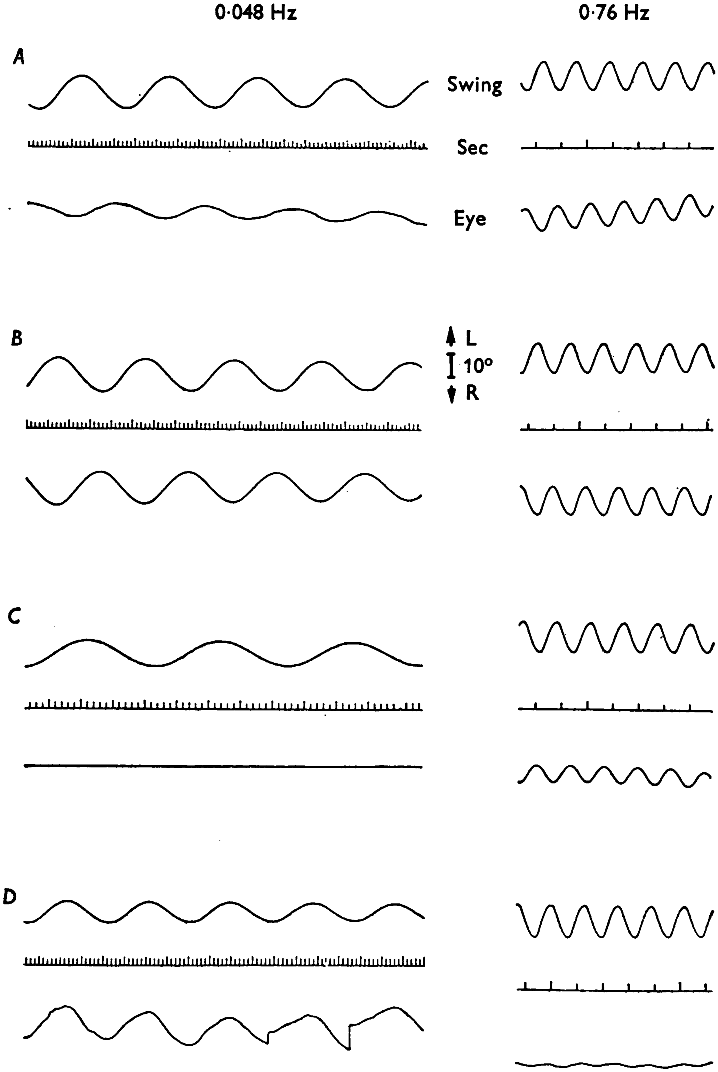

Fig. 1. Examples of compensatory eye movements on the torsion swing, for an amplitude of about 5° and frequencies of 0·048 and 0·76 Hz. *A*: eyes closed. *B*: eyes open, earth-fixed visual surroundings. *C*: eyes open, platform-fixed visual surroundings. *D*: eyes open, earth-fixed surroundings, labyrinthless animal. Calibrations valid for both swing and eye movements, except that polarity of eye movement recording in *D* has been inverted.

Another reason for a lower gain at higher frequencies might be found in the orbital mechanics. In all cases, gain is below unity.

An obvious explanation of non-linearities such as demonstrated in Fig. 2 would be the presence of a threshold in the system. However, the existence of a threshold appears to be highly questionable on the basis of our results.

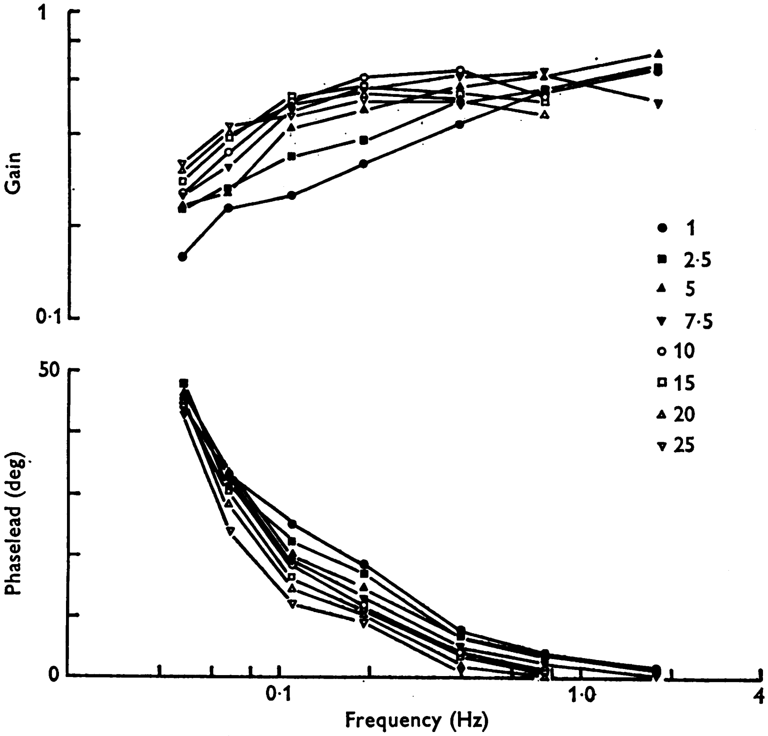

Fig. 2. Gain and phase for canal-ocular reactions (eyes covered) for different frequencies and amplitudes as specified. Average values of seventeen rabbits.

TABLE 1. Average gain and phase lead (all amplitudes pooled) for canal-ocular reactions in seventeen rabbits with eyes closed

Frequency (Hz)	Average gain (± S.D.)	Average phase lead (°) (± S.D.)
0·048	0·24 ± 0·15	45 ± 12
0·068	0·30 ± 0·13	32 ± 7
0·11	0·43 ± 0·21	19 ± 6
0·19	0·50 ± 0·23	13 ± 6
0·40	0·56 ± 0·19	5 ± 4
0·76	0·57 ± 0·20	2·5 ± 2·5
1·8	0·65 ± 0·21	1 ± 1

At the smallest stimulus used (0·048 Hz, amplitude 1°, peak angular acceleration 0·08°/sec^2) a measurable ocular reaction was found in eleven out of seventeen rabbits. With the next stronger stimulus (peak acceleration 0·18°/sec^2) all rabbits showed a measurable reaction. Any threshold compatible with these data would be insufficient to account for the non-linearity observed. Moreover, the lack of measurable reactions in six rabbits at 0·08°/sec^2 is more likely to be due to the insufficient sensitivity of the measuring system as we employed it, than to a genuine threshold.

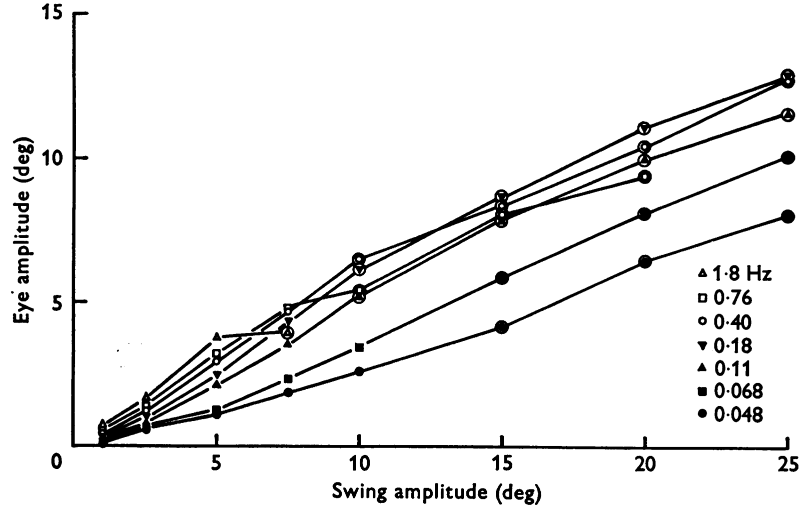

Fig. 3. Input *vs.* output amplitudes of canal-ocular reactions, for different frequencies as specified. Average values of seventeen rabbits. The circled data points were obtained from records that contained saccades.

An argument for the absence of a true threshold is to be found in Fig. 3, where amplitudes of eye and swing have been plotted *vs.* each other for each frequency used. The graphs for the higher frequencies are steeper than for the lower ones, in accordance with the frequency-dependence of the gain (Fig. 2). Although the graphs are not straight lines, all of them seem to approach the origin; none of them appears to be likely to intercept the abscissa at a level different from zero. In Fig. 3, the data points obtained from records containing saccades have been encircled. For the highest frequencies it is seen that, probably due to these saccades, gain as computed from the cumulative slow phase is declining somewhat for the highest amplitudes. For the lower amplitudes and frequencies (left part of Fig. 3) neither a threshold nor saccades present an explanation for the non-linearity in the corresponding part of Fig. 2.

The torsion swing has been demonstrated to produce pure sinusoidal motion (see Methods) and can therefore be excluded as a source of non-linearities.

Another possible cause of non-linear conduct might be velocity- or acceleration-dependence of gain. This possibility was explored by plotting gain (G_v) versus maximal velocity (v_{max}) (Fig. 4*A*) and maximal acceleration (a_{max}) (Fig. 5*A*) of the swing, for the different amplitudes, on logarithmic scales. ($v_{max} = 2\pi fA$ and $a_{max} = (2\pi f)^2A$ if f = frequency in Hz and A = amplitude of the stimulus).

Fig. 4*A* shows a marked amplitude-dependence and does not suggest that gain is a direct function of velocity.

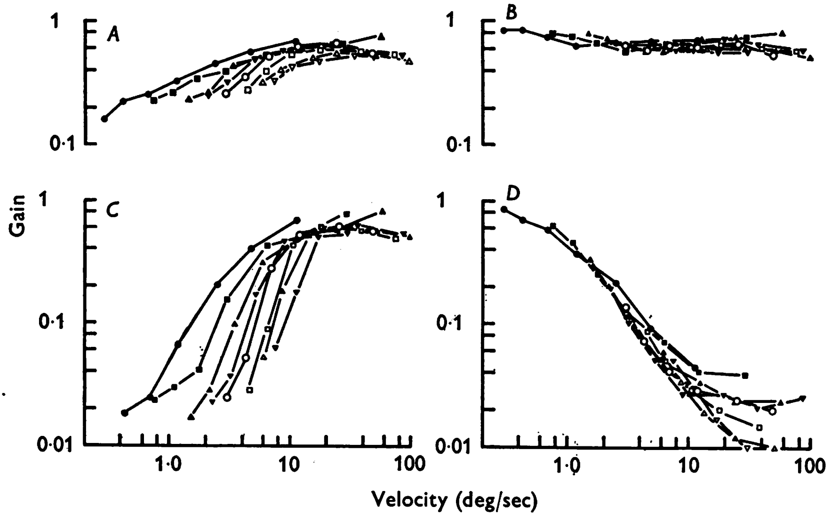

Fig. 4. Gain of eye movements as a function of maximal input velocity. *A*: eyes closed. *B*: eyes open, earth-fixed surroundings. *C*: eyes open, platform-fixed visual surroundings. *D*: eyes open, earth-fixed surroundings, one month after bilateral labyrinthectomy. Average data of seventeen (*A*, *B*) seven (*C*) and five (*D*) rabbits. The symbols indicate different amplitudes as in Fig. 2.

However, Fig. 5*A* shows a remarkable confluence of the different graphs in which the amplitude-dependence appears to be dissolved. Fig. 5*A* does in fact suggest that gain is a function of acceleration, gain being lower at smaller accelerations, and approaching a plateau at high accelerations. It is quite obvious from Fig. 5*A*, that the relation between log gain and log acceleration is not a straight line. Therefore, gain (or amplitude of the eye movement) cannot be expressed as a simple power function of the acceleration. The shape of Fig. 5*A* appears to be better approached by an exponential function. An asymptotic gain value of 1·0 was assumed and by

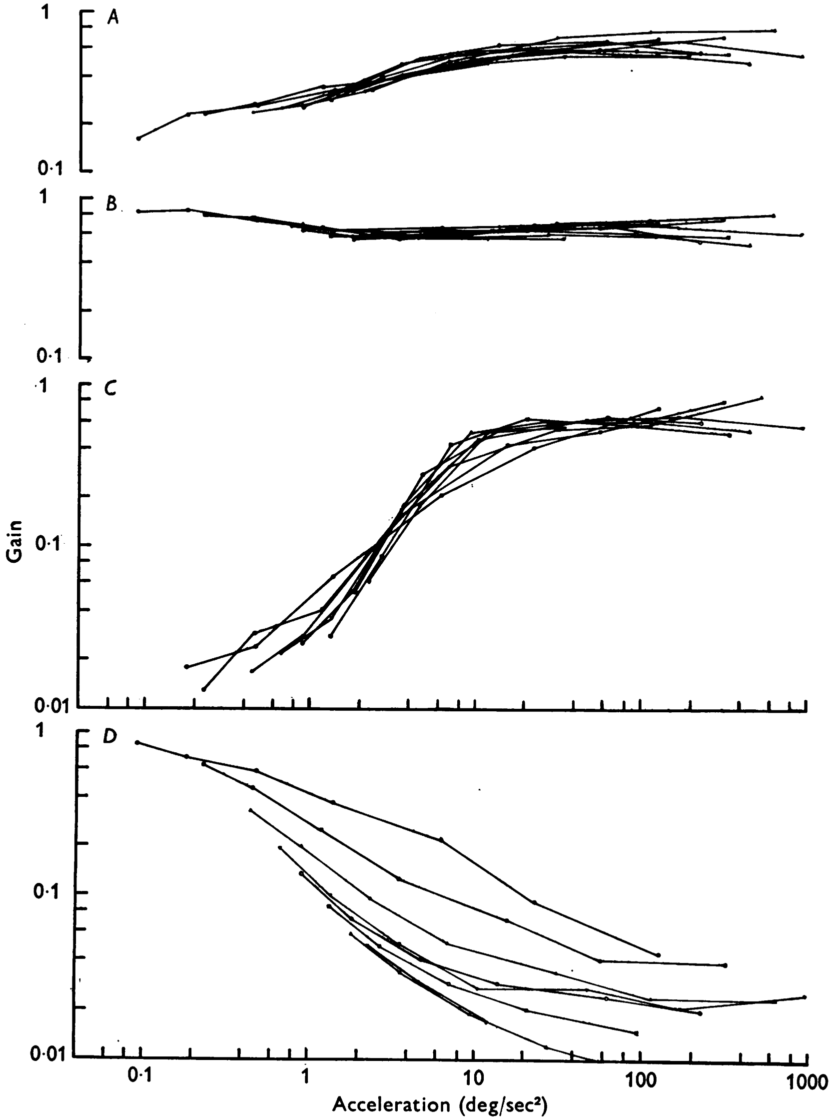

Fig. 5. Gain of eye movements as a function of maximal input acceleration. *A*: eyes closed. *B*: eyes open, earth-fixed visual surroundings. *C*: eyes open, platform-fixed visual surroundings. *D*: eyes open, earth-fixed visual surroundings, 1 month after bilateral labyrinthectomy. Same animals as in Fig. 4, symbols as in Fig. 2.

a regression analysis programme the following function was computer-fitted to our data:

$$\log G_V = -0{\cdot}482a^{-0{\cdot}1667}.$$

Theoretical values of the gain calculated from this function and replotted in the format of Fig. 2, 3 and 4*A* show a remarkable similarity to the average experimental figures, notably they show a similar amplitude dependence.

The absence of a threshold is implicit in this function. The functional significance of the relation is not immediately clear. However, it can be seen that the non-linearity is only distinct for accelerations smaller than about 5°/sec^2. For the higher accelerations, gain is almost independent of acceleration, and in this range the system might well be considered to be approximately linear. A linear approximation of some of the characteristics of the system will be given in the discussion.

A direct harmonic analysis of the eye movements has not been performed.

No systematic asymmetries of the ocular responses were detected in this situation.

Combined (harmonious) vestibular- and optic stimulation

When the same animals were subjected a second time to the same programme of oscillations but this time with their eyes open, in earth-fixed visual surroundings, a considerable improvement of ocular stabilization was seen.

Even at the lowest acceleration (0·08°/sec^2) a measurable eye movement was present in all seventeen animals. Examples in Fig. 1*b* show an increase of the amplitude of eye movements, and the systematic improvement of gain and decrease of phase error is demonstrated in Fig. 6. The combined action of vestibular and optokinetic systems in their natural way results in the following changes with respect to the vestibular reactions only.

(1) Gain is greatly improved for the low, and somewhat improved for the higher frequencies; this results in a rather constant gain over the whole employed frequency range. Values vary between 0·55 and 0·82 (over-all mean 0·62).

(2) Phase lead for the lower frequencies is reduced to maximally 10°, from a maximum of 47° with the eyes covered. A phase lag occurred only rarely.

(3) The systematic effect of amplitude on gain and phase in the vestibular situation is almost abolished in the harmonious situation.

Analysis of variance showed that a statistically significant effect of frequency on phase and gain was no longer present in this situation. The combined systems behaved as an approximately linear system. A small amplitude effect is still present for the lower frequencies, but it is inverted with respect to vestibular stimulation alone.

It appears that the non-linear properties of the canal-ocular reflexes, which are especially apparent for low stimulus frequencies and amplitudes (resulting in low stimulus velocities) are corrected to a great extent when the optokinetic and vestibular system are interacting in the normal way.

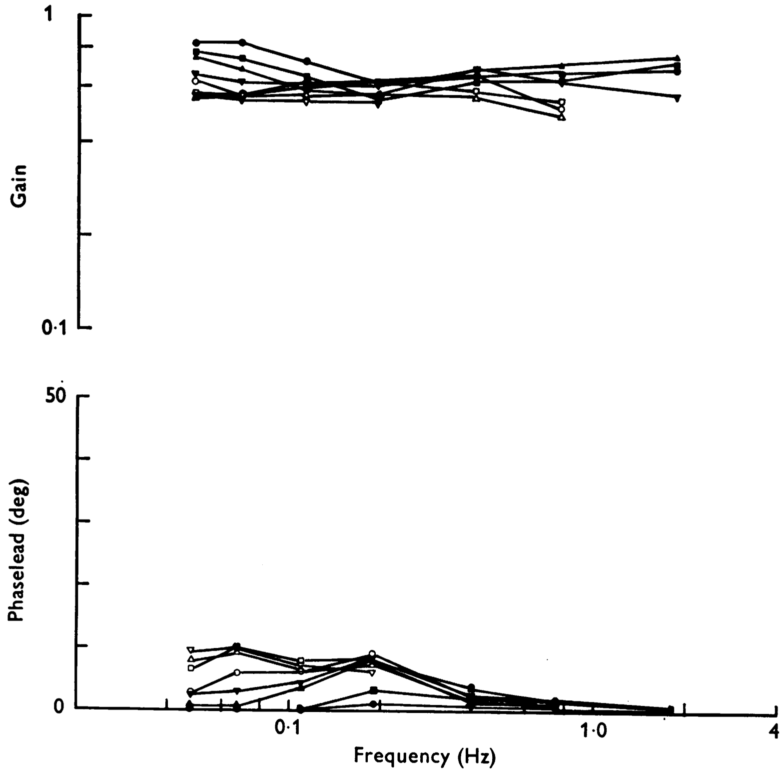

Fig. 6. Gain and phase for canal-ocular and optokinetic reactions combined (earth-fixed visual surroundings). Symbols as in Fig. 2. Average values of seventeen rabbits.

Harmonious gain (G_h) is plotted as a function of maximal stimulus velocity (v_{max}) and acceleration (a_{max}) in Fig. 4*B* and 5*B*. In contrast to Fig. 4*A* and 5*A*, these graphs suggest that gain is practically constant, and therefore independent of velocity or acceleration. This impression was statistically confirmed by computer-fitting a linear function to the data:

$$\ln G_h = p \ln v_{max} + q,$$

p was found to be $-0{\cdot}016$, not significantly different from 0. q was $-0{\cdot}537$. This indicates a constant gain:

$$G_{\mathrm{h}} = \exp - 0{\cdot}537 = 0{\cdot}58.$$

(the actual over-all mean for G_{h} was 0·62).

A similar calculation was done for gain *vs.* acceleration:

$$\ln G_{\mathrm{h}} = k \ln a_{\mathrm{max}} + p$$

k was found to be 0·01, not significantly different from 0. p was $-0{\cdot}542$, which leads again to an estimated constant value of 0·58 for G_{h}.

Also in the harmonic situation, systematic asymmetries of eye movements were not found.

Platform-fixed visual surroundings

In seven of the seventeen rabbits, the same stimulus programme was also administered while a platform-fixed optokinetic drum was rotating with the animal. The conflict between optokinetic and vestibular information inherent to this situation resulted in a considerable reduction in gain, compared to the stimulation of the labyrinth only. Examples of records are shown in Fig. 1*C*. The lowest accelerations of the stimulus programme often did not elicit a measurable eye movement. The smallest effective stimuli (in $^{\circ}/\mathrm{sec}^2$) in the seven animals were distributed as follows: 0·08 (1 ×), 0·18 (1 ×), 0·23 (1 ×), 0·43 (2 ×) and 0·92 (2 ×).

Average gain (G_{s}) and phase for the different amplitudes are plotted in Fig. 7. Several features are immediately obvious.

(1) The system is extremely non-linear under these conditions. Phase and gain are strongly and systematically influenced by stimulus amplitude.

(2) Especially for the lower amplitudes and frequencies, gain is strongly depressed and phase lead increased.

It appears as if the rather small deviations from linearity of the canal-ocular system (Fig. 2), which are largely corrected by normal interaction with the optic system (Fig. 6), are considerably exaggerated when the optokinetic system is opposing, rather than aiding the canal-ocular system in stabilizing the eyes. The same tendency is clearly demonstrated in Figs. 4*C* and 5*C* where gain is plotted against maximal input velocity and acceleration, respectively.

Again, no asymmetry of ocular movements was found.

Optokinetic reactions after bilateral labyrinthectomy

Five animals, in which both labyrinths had been destroyed one month before, were subjected to the same stimulus programme as the normal rabbits. These rabbits showed the classical phenomena of total loss of labyrinthine (and auditory) functions. They moved about very cautiously and awkwardly but ate well and appeared to be in reasonably good condition. Spontaneous nystagmus was not present.

If the eyes were covered, compensatory eye movements could not be elicited by any movement.

With the eyes uncovered in earth-fixed visual surroundings, optokinetic eye movements were produced. Gain and phase of these reactions as a function of frequency are shown (separately for each amplitude) in Fig. 8.

Obviously, gain is strongly influenced by both amplitude and frequency. The main slope of the gain versus frequency graphs is close to -1, which

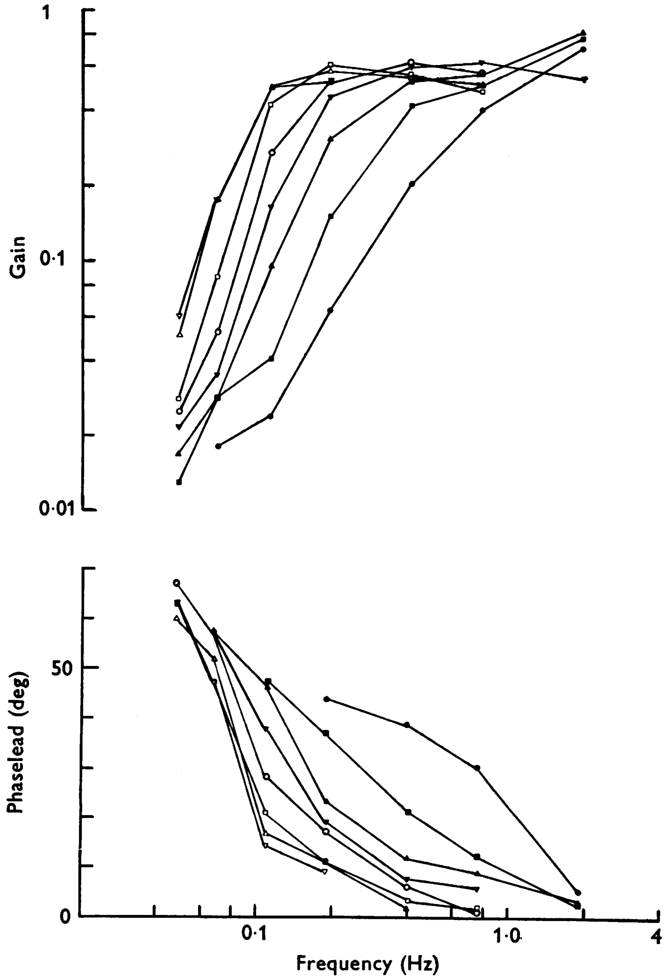

Fig. 7. Gain and phase for canal-ocular reactions, inhibited by optokinetic reactions (platform-fixed visual surroundings). Symbols as in Fig. 2. Average values of seven rabbits.

means that gain is nearly inversely proportional to frequency. The vertical distances between the graphs indicate that gain is also roughly inversely proportional to stimulus amplitude (compare the graphs for 2·5, 5, 10 and 20° amplitude, which are each separated vertically by about 0·3 log units, or a factor 2).

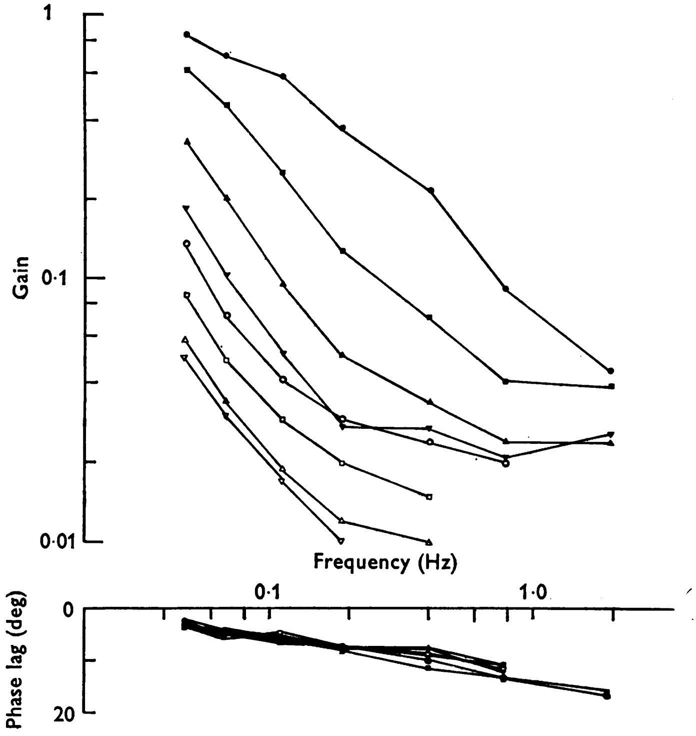

Fig. 8. Gain and phase for optokinetic reactions one month after bilateral labyrinthectomy. Symbols as in Fig. 2. Average values of five rabbits.

These observations suggest, in agreement with earlier results on normal rabbits, that optokinetic gain (G_0) is a direct function of stimulus velocity. Fig. 4*D* shows this relation very clearly. G_0 is decreasing rapidly with increasing stimulus velocities, independent from stimulus amplitude. The following function was computer-fitted to these data:

$$G_0 = -0{\cdot}863 \log v_{\max} - 0{\cdot}521.$$

For the lowest stimulus velocity used (0·3°/sec) this function predicts a G_0 equal to 0·85, in agreement with the actual value. Obviously the relation may not be extrapolated to lower stimulus velocities, since G_0 does never exceed 1. In normal rabbits, maximal values for G_0 around 0·95 have been found for sinusoidal movement (Collewijn, 1969).

The phase-lag (Fig. 8) of optokinetic reactions is in agreement with earlier findings and has been explained largely as a delay of about 75 msec (Collewijn, 1969, 1972*a*).

After bilateral labyrinthectomy the sinusoidal eye movements were still symmetric to the right and left side.

As shown in Fig. 5*D*, G_0 is not a direct function of a_{max}.

DISCUSSION

Canal-ocular reactions

General input–output relations

In the optimal frequency range we found an average gain (G_V) between 0·55 and 0·75, with a decline for frequencies below about 0·2 Hz. Phase was very obviously a function of stimulus frequency and ranged from about 45° advance at 0·048 Hz to about 0° phase error around 1–1·8 Hz. No other data for the rabbit are available for comparison. Ten Kate (1969), using a frequency range between 0·007 and 7 Hz in the pike found a gain increasing with frequency from 0·2 to 0·6 and a phase (eye position *vs.* platform position) between about 110° advance for the lowest frequency to about 5° lag for the highest frequencies. Although a pike is obviously very different from a rabbit, the general trend of these data is similar to ours. Carpenter (1972), using decerebrate cats, rotated the head relative to the body and states that a flat gain of compensatory eye movements between 0·02 and 1 Hz was found, although his illustrations suggest that gain was actually quite variable with frequency. Phase appears to vary in his experiments between about 90° lead and 45° lag for the low and high frequencies, respectively. Neck proprioceptive reflexes may have contributed to the relatively high gain found by Carpenter; his control experiment (negative reactions after sectioning the VIIIth nerves) may have been too traumatic for a definitive answer to this question.

Meiry (1966, 1971) studied human canal-ocular responses. His stimulus parameters were: constant amplitude (about 12°) below 0·6 Hz, constant peak acceleration (about 170°/sec^2) above 0·6 Hz. He found a very constant gain of 0·40 for the frequency range 0·03–2 Hz, although phase varied between about 35° advance and 30° lag, respectively. Benson (1970), using somewhat different but still comparable stimulus parameters (0·01 to 5 Hz, constant maximal velocity of 30°/sec) found a gain increasing from 0·4 for 0·01 Hz to 0·7 for the frequency range 0·05–0·5 with a sharp increase for frequencies above 0·5 Hz, up to 5 Hz, for which gain was even above unity. At 0·01 Hz phase lead was about 53°; for 0·2 Hz and higher frequencies phase error was absent. The absence of a phase lag and the substantially higher gain obviously differ from Meiry's findings.

The phase measurements of Niven & Hixson (1961) agree with Benson's data. Our findings, although somewhat shifted to a higher frequency range, correspond quite well to Benson's findings.

Skavenski & Robinson (1973), using alert monkeys, report a constant gain of about 0·85 over the range 0·02–1·5 Hz. Over the frequency range 0·04–1·5 Hz the eye showed a phase lead of 3°. At lower frequencies the phase lead was quite small: only 6·5° at 0·03 Hz and 20° at 0·01 Hz. These findings are quite unusual and in fact very similar to our data on rabbits with opened eyes. We wonder whether these monkeys may have used some tiny visual cue, although the authors state that a dim Ganzfeld, and in some cases complete darkness was used.

Non-linearities

Our evidence does not indicate the presence of any genuine threshold in canal-ocular reactions of the rabbit. Mechanical factors such as a variable friction between the cupula and the ampulla could possibly produce a threshold for cupular deviation. Since all further signal handling in the system is done by modulation of resting discharges there is no compelling reason why the nervous part of the system should have a threshold. The only intrinsic limitation could be the overall noise level of nervous system and measuring apparatus, which will limit the discrimination of responses, but not the response itself. This seems true both for psychophysical and instrumental observations. Ten Kate (1969) found a threshold of the order of one degree per sec in pikes with a body length of 20 cm at a frequency of 0·1 Hz, using a similar extrapolation procedure as in our Fig. 3. In the low frequency region the threshold values of different sized pikes varied between 5 and 0·7 degrees per sec for pikes between 5 and 87 cm body length. De Vries & Schierbeek (1953) applied essentially the same method to angular velocity perception in human observers and found no true threshold. Also Goldberg & Fernandez (1971) found no support for a threshold in their input–output relations of single afferent fibres of semicircular canals, but they used no stimuli smaller than $5^\circ/\mathrm{sec}^2$.

The occurrence of saccades in part of our responses introduces in itself a non-linear element. If these fast movements are considered as a genuine part of canal-ocular reactions our use of cumulative slow phase as a response parameter could be questioned.

Sugie & Jones (1971) have proposed a model containing a primary (smooth) and secondary (saccadic) component. They argue that the introduction of fast phases in the response results in considerable improvement of gain and reduction of phase lead. Unfortunately, their distinction of two components is entirely based upon differential sensitivity to ether anaesthesia. At a level where saccades no longer occur it is quite likely that neuronal processing (e.g. integration) of vestibular signals will be severely affected too. Our data for gain (Figs. 2, 3) and phase (Fig. 2) do not suggest that the occurrence of fast phases has any functional advantage other than resetting the system and preventing saturation phenomena.

A non-linearity in the sense of an acceleration-dependent gain such as we found has not been reported, neither for vestibulo-ocular reactions nor for vestibular afferent fibres. However, a systematic search for non-linearities in a wide stimulus range has not often been made. Meiry (1966, 1971) and Benson (1970) use only a single amplitude at each frequency. Hixson & Niven (1962) carefully examined non-linearities (for phase only) in human subjects. They found an increase in phase lead with acceleration, which is opposite to our results. However, a straightforward comparison is difficult, since they used accelerations of 10–80°/sec^2 even for very low frequencies, which means that at 0·04 Hz they must have used amplitudes between 320 and 1280°, while we used 1–25°.

Ten Kate (1969) found a linear relation between the amplitude of the eye and the amplitude of the turning table at 0·1 Hz, apart from a threshold. Fernandez & Goldberg (1971), in their study of responses of semicircular canal fibres to sinusoidal stimulation, found no evidence for an amplitude dependence and consider the canal system as linear, but they did not study accelerations smaller than 5°/sec^2, which is the range where in our case deviations were most clear. Jones & Milsum (1970) found that gain decreased monotonically with stimulus amplitude in canal-dependent units in vestibular nuclei. This tendency again appears opposite to our results.

All together, in view of the many conceivable sources of non-linearities in neuronal sensorimotor responses, it is probably more appropriate to emphasize the quasi-linear characteristics of the system, than to dwell very long on the rather minor deviations from linearity, which may depend on experimental conditions.

Linear approximation

The analysis of the semicircular canal responses as a second order system has been extensively dealt with in the literature. For a detailed account we refer to Jones & Milsum (1971).

The cupula-endolymph system is generally treated as a heavily overdamped torsion pendulum, with a long and a short time constant, T_1 and T_2. In the frequency range below $1/T_1$ rad/sec the cupula will move approximately in phase with angular acceleration. In the middle range, between $1/T_1$ and $1/T_2$ rad/sec, the cupula deviation is approximately in phase with angular velocity of the head. Finally a high frequency range (above $1/T_2$ rad/sec) should exist where the cupula moves in phase with angular position of the head.

For the middle range of frequencies, which roughly corresponds to the physiological range of head movements, compensatory eye movements are approximately in counter phase with head movements. For the low frequency range the eye will lead the head movement. This notion implies that an integration, introducing a phase lag of 90°, must be performed upon the signal of the semicircular canals. Part of this integration may be accounted for by the orbital mechanics. The existence of a neuronal integration has been postulated in addition, since orbital mechanics could probably not account for the phase relations observed for low frequencies (Robinson, 1968, 1971). Carpenter (1972), on the basis of ablation experiments in cats, argues for a cerebellar localization of the integration, while Cohen & Komatsuzaki (1972) provide evidence (based on stimulation studies) for a step of integration in the pontine reticular formation. A similar integrator seems to be required for the optokinetic system (see Collewijn, 1972*b*). Recently, Skavenski & Robinson (1973) recorded discharge rates in the abducens nucleus during sinusoidal rotatory stimulation and demonstrated conclusively that integration of the ampullar nerve signal is performed central to the lower oculomotor neurone.

In view of these findings, estimates of the properties of the semicircular canal on the basis of eye movements must be viewed with extreme caution. According to Skavenski & Robinson's data, this is especially so for frequencies above 0·1 Hz.

Our data for gain and phase (Fig. 2) are entirely compatible with the data of Jones & Milsum (1971) for canal dependent units in the vestibular nuclei of the cat (their Fig. 7), if one step of integration is allowed for. This may indicate, that the frequency response of canal-ocular reflexes, in mammals of the size of cats and rabbits, is indeed governed by the mechanics of the semicircular canal in the low frequency range. At our lowest frequency (0·048 Hz = 0·30 rad/sec) phase lead was close to 45° for all amplitudes used. Under the assumptions specified above, this leads to an estimate of 1/0·30 = 3·3 sec for T_1, the long time constant of the cupula-endolymph system (the spread in the individual experiments would indicate a standard deviation of roughly ± 25 % for this value). The value of 3·3 sec is in reasonable agreement with the estimates by Jones & Milsum (1971) in the cat (4 sec) and Fernandez & Goldberg (1971) in the spider monkey (5·7 sec), both based on direct measurements of canal-dependent neuronal activity.

Vestibulo-ocular responses in man have led to estimates of T_1 as 10 sec (van Egmond, Groen & Jongkees, 1949), 6·7–10·2 sec (Niven & Hixson, 1961) and 8 sec (Meiry, 1966). Benson's (1970) data also suggest a T_1 of 10 sec. The species differences may be largely explained in terms of animal size and frequency content of natural head movements, as has been discussed by Jones & Spells (1963).

Optokinetic reactions after labyrinthectomy

In earlier experiments on intact rabbits (Collewijn, 1969) optokinetic gain was found to be up to 0·95 for sinusoidal motion with maximal velocities up to 1°/sec, and to decline steeply for higher velocities. These findings have been interpreted in terms of a non-linear velocity sensitivity of the system (Collewijn, 1972*b*).

The present data obtained from labyrinthless animals differ in some respects from these earlier results. The rate of decline of gain at higher stimulus speeds is very similar in both groups, but after labyrinthectomy the decline in gain is already obvious for stimulus speeds much lower than 1°/sec. For the lowest stimulus speed used in the present experiments (0·3°/sec) gain is about 0·85, which is still below the value of 0·95 found in normal rabbits (Collewijn, 1969). Possibly, gain may be higher for still lower velocities. It must be concluded that in the entire tested range gain is subnormal.

Only a few reports exist on the effect of labyrinthectomy on optokinetic reactions. Gutman, Zelig & Bergmann (1964) investigated optokinetic reactions in labyrinthectomized rabbits, using frequency of fast nystagmic phases as an index of response. A marked decrease of the number of beats/min was found for all velocities tested (roughly 1–100°/sec), while the general shape of the response as a function of stimulus velocity was preserved. However, since the amplitude of the fast movements was not measured, the overall effect on slow phase velocity is somewhat uncertain.

Honrubia, Jenkins, Downey & Ward (1971) made a similar study in cats. They also found a decrease in the frequency of nystagmic beats. However, the frequency-amplitude product ('intensity'), which is directly comparable to our slow phase velocity, was not different before and after bilateral labyrinthectomy. Whether labyrinthectomy in itself affects the gain of optokinetic reactions specifically or indirectly as a result of somewhat poorer general conditions of the animal is unclear at this time.

Combined vestibular and optokinetic stimulation

In earth-fixed visual surroundings, a certain part of the movement of the skull relative to the surroundings will be compensated by the vestibulo-ocular eye movement. The remaining retinal slip will serve as the input signal to the optokinetic system. The two systems are complementary in a highly meaningful way. Canal-ocular reactions function especially well for relatively fast movements, while the optokinetic system is tuned to low velocities. The result of their cooperation is a practically constant gain and negligible phase error for the range of stimuli tested (Fig. 6).

Assuming a linear interaction between vestibular and optokinetic system we can expect the following relation:

$$G_h = G_0(1-G_v)+G_v$$

in which

$$G_h = \text{total, harmonious gain,} \quad G_0 = \text{optokinetic gain}$$

and

$$G_v = \text{vestibular gain.}$$

In platform-fixed visual surroundings, the output of the vestibular system itself will be the input to the optokinetic system. The optokinetic system will oppose any eye movement relative to the visual surroundings. In principle, we can expect

$$G_s = G_v - G_o\, G_v$$

in which G_s = gain in platform-fixed surroundings. Both G_v and G_0 are amplitude- and frequency-dependent. For each amplitude-frequency combination G_v is known and G_0 can be calculated for the effective optical stimulus by means of the optokinetic input–output relation, such as the one found for normal rabbits (Collwijn, 1969).

In this way, we calculated theoretical values of G_h and G_s for all amplitude-frequency combinations of the swing. The obtained figures very markedly showed the characteristics of Fig. 6 and 7, in particular an obvious improvement of gain and reduction of non-linearity for the harmonic case and deterioration of gain and enhancement of non-linearity for the platform-fixed surroundings, both with respect to pure canal-ocular stimulation. A perfect fit between predicted and actual values for G_h and G_s was not obtained, which may be due to several factors:

(1) the used values for G_0 had not been determined in the same animals for which G_v, G_s and G_h were measured,

(2) phase errors and delays have been entirely neglected in this approach,

(3) the assumption of a linear interaction between optokinetic and vestibular reactions may be erroneous. For instance, unforeseen saturation effects might occur at some stage common to both systems. The fact that optokinetic gain is decreased after labyrinthectomy, if specific, might indicate some non-linear interaction.

A more rigorous quantitative investigation of the interaction between these systems would require measurement of all types of gain in the same animals, as well as analog computer models of both systems and their interaction, inclusive delays and non-linearities.

Interaction experiments somewhat similar to ours have been done in man by Meiry (1966). In his experiments, foveal fixation of a small target (earth-fixed or platform-fixed) was attempted by the subject during sinusoidal oscillation. With earth-fixed fixation perfect smooth tracking of amplitude was reached (gain = 1·0), though with a rapidly increasing phase lag beyond 0·5 Hz. (The latter finding contrasts with Benson's (1970, 1971) reports.) With a platform-fixed fixation target, vestibular eye movements were counteracted by a rapid sequence of small saccades, which kept the eye within 0·5° from the mean position. The occurrence of these fixation movements, which are not found in the rabbit, makes any comparison with our data difficult.

Mr H. Werner kindly undertook the curve fitting and analysis of variance, using the Varian/02 programme by T. Kwaaitaal and E. Roskam, University of Nijmegen. Thanks are also due to Dr H. G. Stassen for Fourier analysis of the stimulus and Dr J. H. ten Kate for helpful criticism.

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