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EYE AND HEAD MOVEMENTS IN THE PIGMENTED RAT*

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Abstract—Vestibular, optokinetic, and spontaneous eye and head movements have been examined in the hooded rat. Eye movement range was 18–20°, and frequency of ocular saccades was 5–20/min; there was a weak linkage of eye and head movements and a weak vestibulocollic reflex. Response to optokinetic stimulation with unity gain (eye velocity matches drum velocity) was seen only at velocities below 1 deg/sec; maximal eye velocity evoked by drum velocities of over 20 deg/sec never exceeded 4–6 deg/sec. These motor responses were not altered by head movements: thus gaze velocity is not improved by optocollic (head movement) responses, and such optocollic activity occurs only when substantial retinal image motion is present.

Vestibular Optokinetic Eye movements Head movements

INTRODUCTION

The laboratory rat is used in physiological and anatomical studies of vestibular and visual reflex systems and in other behavioral studies in which visually directed behavior is required. Because eye movements are difficult to measure in a small animal, head movements are commonly used to assess vestibular and optokinetic reflexes in the rat. The latter reflex, in which the rat moves its head in the direction of full field movements, referred to here as the optocollic reflex (OCR), has been observed in the guinea pig (Gresty, 1975) and the rabbit (Brecher, 1936, Fukuda and Tokita, 1957) as well. Since all three species have been shown to have a vestibulo-ocular reflex (VOR), it seems strange that head movements should be evoked by optokinetic stimulation, since the VOR under optimal conditions would cancel any benefit the head movements might contribute to reduction of retinal image motion. While this question is of major interest in this study, consideration of visual-vestibular interactions which occur in the OCR requires examination of oculomotricity in general, and various aspects of eye-head coordinated movements. For example, head movements might be beneficial if eye movements are generally very small or slow, or if the VOR gain is low. Thus, before examining when and why head movement is evoked by optokinetic stimulation, some information is required on the independence or dependence of eye and head movements and other ancillary behavior. In this context, certain characteristics of rat saccades, of the vestibulo-collic reflex (VCR) and of the optokinetic (eye) reflex (OKR) which have not been reported, are examined.

METHODS

Five adult (200–300 g) Long-Evans hooded rats were anesthetized with pentobarbital and surgically prepared for chronic behavioral studies as presented in detail elsewhere (Fuller, 1981).

Surgical preparation

A pedestal containing a tubular aluminum socket made of 1/4" rod (1/8" inside diameter) and a set of connector pins was affixed to the skull. The oculogram was measured with silver–silver chloride electrode balls, 1 mm in diameter, placed as close as possible to the lateral and medial canthi of each eye: a 1–2 mm incision was made in the skin, and the subcutaneous tissue was freed from the overlying skin behind the incision, forming a pocket or recess. The two oculogram leads from each eye were threaded under the skin to the pedestal; the silver–silver chloride ball was drawn into the subcutaneous recess behind the incision, and the leads were taken to the pedestal connecting pins (a fifth, indifferent pin was implanted in the skull). The incision was closed with fine surgical suture. It should be noted that the bony orbit in the anterior-posterior axis of the rat skull is 15 mm long, measured across the center of the eye, whereas the eye is about 6 mm in diameter in this axis with the remaining 9 mm occupied by soft tissue (Hughes, 1979); inserting the electrode in bone places it too far away from the corneo-retinal potential to

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obtain a measurable signal. Dependable recording stability lasted 3–5 days following surgery, after which d.c. drift and variable gain occurred.

Vestibular and optokinetic stimulation

Upon recovery from surgery, the animals were placed on a platform which rotated about a vertical axis passing through the first and second cervical vertebral junction. The animal's head could be freed to allow voluntary or reflex head movements about this axis or fixed for passive whole-body rotation through the same axis. Strain gauges mounted on the shaft measured head torque. The animals were loosely restrained in a box which allowed freedom of movement above the upper thoracic vertebrae. The rats were placed in the prone (sphinx-like) position and usually adapted to this posture within 1/2 hr. Other postures were tested, but were less well tolerated. The animals faced an optokinetic drum of 57 cm radius described elsewhere (Fuller, 1980).

Calibration of the oculogram

Due to the small signal of the EOG and artifacts presumably due to respiration (see Fischer *et al.*, 1979), the signals from the two eyes were summed to increase the signal amplitude and cancel the respiration-related noise; the latter was eliminated by adjusting the two oculogram signals from each eye until the noise was equal (but opposite in polarity) from both leads. This method has been described previously (Fischer *et al.*, 1979). The summed oculogram amplifier gain was adjusted while monitoring the gaze signal, which is the sum of horizontal eye movement (HEM) and platform angular deviation (PAD). In Fig. 1, the rat was rotated ($\pm 30°$, $\pm 20°$/sec, at 0.11 Hz) with full-field vision. In all figures rightward movements are positive.

Figure 1 shows that the intersaccadic gaze signal is frequently sloped in the direction of platform rotation, indicating compensatory eye movements are smaller than the stimulus. This is normal and, as thoroughly discussed elsewhere (Fuller, 1981), is likely due to visual inattention. The initial calibration of the oculogram gain was considered complete if, during several minutes of rotation, there were occasional intersaccadic gaze intervals which were flat (eye equals platform rotation), and no intervals in which gaze sloped opposite the platform (eye greater than platform rotation). Since there were no objects between the rat and the experimental visual field (stationary checkered pattern), it is unlikely that there was accommodation of near objects—which would increase the eye signal relative to platform rotation (Blakemore and Donaghy 1980). Other corroborative tests of oculogram calibration are given below.

RESULTS

Oculomotricity

In the present study, spontaneous saccades were seen when the rats were stationary with heads fixed; the frequency ranged between 5 and 20/min. The most eccentric excursion of the eyes in the orbit was 18–20°, and maximal excurison was most often elicited by full-field optokinetic stimulation. The largest voluntary saccade was 17° eccentric. Voluntary saccadic amplitude and velocity were related with a slope of $20 \pm 3°$/sec/deg (Fig. 2). Saccadic duration increased with amplitude, although it was highly variable (Fig. 2). Saccades smaller than 3° were not measured; duration was measured accurate only to 5 msec. The fastest eye movement was 400°/sec for a 20° saccade, elicited by optokinetic stimulation.

Head on trunk movements

Both passive and active head movements were studied. In Fig. 3 the platform was stationary, the head was freed and manually (passively) rotated

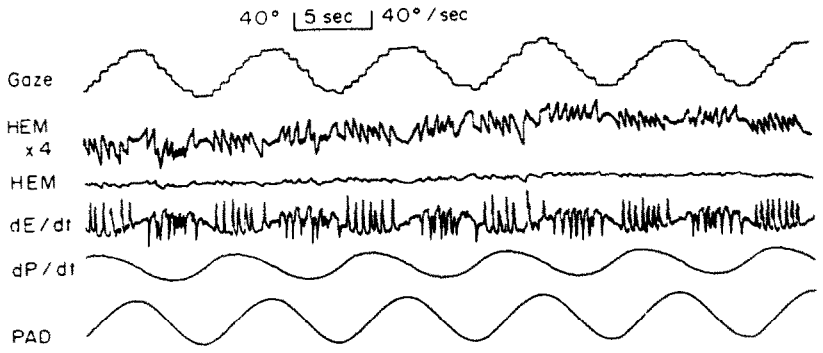

Fig. 1. Calibration of the oculogram signal. Animal is rotated with full-field vision and head fixed to the platform. Horizontal eye movements are shown at unity gain (HEM) and at four times unity gain (HEM × 4) for illustrative purposes. Abbreviations: HEM, horizontal eye movement; PAD, platform angular deviation; gaze, sum of HEM and PAD; dE/dt and dP/dt, velocity of HEM and PAD respectively.

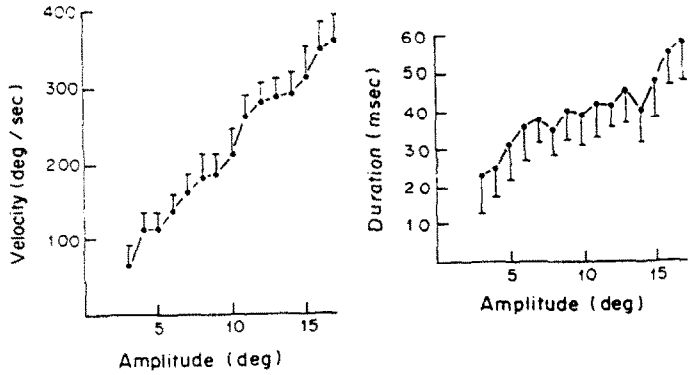

Fig. 2. Characteristics of rat saccades. Amplitude is related to peak velocity (left) and duration (right). Each point represents 10 movements from 2 to 3 rats, with the exception of points above 15 deg, in which 3–5 movements represent each point. Vertical lines represent one standard deviation.

about the C_1–C_2 junction. At low or high velocities, intersaccadic gaze is flat, and the differentiated eye signals have the same profile as head movement (dN/dt is inverted for easier comparison with the differentiated oculogram signal).

While passive rotation of the head provides verification of oculogram gain and additional information on the range of amplitudes and velocity of eye movements, spontaneous active movements provide more realistic measurements (Fuller, 1981; Collewijn *et al.*, 1983). However, voluntary head movements about the vertical axis were quite rare; for example, Fig. 3 shows two spontaneous eye-head movements from one rat, which were selected from 15 head movements, observed over a total period of three hours and distributed over 5 recording sessions. This figure was typical for all rats, and is in contrast to saccades independent of head movements, which as noted above occur at a frequency of 5–20/min.

The pattern of eye and head movements in Fig. 3(B1) somewhat resembles that in other animals: a single ocular saccade is slowed proportionally with head velocity (i.e. eye and head movements are summed; Fuller *et al.*, 1983). This is followed by a counter-rotary eye movement of equal and opposite amplitude to the head movement (confirming proper oculogram gain). However, only two out of the 15 head movements made in the absence of trunk movements had this profile. Figure 3(B2) illustrates the more common profile with two or more ocular saccades in the direction of gaze transition. During a brief period while the head was moving, the eyes were stationary in the orbits (marked by a horizontal bar). This has been described in cat (Fuller *et al.*, 1983) but is not seen in this species during multiple step gaze shifts [which Fig. 3(B2) is], but only in single step gaze shifts [which Fig. 3(B1) is]. Thus, as with many species, single step gaze shifts can be made with saccadic-vestibular summation, but there are frequent occasions when the VOR appears not to be functional (Fuller *et al.*, 1983).

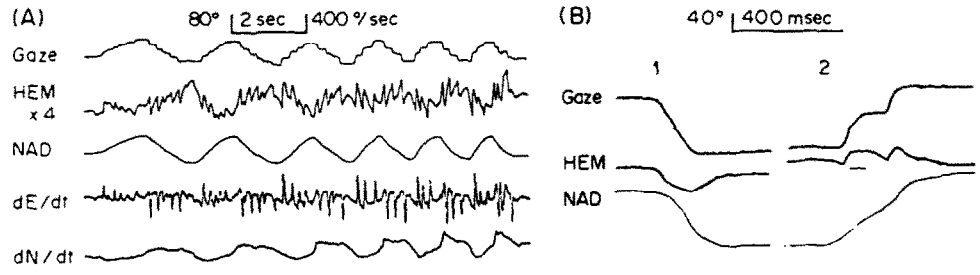

Fig. 3. Passive and active head-on-trunk movements. (A) With full-field vision, animal's head is passively rotated (measured as neck angular deviation, or NAD) on its stationary trunk. Note that as in Fig. 1, gaze is generally flat during intersaccadic intervals. Saccadic velocity (dE/dt) is not clipped as in Fig. 1, thus the peak velocity at a variety of amplitudes can be compared. Head movement velocity, or dN/dt, is inverted for ease of comparison with dE/dt. Note that the HEM signal is amplified four times the other signals. (B). Voluntary (spontaneous) head movements from one rat. (1) A single leftward saccade precedes head movements; note unchanged slope of gaze as NAD accelerates, indicating summation. (2) Multiple rightward saccades interspersed with counter-rotary eye movements; at one point during the head movement the eyes were stationary in the orbit (bar under HEM).

Vestibulo-ocular reflex

When the animal was briefly (10 sec) deprived of a textured visual field by placement of a Ganzfeld (Fuller, 1980), eye movement amplitude during whole-body rotation was unaffected. This held for frequencies of 0.08 ± 0.5 Hz and velocities of ± 5 to 100°/sec; however, in agreement with Lannou *et al.* (1982), placement of the Ganzfeld produced a phase advance of about 10–40°. Furthermore, manual rotation of the animal's head in the absence of a textured visual field produced the same results; thus, the data illustrated in Figs 1 and 3 are comparable to those obtained when vision was excluded for short periods of time (ca 10–30 sec), with the exception of a small phase lead.

Head movements elicited by vestibular stimulation

The rat tends to partially stabilize its head in space during whole-body rotation; this is presumably effected by the vestibulo-collic reflex (VCR). This reflex can be assessed in the open loop condition by measuring attempted head movements (head torque) of the rat when rotated with its head fixed to the platform. In Fig. 4(A), occasionally slow and fast phases of horizontal head torque (HHT) loosely correspond to the slow and fast phases of eye movements (best seen at the beginning and end of the trace), but the correspondence is rarely consistent and does not show a temporal linkage with the eye movements.

Corresponding to the weak attempted head movements is a relatively variable VCR, shown in Fig 4(B) and (C). While it may appear that there is a physical limitation at the extremes of eccentricity, the neck angular deviation (NAD) trace in Fig. 4(B) has a leftward d.c. drift (i.e. the rat is slowly moving its head to the left), indicating that the animal is, in fact, able to move its head beyond the apparent extreme. Thus, the small extent of head-on-trunk movements (a gain—NAD/PAD—of 0.3) reflects a rather slight VCR rather than physical limitations of the restraining apparatus on head movement. Figure 4(C) at the far right shows the maximum gain (0.76) seen

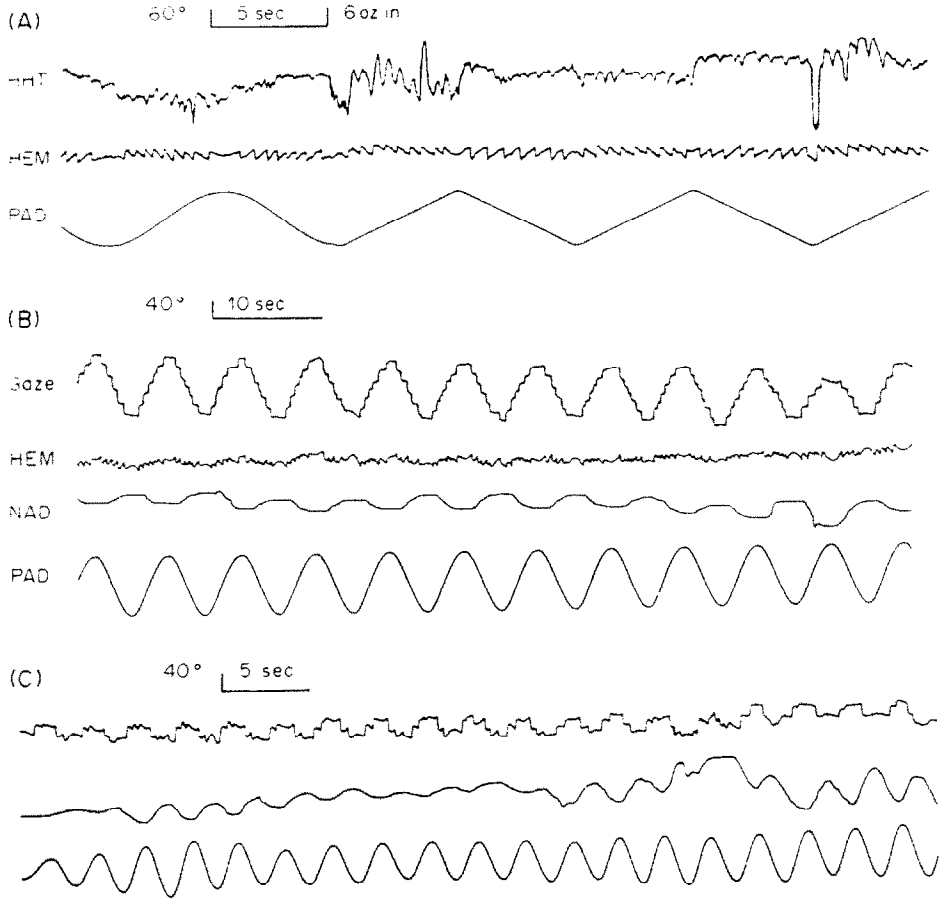

Fig. 4. Vestibulo-collic reflex. (A) Animal is rotated with head fixed to platform to demonstrate attempted head movements, shown as horizontal head torque (HHT). (B) Continuous trace of rat being rotated with free head. Rotation is effected by a servo controlled motor. Gaze is the sum of HEM, NAD, and PAD. (C) Rotation was imposed by manually flexing a torsion spring attached to the platform. Note that at end of trace, the reflex gain is highest and most closely resembles the platform angular deviation signals. Traces are in same order as (B) except gaze is not included.

in these studies. The gain for all rats averaged 0.32 (S.D. 0.21). In the last four cycles of Fig. 4(C), there are repeated ocular saccades opposite NAD and in the same direction as the platform; this was frequently observed at high rotational velocities and is similar to the pattern seen in rabbit (Fuller, 1981). In Fig. 4(B), the contributions of the eyes and head to gaze stability are inversely related such that gaze is fairly stable (with reference to earth-fixed surroundings) throughout the trace of Fig. 4(B); this unchanged gaze profile with variable NAD contribution also corroborates oculogram calibration (see Fuller, 1981, p. 378).

Measurement of optokinetically-induced eye movements

The calibrated drum potentiometer signal (optokinetic drum, or OKD) was inverted and summed with the oculogram signal; the resulting signal is referred to as "gaze relative to drum" (GRD). (The head is fixed and the platform stationary; thus HEM equals gaze.) The GRD and OKD signals were then reinverted and displayed with their original polarities for ease of analysis. Thus, in Fig. 5(A) (left), the HEM signal shows rightward (positive) slow and leftward saccadic eye movements. Note that the GRD signal shows ocular saccades in an inverted form. Parallel lines are provided to indicate a unity match of eye movements and drum movements. If the animal's eyes are moving more slowly than the drum, the intersaccadic GRD signal will slope in the same direction as the drum signal. Thus, the GRD signal in this figure reflects the oculogram relative to drum movements.

Optokinetic reflex

The maximum drum velocity at which eye movements consistently produced a "flat" GRD signal (i.e., identical slope of eye movement and optokinetic drum movement) was approximately 0.9°/sec: in Fig. 5(A) (left), the drum velocity was 0.87°/sec. In Figure 5A (right), the drum velocity was 2.7°/sec, and while there are occasional intersaccadic periods in which the GRD signal is flat, the majority of slow eye movements are slower than the drum, and the GRD signal has a slope of 0.5–1.0°/sec. Continuous rotation for many minutes did not alter the response.

Figure 5(B) shows the response to triangular waveform stimulation at velocities of ±2.8°/sec. Despite brief periods of a flat GRD signal, the gaze is generally sloped in the direction of drum movement; at faster velocities (±4°/sec) to the right of Fig. 5(B), there is under-compensation exclusively. The latency between drum reversal and eye movement reversal is shorter than 1 sec, and the slope of eye movements after the reversal is generally consistent after the second or third intersaccadic interval.

Figure 6 shows the responses of the animals to continuous rotation. Measurements were made after at least 30 sec of constant velocity stimulation. Each point below 2.0°/sec represents 15 measurements: 5 consecutive intersaccadic eye movement velocities

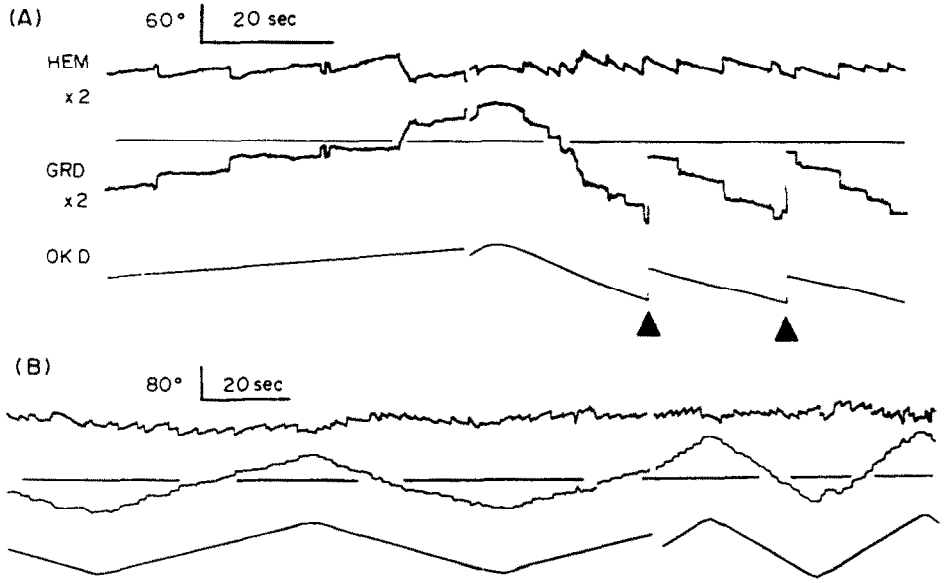

Fig. 5. Full-field optokinetic stimulation with the head fixed. (A) Continuous rightward drum rotation until the middle of trace, when direction of rotation is reversed. Triangles represent instances in which the OKD (and, therefore, RS) signal has had a voltage step applied to it. When the RS signal is parallel to the reference line, HEM and OKD have identical slopes. See text for fuller explanation. (B) Triangular stimulation with same conditions as in (A). Order of traces is the same as in (A), and only HEM is twice (2×) unity gain, whereas RS is at unity gain. Abbreviations: OKD, optokinetic drum; RS, sum of OKD and HEM.

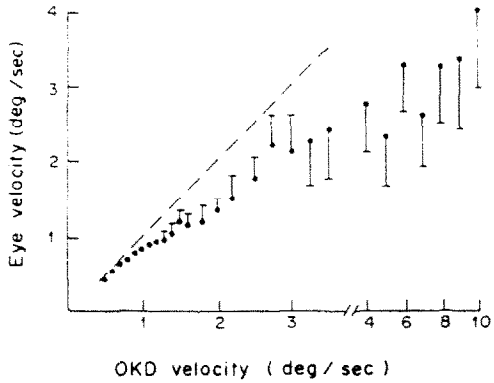

Fig. 6. Response to optokinetic stimulation. Rats with their head fixed faced a constant velocity rotating drum. Points represent 5–10 intersaccadic intervals from each of 3–5 rats. Vertical lines represent one standard deviation (SD); upward or downward SD lines are for illustrative convenience only. SD below 1.2°/sec was too small to illustrate, and was 0.05–0.08 below 0.9°/sec, and 0.06–0.1 up to 1.2°/sec. The broken line represents a gain of 1.0.

were measured for three rats; all 15 were then averaged. Velocities below 0.5°/sec were not sufficiently constant to measure the response. Measurements of responses above 2°/sec represent 10 consecutive movements in all 5 rats. Measured in this way, it can be seen that the optimal response (minimal image movement on the retina) occurred below 0.9°/sec, with a drop above 1.1°/sec. Responses to velocities above 2.5°/sec were extremely variable.

Optokinetic stimulation and head movements

Based on the above oculomotor responses, one might expect that if the rat's head were free, increasing gaze velocity by head movements would reduce retinal slippage if the drum velocities were greater than 1°/sec. This was not the case; head movements did not reduce the GRD slope. In Fig. 7(A) and (B), there are brief periods of a flat GRD signal during drum rotations between 3.5°/sec and 6.3°/sec; however, the GRD signal was most often sloped in the direction of drum rotation, indicating undercompensation. Nystagmus-like head movements were rare and bore little resemblance to the more periodic and rhythmic eye movements elicited by a moving field. Furthermore, during periods of substantial undercompensation [Fig. 7(C)], head movements did not increase gaze velocity; head velocity reduced eye movements and the gaze slope remained unchanged. Head movements were rarely (2 of 100 trials) evoked by drum velocities below 2°/sec, frequently (20 of 100 trials) with velocities of 4–10°/sec, and consistently with velocities greater than 10°/sec. That is, only when there was substantial retinal image motion were head movements evoked. However, the GRD signal at high velocities was never remotely close to being flat; velocity in Fig. 7(C) was increased from 12 to 22°/sec, whereas gaze velocity was 3°/sec and did not increase when drum velocity was increased; i.e. gaze was unchanged by head movement contribution.

In summary, beyond about 0.9°/sec, the GRD signal slope nearly always progressively increased with higher drum velocities, whether the head was free or fixed. However, with both fixed [Fig. 5(B)] and free [Fig. 7(A)] head, there were short intervals during which gaze velocity reached 4–6°/sec and matched that of the drum; this may reflect heightened arousal or attentiveness.

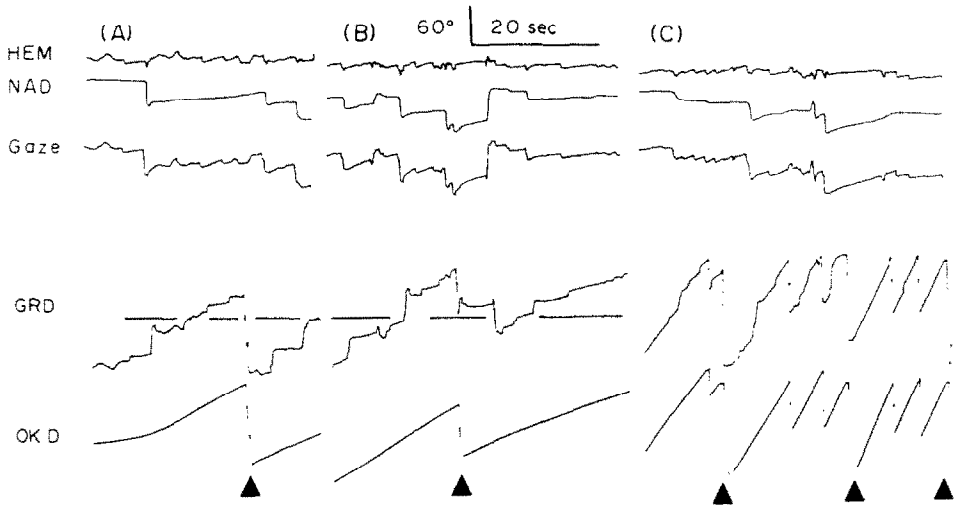

Fig. 7. Optokinetic stimulation with free head. (A) and (B) show periods with velocities of 3–6°/sec. In (C), drum velocity is gradually increased from 12 to 21°/sec. In (A) and (B) the triangle indicates when a voltage step is applied, as in Fig. 5. The OKD potentiometer recorded 335° of rotation; thus in (C), as the drum passed between 335° and 360°, a "dead zone" in which no rotation is recorded is marked by a triangle below the OKD signal. Abbreviations as in previous figures.

DISCUSSION

These preliminary data on oculomotricity demonstrate that the rat is not greatly different from other species. Saccadic amplitude and velocity are related with a slope of 20°/sec/deg; this is less than that seen in monkey (40°/sec/deg), greater than that of rabbit (13°/sec/deg), and close to that in man (20°/sec/deg) (Evinger and Fuchs, 1978). The maximum saccadic velocity seen in rat (400°/sec) also falls into the intermediate range. The oculomotor range (20°) compares favorably with results from superior collicular stimulation in the rat (McHaffie and Stein, 1982), and is close to that of the rabbit (Collewijn, 1977).

Eye-head coordination

The frequency of saccades with either free or fixed head in rats is about 10/min, while eye-head movements occur at a rate of fewer than 1/min. While the rarity of horizontal head movements may reflect the method of restraint, the same restraint technique was used for rabbits (Fuller, 1981), and by comparison, rats moved their head far less and their eyes far more than rabbits under the same conditions: rabbits with a fixed head made ocular saccades at a rate of 1–5/min and eye-head movements with a free head at a rate of 10–20/min (unpublished observations); completely unrestrained rabbits make eye-head movements at a rate of 30–40/min (Collewijn, 1977).

The vestibulo-collic reflex in rat is weakly manifested, which is reflected in the head torque (attempted head movements) and which showed only a slight modulation during head-fixed rotation. Not unexpectedly, the peak torque was small, about 1/5 of that produced by the rabbit (Fuller, 1981). In Fig. 4(A), the head torque signal occasionally demonstrates a slow modulation in phase with velocity during sine wave rotation or a square wave appearance during triangular wave forms. (Actually the peak of the slow torque change is 180°, or reversed in polarity, with respect to velocity; i.e. a leftward ramp produces a rightward step in torque.) This has been seen in all mammals studied by the present author and probably represents more a "voluntary" response of the animal to whole-body rotation rather than a vestibular response (see Fuller, 1981, for detailed discussion); as illustrated here, it is highly irregular.

It is surprising that rats do not demonstrate larger vestibularly driven head movements (VCR), since by contrast guinea pigs and rabbits (a lower mammal, but not a rodent) both show quite strong VCR. In the case of guinea pigs, the strong VCR is seen with a completely free head (Gresty, 1975) or in exactly the same apparatus (Fuller, unpublished observations) used for rats. Thus the small extent of head movements is not necessarily due to the method of restraint. The additional fact of a high frequency of eye movements independent of head movements, and of a weak eye-head linkage also are in contrast to rabbit (Fuller, 1981). A possible inference is that rats rely more heavily on eye movements for visual exploration than do rabbits, in which there is a fairly compulsory linkage between the two. Nevertheless, if the above observations are taken to demonstrate a reliance on eye, rather than head movements for gaze shifts (compared to rabbit), this would deny the present data, in which rats do indeed exhibit an OCR and previous observations in which rabbits also show an OCR (Fukuda and Tokita, 1957).

Optokinetic eye movements

The most extensively studied lower mammal is the rabbit, and comparing its OKR with the rat can be instructive. One report on the rabbit (Collewijn, 1969) stated that the gain is near unity (0.9) at velocities of 1°/sec; the response is based on averaged eye velocities, and by this measure rats and rabbits appear to be similar. Another account placed the upper limits of the rabbit OK system at about 3–8°/sec (Fig. 11 of Barmack and Simpson, 1980); the response was based on peak eye velocity. As noted by Collewijn (1969) and shown here in Fig. 5 the optokinetic response is variable, and like the VOR-visual response (Fig. 1), the match between eye velocity and stimulus velocity varies from one intersaccadic interval to the next.

To conform to convention, the OK response in this study is reported as average velocity; a more representative, but cumbersome, measurement would be to evaluate the number of intersaccadic intervals which show no detectable GRD slope (in this study about 0.05°/sec was the smallest measurable slope). Using this method, the data were as follows: at 0.5°/sec, 90% of 100 consecutive intervals were flat (a gain of 1.0). This percentage was the same (within 1–2%) for all five rats for rates up to 0.9°/sec. The percent of intersaccadic intervals with no GRD slope dropped to 86% at 1°/sec, to 67% at 1.5, and 57% at 2.0°/sec. At 4°/sec the value was 20%. Thus, using this more cumbersome method, inferiority of the rat OKR is emphasized, since in rabbits occasional velocities of 10°/sec are seen in response to drum rotations of 10°/sec (Barmack and Simpson, 1980).

A second reflection of rat's inferior OKR is the fact that optokinetically-induced eye movements in the rat never exceeded 4 to 6°/sec even at drum velocities of 30°/sec, while optokinetically-induced eye movements in the rabbit can reach up to 20–30°/sec by employing drum velocities up to 50°/sec (Collewijn, 1969; Barmack and Simpson, 1980). Apparently, in this respect, the rat has an upper limit of velocity capacity which is far below that of the rabbit; this may also suggest a difference in velocity storage (by a neural integrator) in the two species. This issue becomes important when head movements are allowed during optokinetic stimulation.

Optokinetically induced head movements

When the rat moves its head during optokinetic stimulation, gaze velocity does not appear to in-

crease. This is in agreement with observations in primates (Kubo *et al.*, 1981). One possible explanation for this is that vestibular and visual reflexes are summed, as is illustrated by the following example: in Fig. 7(C), despite an apparent retinal image movement of nearly 20°/sec, a 3°/sec head movement nearly cancels the eye movements, indicating that there is a 3–4°/sec internally generated optokinetic slip signal. This is most easily explained by assuming that vestibular and optokinetic signals sum to eliminate eye movement at this velocity; it does not, however, explain why a remaining retinal slip fails to continue to drive the eyes (Fuller, 1985).

Since the optokinetically elicited eye movements are of variable gain, especially above 1°/sec, it is expected that visual and vestibular interaction will also be variable, and that the only time at which head movement could increase gaze velocity would be when retinal image slip is sufficiently massive so as to override any oculomotor drive resulting from vestibular stimulation accompanying head movement. Conversely, vestibular stimulation must be weak so as not to override optokinetic drive. Therefore, only if vestibular drive is less than optokinetic drive will head movements increase gaze velocity; it follows that such head movements cannot result in image stability. It is noted that the time constant for charging and discharging of optokinetic and vestibular activity will also influence visual and vestibular interactions; since the velocities involved in the rat are so small, this was not practical to examine. However, as suggested by the very low maximal OKR (4–6°/sec) and by the lack of increase of gaze velocity by head movement, the rat neural integrator may be very weak.

The above observations can be summarized in regard to the optimal stimuli for evoking head and eye movements and in regard to the question posed at the outset—do head movements improve the optokinetic response? Large, active head movements are elicited by optokinetic stimulation, although velocity is rather low; higher velocity, but lower amplitude head movements are elicited by vestibular stimulation. The rat has an extremely limited velocity capacity in response to optokinetic stimulation; head movements do not extend the range of the response.

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