COMPENSATORY EYE MOVEMENTS TO MINIATURE ROTATIONS IN THE RABBIT: IMPLICATIONS FOR RETINAL IMAGE STABILITY

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(RECEIVED 20 SEPTEMBER 1978)

Abstract—Compensatory eye movements of Dutch belted rabbits were measured with the search coil technique during small (<1°) sinusoidal horizontal rotations at frequencies ranging from 0.063 to 11.5 Hz. Oscilloctometer compensation was substantial but not perfect. Gain ranged from 0.2 to 0.6 in the dark and from 0.4 to 0.8 in the light. This means that retinal image motion is considerable even when head movements are minimal. Also, gains obtained with small rotations were lower than those obtained with large rotations—a result which suggests that the oscillometer system adjusts gain so that retinal image motion is sufficient to prevent perceptual fading but not so great as to produce visual blurring.

INTRODUCTION

It is often suggested that the purpose of the small eye movements that occur during attempted fixation is to produce sufficient retinal image motion to prevent fading of the visual percept. This suggestion is based on the fact that stimuli, stabilized on the retina, disappear. However, recent measurements of retinal image motion during foveal fixation and body movement show that, at least in man, eye movements are not completely compensatory and thus retinal image motion is guaranteed in natural situations (Winterborn et al., 1975; Skavenski et al., 1975; Skavenski et al., 1972; Seiutum and Collewijn, 1974). These authors found that mean retinal image speeds of subjects sitting or standing quietly ranged from 20 to 40 min anscode, always greater than the mean retinal image speeds when the head was stabilized artificially on a headboard. Such image speeds occurred because oscilloptometer compensation to natural head movements was incomplete. The most effective oscilloptometer response to small forced rotations in these subjects ranged from 40% to 60%. In view of these results it seems unlikely that the small intralateral eye movements observed during the pursuit of a target in the dark is stabilized a safety margin from the loss of stability that may arise from extraneous pressures to destabilize the retinal image—at least in man.

It is impossible to compensate in animals that have evolved under different extraneous pressures than man. The rabbit, which is lateral eyed, herbivorous and prey to many predators, is a sufficiently distant relative of human beings to begin to answer this question. It was already known that oscilloptometer compensation to large and low frequency rotations was far from perfect in the rabbit, i.e. Baarsma and Collewijn (1974) reported gains from 0.5 to 0.8 for oscilloptometer compensation to rotation in the light.

These values are sufficiently far from 1.0 to guarantee perceptual retinal image motion. What had been left unreported was compensation for very small and high frequency rotations likely to occur when the rabbit is sitting quietly or in the "freeze" position—natural activities that might lead to better compensation and, therefore, relative stabilization of the retinal image. The results we report explore this region and show that compensation is incomplete which means that, in the rabbit, as in man, the retinal image will move even when the motion of the head and body are minimal.

METHODS

Horizontal eye rotations of 6 young adult Dutch belted rabbits were measured with the magnetic field search coil technique (Rockstein, 1963). The peak-to-peak movement range of the eye movement recording was 0°. Rabbits were rotated sinusoidally by suspending the body of the animal in a hammock in a torsion swing. The head was firmly bolted to the torsion swing with a dural acryl head plate. Three of these rabbits were sacrificed at high as well as low frequencies. In these animals additional search coil was attached to the skull by embedding it in the acrylic head plate to ensure that the head was not moving with respect to the torsion swing when high swing frequencies were used. The two coils generating the magnetic field were bolted firmly to the torsion swing so that eye position was measured with respect to the head. Rotation of the torsion swing was monitored with a high precision transducer. The torsion swing was rotated in such a way that could be modulated from 0.033 Hz to 11.7 Hz by either adding weight or by stopping the swing at each end. Noise by shaft spring.

Angular signals proportional to angular eye position, angular swing position, and angular head position were recorded on a Grass polygraph and on an IVM tape recorder. All analyses were based on the polygraph record. For high frequencies tape recorders were played back at a slower speed onto the polygraph which made it possible to measure phase to about 1° over the entire range of frequencies shied (see Figs. 1 and 10) and high frequency records. At small amplitudes and low frequencies the responses were often proportionally and slightly compared to the spontaneous swings that disturbed eye position in darkness (Collewijn, 1970). This led to some ambiguity as to whether points in the eye movement record should be selected to compute phase and gain.

Therefore, to all measurements of small amplitude low frequency responses a smooth curve was fitted through the eye...
movement record to approximate the fundamental frequency. The points of maximum and minimum excursion of the fitted curve were used to calculate phase and gain. Gain and phase were computed over successive half cycles for rotations selected to be within 10% of the following amplitudes: 30, 20, 15, 5, and 2.5° arc. Values reported for gain and phase are averages of at least 6 half-cycles (3 in each direction). Frequently, as many as 20 half-cycles (10 in each direction) were averaged for each rabbit. Measurement of ocularmotor compensation were made under two conditions: in total darkness in order to study the vestibulo-ocular response (VOR) alone and in the normally illuminated laboratory to assess the improvement in compensatory eye movements when vision was allowed.

RESULTS
Compensatory eye movements were observed in all rabbits over the entire frequency-amplitude range tested when the room was normally illuminated. In the light average gain ranged from 0.25 to 0.56 and phase error was less than 6° as can be seen in Fig. 2. The functions plotted in this figure are repre-

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Fig. 1. A: Typical compensatory eye movements (E) elicited by horizontal sinusoidal rotation at 0.68 Hz (S). Amplitude of rotation is 30° min arc. Time proceeds to the right. (B): Typical compensatory eye movements (E) elicited by high frequency (0.6 Hz) horizontal sinusoidal rotation (S). Amplitude of rotation is 30° min arc. The bottom most trace (H/C) represents head position with respect to field coils and torsion swing. Time proceeds to the right.

Fig. 2. Gain and phase in the light (A) and in the dark (B) of the compensatory eye movements to measure horizontal sinusoidal rotations. Each point represents the average value for 3 rabbits and 5 amplitudes: 2.5, 5.0, 10.0, 20.0 and 30.0° min arc. Thus 25 values were used for the computation of each mean. The error bars above and below each point show ± SE of the mean.
sensitive of performance for all amplitudes and rabbits. Note that gain was relatively low which means that there was considerable retinal image motion. This result is similar to the result obtained with large amplitude rotations (Ba骃tia and Collewijn, 1974). R豚ina image motion is appreciable when the rabbit moves very little; as well as when it moves a great deal. The vestibular contribution to ocularmotor compensation in the frequency-amplitude range examined in the present study was considerable. The VOR can account for somewhat more than half of the compensation. The contribution of visual input was also evident with respect to the phase of the response. Phase leads were substantia4 in the dark but negligible in the light. These results are comparable to those observed for large amplitude rotations for the same range of frequencies. The main difference is that gain, both in light and in the dark, were lower than gain observed with large amplitude (> 1°) rotations (Ba骃tia and Collewijn, 1974).

Compensatory ocularmotor response to high frequencies is summarized in Fig. 3. The data shown for the low frequencies (< 1 Hz) in this figure are the values obtained for the three animals whose high frequency responses were measured. Once again, these average functions are representative of all amplitudes and rabbits. For frequencies below 4 Hz compensa-

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**Fig. 3.** Gain and phase in the light (A) and in the dark (B) of compensatory eye movements to miniature horizontal sinusoidal rotations. Each point represents the average value for 3 rabbits and 5 amplitudes: 2.5, 5.0, 10.0, 20.0 and 30.0 min arc. Ten values were used for the computation of each mean. The error bars show ±SE of the mean above and below some means, however, for graphic simplicity some are shown only above or below.

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**Fig. 4.** Amplitude (in min arc) of sinusoidal eye angular position (Eye Amplitude) during sinusoidal horizontal rotations as a function of amplitude in min arc of rotatory (Swing Amplitude) for three frequencies of oscillation: 0.08 Hz (A), 0.44 Hz (B) and 0.23 Hz (C). Each point represents values averaged over 3 rabbits.
tory eye movements in the light and in the dark showed gain and phase characteristics similar to those described above (see Fig. 1) for the 5 rabbits which served in the low frequency small amplitude experiments and were also similar to the compensatory eye movements to large amplitudes studied by Baarsma and Colliewijn (1978). At high frequencies (＞ 4 Hz), however, the improvement of compensation due to the presence of visual input disappeared. There was no difference either in gain or in phase between perform inance to slit light and in the dark. This result was expected because the optokinetic reflex, which provides assistance to the vestibuloocular response at low frequencies, responds poorly or not at all when retinal image frequency becomes high (Colliewijn, 1969). This situation in the rabbit is similar to that found in primates (Skavenski et al., 1979; Bessin, 1970; Skavenski and Robinson, 1973).

In summary, the rabbit's compensatory ocularmotor responses to small rotations is consistent with the rabbit's response to large rotations. The only difference observed was that gain was lower when the amplitude of rotation is less than 1°. The degree of agreement between the present study of small rotations with prior research on large rotations can be illustrated by consideration of the amplitude threshold of the vestibulo-ocular response. Baarsma and Colliewijn (1974) argued that there was no threshold for this response because the functions of amplitudes of eye movement to amplitudes of swing rotation, when extrapolated below 1° of swing amplitude appeared to have an intercept of near zero (see their Fig. 3). We supported this argument by plotting similar functions for our small amplitudes rotations. These functions tended toward zero rotation amplitude. Indeed, linear regression functions fitted to these data have intercepts very near zero ranging between 0.5 to 1.1° of eye amplitude (see our Fig. 4). Note that the swing amplitude intercepts are not only close to zero, but they are negative, as well, which clearly is opposite to an intercept expected if there were a threshold.

**Discussion**

Oculomotor compensation to small amplitude and high frequency visual stimuli is substantial, but far from perfect in the rabbit. Compensation provided by the vestibulo-ocular response alone was quite poor—average gains obtained in darkness ranged from 0.2 to 0.4. Compensation was somewhat better when visual input was provided—gains obtained in the light ranged from 0.2 to 0.6. Such incomplete compensation means that there was considerable reso-nidual retinal image motion. For example, when head rotation had an amplitude of 30° arc, average peak retinal image speed ranged from 18 arcsec at 0.32 Hz to 94 arcsec at 3.2 Hz. Average retinal image speeds under these conditions ranged from 1.5 to 5.5 arcsec at 40 arcsec. At higher frequencies, with rotations of the same amplitude, retinal image speed was considerably higher. 6.4 arcsec at 3.8 Hz to 22 arcsec at 11.6 Hz, which is sufficient to generate a substantial retinal image motion when the rabbit rotates through small angles.

This conclusion is at variance with a prior report by one of us in which it was concluded that the eye was stable with respect to space in a freely moving rabbit (Colliewijn, 1977). Note, however, this conclusion was based on relatively low resolution records needed to register the very large saccadic eye movements typical of freely moving rabbits. The discrepancy between our conclusion and the prior one can be resolved by a close inspection of the published records where intersaccadic slow eye movements ranging from 1 sec to 14 sec can be found (see Figs. 6, 9 and 11 in Colliewijn, 1977). So, the conclusion in the prior report was a false assumption. The eye was "stable" when the head was moving but a close inspection provided by the present results reveals that the eye was not completely stable. The retinal image was, in fact, moving appreciably.

Our results with the rabbit are consistent with what is already known about retinal image motion in the human in two respects. First, oculomotor compensation of head rotations is not perfect and, therefore, retinal image motion can be considerable. Second, our data lends us to conclude with a suggestion made by Skavenski et al. (1979) that the oculomotor compensatory machinery may adjust gain so as to maintain optimal retinal image motion. This hypothesis was offered when it was found in humans that the gain of compensatory eye movements was relatively low when head movements had a small amplitude and was higher when the head moved through larger angles. For example, one of the subjects in their report was rotated at amplitudes greater than 3 deg arc. Gain was found to be 0.8 in the dark as compared to 0.6 when amplitude was less than 0.25 deg arc. In the light, gain jumped to 0.95 for large amplitudes as compared to 0.6 for small amplitudes. The situation is similar in the rabbit. Gains obtained for small rotations were lower, both in the dark and in the light, than with large rotations (Baarsma and Colliewijn, 1974). For amplitudes of 30 arc deg and less, gains in the dark ranged from 0.2 to 0.4 and from 0.6 to 0.6 in the light. Baarsma and Colliewijn (1974), who had previously determined that the range from 25° to 30° gained in the dark to be 0.4 to 5.6° and 0.7° in the light. These differences in gain in the rabbit parallel differences observed in man (Skaveski, et al., 1979)—a result which supports the concept of the rabbit as a model that allows changes in gain to be evaluated in this respect...
Compensatory eye movements in the rabbit


