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

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Abstract—Compensatory eye movements of Dutch belted rabbits were measured with the search coil technique during small ($< 1°$/arc) sinusoidal horizontal rotations at frequencies ranging from 0.063 to 11.5 Hz. Oculomotor compensation was substantial but not perfect. Gain ranged from 0.2 to 0.4 in the dark and from 0.4 to 0.6 in the light. This means that retinal image motion is considerable even when head movements are minuscule. Also, gains obtained with small rotations were lower than those obtained with large rotations—a result which suggests that the oculomotor system adjusts gain so that retinal image motion is sufficient to prevent perceptual fading yet 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 natural head and body motion show that, at least in man, eye movements are not completely compensatory and thus retinal image motion is guaranteed in natural situations (Winterson *et al.*, 1975; Skavenski *et al.*, 1975; Skavenski *et al.*, 1979; Steinman and Collewijn, 1978). These authors found that mean retinal image speeds of subjects sitting or standing quietly ranged from 20 to 40 min arc/sec, always greater than the mean retinal image speeds when the head was stabilized artificially on a biteboard. Such image speeds occurred because oculomotor compensation to natural head movements was incomplete. The most effective oculomotor response to small forced rotations in these subjects ranged from 40% to 90%. In view of these results it seems unlikely that the small fixational eye movements observed while the head is stabilized artificially arose from evolutionary pressures to destabilize the retinal image—at least in man.

Is compensation also incomplete in animals that have evolved under different evolutionary pressures than man? The rabbit, which is lateral eyed, herbivorous and prey to many predators, is a sufficiently distant relative to human beings to begin to answer this question. It was already known that oculomotor compensation to large and low frequency rotation was far from perfect in the rabbit, i.e. Baarsma and Collewijn (1974) reported gains from 0.5 to 0.8 for oculomotor compensation to rotation in the light. These values are sufficiently far from 1.0 to guarantee appreciable retinal image motion. What had been left unexplored 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 motions of the head and body are minuscule.

METHODS

Horizontal eye rotations of 8 young adult Dutch belted rabbits were measured with the magnetic field search coil technique (Robinson, 1963). The peak-to-peak noise level of the eye movement recording was 18″ arc. 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 dental acrylic head plate. Three of these rabbits were oscillated at high, as well as low, frequencies. In these animals an additional search coil was attached to the skull by imbedding 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's natural frequency could be modulated from 0.063 Hz to 11.7 Hz by either adding weight or by coupling the swing to an earth-fixed frame by stiff springs.

Analog signals proportional to angular eye position, angular swing position, and angular head position were recorded on a Grass polygraph and also on an FM tape recorder. All analyses were based on the polygraph records. For high frequencies tape recordings 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 studied (see Figs 1A and 1B for low and high frequency records). At small amplitudes and low frequencies the compensatory response was often proportionately small compared to the spontaneous eye drifts that disturb eye position in darkness (Collewijn, 1970). This led to some ambiguity as to which points in the eye movement record should be selected to compute phase and gain. Therefore, in all measurements of small amplitude low frequency responses a smooth curve was fit through the eye
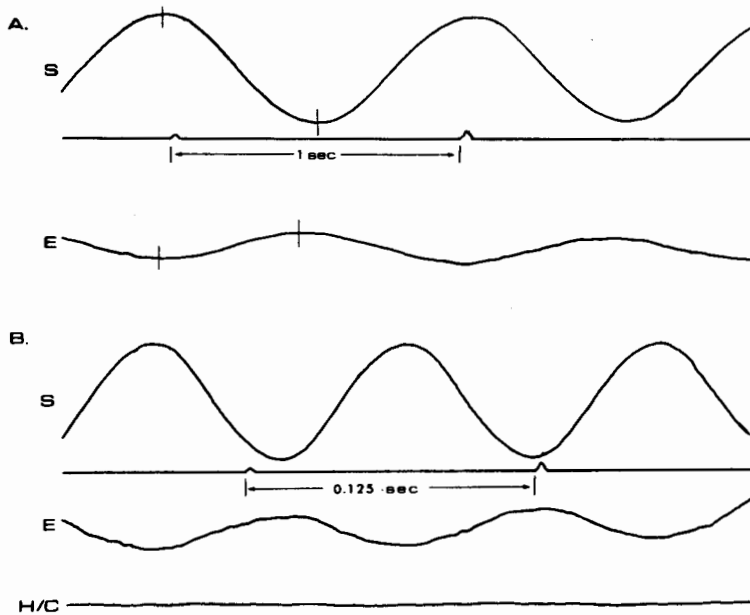
Fig. 1. A: Typical compensatory eye movements (E) elicited by horizontal sinusoidal rotation at 0.88 Hz (S). Amplitude of rotation is 30 min arc. Time proceeds to the right. (B): Typical compensatory eye movements (E) elicited by high frequency (9 Hz) horizontal sinusoidal rotations (S). Amplitude of 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.

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, 10, 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. Measurements of oculomotor compensation were made under two conditions: in total darkness in order to study the vestibulo–ocular response (VOR) alone and in the normally illu-minated 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-
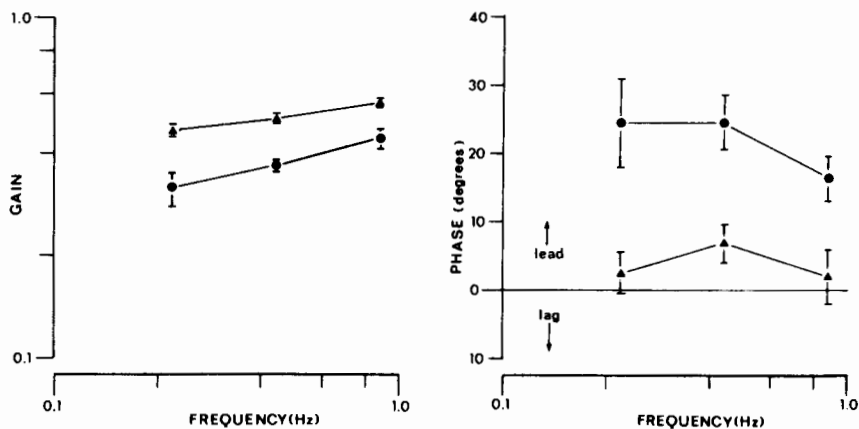

Fig. 2. Gain and phase in the light (▲) and in the dark (●) of the compensatory eye movements to miniature horizontal sinusoidal rotations. Each point represents the average value for 5 rabbits and 5 amplitudes: 2.5, 5.0, 10.0, 20.0 and 30.0 min arc. Thus 25 values were used for the computation of each mean. The error bars above and below each point show 1 SE of the mean.
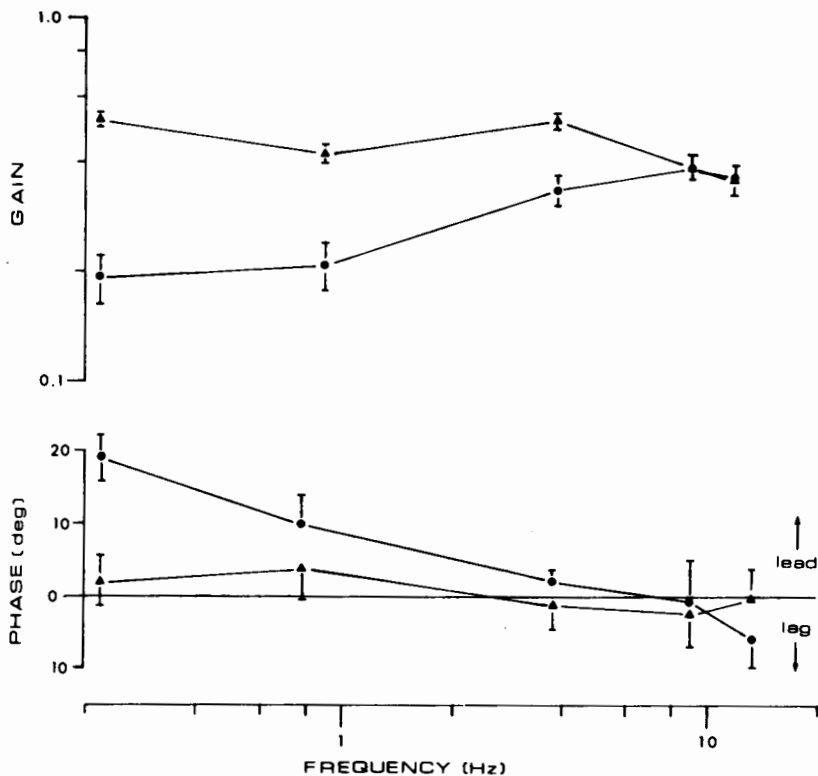
Fig. 3. Gain and phase in the light (▲) and in the dark (●) of compensatory eye movements to miniature horizontal sinusoidal rotations. Each point represents the average value for 3 rabbits and 5 amplitudes: 2.5, 5.0, 10.0, 20.0 and 30.0 min arc. Thus 15 values were used for the computation of each mean. The error bars show 1 SE of the mean above and below some means, however, for graphic simplicity some are shown only above or below.

sentative 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 (Baarsma and Collewijn, 1974). Retinal image motion is appreciable when the rabbit moves very little as well as when it moves a great deal. The vestibular contribution to oculomotor 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 substantial 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 gains observed with large amplitude (> 1°) rotations (Baarsma and Collewijn, 1974).

Compensatory oculomotor 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-
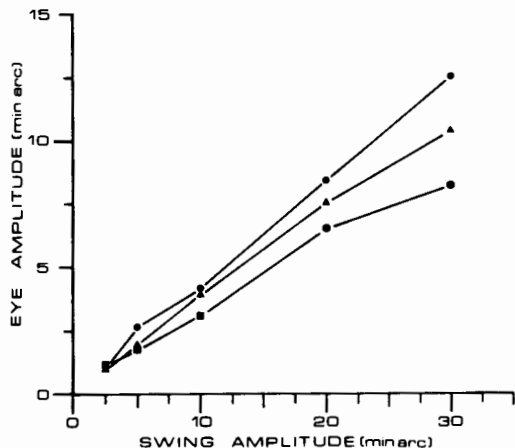

Fig. 4. Amplitude (in min arc) of sinusoidal eye angular position (Eye Amplitude) elicited during sinusoidal horizontal rotations as a function of amplitude in min arc of rotation (Swing Amplitude) for three frequencies of oscillation: 0.88 Hz (●), 0.44 Hz (▲), and 0.22 Hz (■). Each point represents values averaged over 5 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 who served in the low frequency small amplitude experiment and were also similar to the compensatory eye movements to large amplitudes studied by Baarsma and Collewijn (1974). 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 performance in the light and in the dark. This result was expected because the optokinetic reflex, which provides assistance to the vestibulo-cular response at low frequencies, responds poorly or not at all when retinal image frequency becomes high (Collewijn, 1969). This situation in the rabbit is similar to that found in primates (Skavenski et al., 1979; Benson, 1970; Skavenski and Robinson, 1973).

In summary, the rabbit's compensatory oculomotor 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 Collewijn (1974) argued that there was no threshold for this response because the functions of amplitude of eye rotation to amplitude 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 amplitude rotations. These functions tended toward zero rotation amplitude. Indeed, linear regression functions fitted to these data have intercepts very near zero ranging between 0.52 to 1.1' arc 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 sinusoidal rotations 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 0.4 to 0.6. Such incomplete compensation means that there was considerable residual retinal image motion. For example when head rotation had an amplitude of 30' arc, average peak retinal image speed ranged from 18' arc/sec at 0.22 Hz to 88' arc/sec at 0.88 Hz. Average retinal image speed under these conditions ranged from 11' arc/sec to 55' arc/sec. At higher frequencies, with rotations of the same amplitude, retinal image speed was considerably higher: 6.4° arc/sec at 3.8 Hz to 22° arc/sec at 11.7 Hz. We conclude that there is considerable 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 (Collewijn, 1977). Note, however, this conclusion was based on relatively low resolution recordings 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 movement speeds ranging from 1°/sec to 14°/sec can be found (see Figs 6, 9 and 11 in Collewijn, 1977). So, the conclusion in the prior report was a first approximation. The eye was "stable" when the head was moving but a close inspection provoked 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 leads us to concur with a suggestion made by Skavenski et al. (1979) that the oculomotor conpensatory 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 0.67 when amplitude was less than 0.25 deg arc. In the light, gain jumped to 0.95 for large amplitudes as compared to 0.80 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 Collewijn, 1974). For amplitudes of 30' arc and less, gains in the dark ranged from 0.2 to 0.4 and from 0.4 to 0.6 in the light. Baarsma and Collewijn (1974), who used amplitudes of rotation which ranged from 1 to 25°, found gains in the dark to be 0.4 to 0.6 and 0.7 to 0.9 in the light. These differences in gain in the rabbit parallel differences observed in man (Skavenski, et al., 1979)—a result which supports the contention of these authors that such changes in gain have functional significance—namely, gain of the oculomotor response is adjusted to the amplitude of head rotations so that retinal image speed is kept at some optimal value. The value is optimal because it guarantees image speeds sufficiently high to prevent perceptual fading but sufficiently low to prevent blurring of visual objects.

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