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THE EFFECT OF LUMINANCE ON HUMAN SMOOTH PURSUIT OF PERIFOVEAL AND FOVEAL TARGETS[1]

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Abstract—Two subjects tracked targets located in the perifovea (6° below the line of sight) while oculomotor performance was recorded with an infrared contact lens optical lever. A point target was either 1.85 log units above absolute foveal threshold (photopic) or 0.5 log units above absolute scotopic threshold. Transfer characteristics of smooth pursuit of sinusoidal motion (amplitude = 2.18°, frequency = 0.13–5.00 Hz) were measured.

It was found that (1) eccentric smooth pursuit is easily accomplished with no practice, (2) smooth pursuit characteristics were largely uninfluenced by target luminance, (3) the phase of smooth pursuit showed greater lag with the scotopic target than with photopic target, and (4) predictive tracking occurs in the perifoveal retina. Similar results were obtained in the fovea where overall smooth pursuit gain was higher but, once again, large variations in luminance did not have systematic or large effects on smooth pursuit gain.

INTRODUCTION

The oculomotor system, unlike the visual system, has been shown to be largely independent of stimulus parameters in the sense that the ability to maintain eye position is influenced little by conditions of stimulation that cause the visual world to have very different appearances. For example, the line of sight can be maintained within or at the edges of a variety of forms as well as it can be maintained by a single visual detail (Murphy, Haddad and Steinman, 1974). The size of a foveal fixation stimulus also has trivial effects on control of the line of sight (Steinman, 1965; Rattle, 1969), as does spectral distribution and luminance above foveal threshold (Steinman, 1965; Boyce, 1967).

However, oculomotor control can be affected when luminance of the stimulus falls into the scotopic range. Subjects attempting to maintain the position of a target below foveal threshold on extra-foveal retina where it was visible would invariably show a maladaptive and stereotyped eye movement pattern which brought the stimulus image onto the fovea where it would disappear. A photopic stimulus with a luminance that made its appearance and disappearance as equally likely as that of the scotopic stimulus did not elicit this stereotyped and counter-productive eye movement pattern even when it fell on the same parts of extra-foveal retina (Steinman and Cunitz, 1968). This difference in oculomotor control suggested the possibility that oculomotor performance under scotopic conditions might be profoundly different than under photopic conditions.

This intriguing possibility found further support in a study which had reported that smooth pursuit could be particularly vulnerable to the effects of luminance (Wheeless, Cohen and Boynton, 1967). This control system analysis in which luminance was varied from low scotopic to moderate photopic levels showed systematic influences of target luminance on smooth pursuit performance. Overall gain decreased as the luminance of the tracking target decreased. More interestingly, the high frequency cut-offs of the gain transfer functions obtained when target luminance was scotopic were lower than when the target luminance was photopic. These data also suggested a fundamental difference between photopic and scotopic oculomotor control. But the luminance conditions of this study were confounded by another factor. The tracking target was not equally visible to the subjects under all conditions. When the target luminance was scotopic, and thus below foveal threshold, the target was invisible at least part, if not all, of the time the subjects were attempting to track.

Therefore, we decided to re-examine the effect of luminance on smooth pursuit in the present experiments in such a way that the target was always clearly visible during smooth pursuit. This was accomplished by presenting photopically effective and scotopically effective targets on perifoveal retina where both cone and rod receptors are numerous (Polyak, 1941, p. 213). Presenting targets on the perifoveal retina allows the target to be visible when its luminance is very low as well as when its luminance is high.

We found that (1) sinusoidal tracking was easily accomplished without special effort or practice with targets moving outside of the fovea, (2) overall characteristics of smooth pursuit of sinusoidal target motion of different frequencies was largely unaffected by the luminance of the target, (3) smooth pursuit gain at all frequencies at all luminances was less than 1, (4) luminance affected the lag of smooth pursuit—lag was greater with scotopic targets, and (5) both subjects showed predictive smooth pursuit at certain frequencies. We were therefore forced to abandon the

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notion that there were fundamental differences between photopic and scotopic smooth pursuit.

Having found that luminance did not have powerful or systematic effects on smooth pursuit gain in the perifovea, where this variable could be manipulated over a wide range, the measurements were repeated with foveally presented targets with the same result, namely: (1) overall characteristics of smooth pursuit were unaffected by more than a 10-fold variation in luminance—this was true even when overall system response was measured, i.e. saccades were not eliminated before analysis, (2) lag tended to be greater with low luminance targets, and (3) predictive smooth pusuit was observed. It was also found, as might be expected, that overall smooth pursuit gain was higher in the fovea than in the perifovea.

METHODS

Conditions of stimulation

The target. The tracking target was a "green" oscilloscope point (Tk model 503, P-1 phosphor) situated 1.3 m from the subject's right eye (left eye was covered and closed). The luminance of this target was adjusted by inserting neutral density filters in the optical path. For most of the experiments two luminances were used. One was moderately high in the photopic range (1.85 log units above absolute foveal threshold) where it appeared as a focused green point. The other was low in the scotopic range. It was adjusted to be 0.5 log units above absolute scotopic threshold where it appeared in an achromatic blurred mass surrounded by *rayons*. The target, at both luminance levels, was presented 6° below the subject's line of sight when he fixated a photopically effective pre-trial red point-target. Thresholds were measured with the target stationary.

Rationale for target placement. Both rod and cone receptors are well represented in this part of the perifovea (Polyak, 1941) and important scotopic visual functions are best in this region. For example, Gordon (1947) reports that scotopic visual acuity is lowest (MAR = 36 arc min) as is movement threshold (50'/sec) in a region 5–7° away from the preferred foveal fixation locus. The target was placed below the line of sight so as to fall above the fovea because visual reaction times are shorter here than elsewhere on extrafoveal retina, again minimizing the effects of eccentric target placement (Woodworth, 1937, pp. 327–328).

Target motions. Sinusoidal target motions were produced by a signal generator whose output was applied to the x-axis of the oscilloscope. Their frequencies ranged from 0.13 to 5.00 Hz with amplitude set at 2.18°. Each target motion was tracked for 20 sec. These frequencies of sinusoidal motions were chosen on the basis of human oculomotor system response observed in prior investigations. Their amplitude was chosen so as to be comparable to the amplitude used in the only prior experiment on low luminance tracking, permitting comparison of the present with prior results.

Recording of eye motions

Two-dimensional eye movements were recorded by an infrared electronic contact lens optical lever device (Haddad and Steinman, 1973). The noise level of the instrument, as used in the present experiments, was less than 10 arc sec. Voltage analogs proportional to vertical and horizontal eye position, proportional to stimulus position, and a trial marker were recorded on a Tandberg model 100 FM tape recorder and subsequently computer analyzed.

Experimental protocol

Two experienced eye movement subjects—the authors—performed in the experiment. Neither had prior experience with eccentric tracking. They dark adapted for 30 min prior to each recording session and inserted their contact lenses as rapidly as possible in the dimmest suitable illumination. They continued dark adapting for 5 min before data were collected. Each recording session began with photopically effective targets. Recording with such targets was followed by trials with scotopic targets. Half of the data with photopic targets was obtained at the beginning of each recording session. The other half of the photopic data were obtained at the end of each session—after all scotopic recordings had been made. Systematic changes in performance were not observed within experimental sessions nor were there any obvious day-to-day variations. There were no practice sessions. The stimulus thresholds were measured and the recording system aligned in a single session. Formal data collection began the next day.

At the beginning of each trial the subjects fixated a red point of light and noticed a small green point or a large whitish mass moving horizontally below the line of sight. When the subject felt ready to track the moving target, he started the trial at which time the red fixation light disappeared and the subject smoothly pursued the eccentric target while maintaining its vertical position. Saccades were used to correct vertical drifts towards or away from the moving target as horizontal pursuit continued.

The reader, like the authors, may suspect that such demands are infrequently made upon the oculomotor machinery in everyday life. Eccentric smooth pursuit was, however, easily achieved and required no practice whatsoever. This is illustrated in Fig. 1, where the very first attempt at eccentric sinusoidal tracking is reproduced for the less experienced oculomotorist.

Data reduction and analyses

General. The tape-recorded stimulus and eye position analog voltages were digitized, after all of the data were collected, by a 12-bit A/D converter controlled by a minicomputer (Nova 2/10). Average eye and average stimulus position samples were obtained every 10 msec. These averages were based on four samples obtained for each of the three variables (horizontal eye, vertical eye and stimulus position) within the same millisecond. Only horizontal eye and stimulus position averages were stored. The vertical eye position was used only to determine whether the horizontal eye and stimulus position data were suitable for further analysis. Horizontal eye and stimulus position data were accepted only when vertical eye position showed that the target was in the region 5° to 7° below the line of sight. About 90% of the horizontal eye and stimulus position data were acceptable by this criterion—both subjects were generally successful in maintaining the target at the appropriate distance from the preferred foveal fixation locus. Most discarded data were caused by blinks.

Saccade removal during smooth pursuit. Saccades were detected by an acceleration criterion. Detected saccades were removed and replaced by the average eye velocity observed in the period preceding and following the saccade. This technique assumes that if the saccade had not occurred the eye would have continued to smoothly pursue. This technique was successful, as can be seen in Fig. 1 which shows a saccade-free reconstruction along with its original eye movement record. All computer analyses were verified in this manner—saccade-free reconstructions were plotted for all digitized eye movement records.

Next, the peaks and troughs in the eye and stimulus data were located by finding those times where average velocity of the stimulus and the saccade-free reconstruction of eye position fell to zero. All such times were marked with pointers on the stimulus and eye position records. Generally, the algorithm proved effective, as can be seen

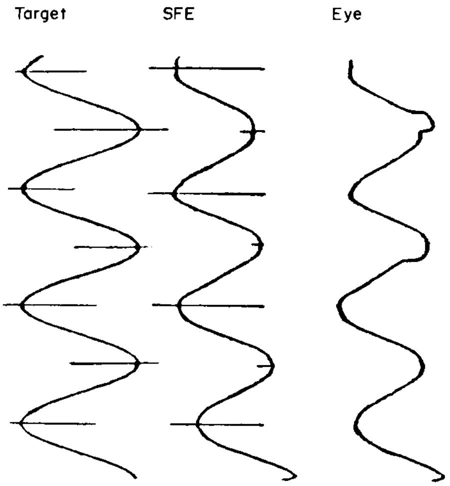

Fig. 1. An analog record of subject BW's first attempt at smooth pursuit of a target moving sinusoidally (frequency = 0.26 Hz, amplitude = 2.18°) in her perifovea. Target luminance was 0.5 log units above absolute scotopic threshold. The complete horizontal eye movement pattern is shown on the right. The horizontal stimulus pattern is shown on the left. The center trace (SFE) shows the smooth pursuit eye movement pattern after saccades had been removed. The horizontal lines show when the computer algorithm located a peak and a trough in the target and saccade-free eye movement data. The record begins at the bottom and the target and eye traces are written with the same scale factor.

in Fig. 1. Successfully detected peaks and troughs were subsequently used to compute the phase and gain of the eye's response over each half-cycle of the sinusoid.[3]

OBSERVATIONS

Smooth pursuit of sinusoidal target motions

Subjects tracked sinusoidal target displacement (amplitude = 2.18°) with frequencies ranging from 0.13 to 5.00 Hz. Tracking trials were initiated by the subject and lasted for 20 sec. Only data obtained when the stimuli fell between 5° and 7° from the line of sight were analyzed.

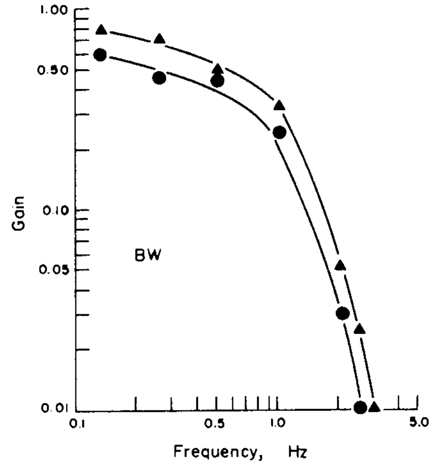

Fig. 2. Subject BW's smooth pursuit gain as a function of the frequency of sinusoidally moving targets. The photopic target (1.85 log units above absolute foveal threshold) is shown by triangles and the scotopic target (0.5 log units above absolute scotopic threshold) is shown by circles.

Large differences in luminance had only modest effects on smooth pursuit. Furthermore, the effect of luminance was not only small, it was different in each subject. These results are summarized in Figs 2 and 3. BW pursued photopic targets better than she pursued scotopic targets. This was true with respect to gain and corner frequency. RS was better with scotopic targets. The effects of luminance in both subjects, however, were small. For example, maximum gains differed by only 0.23 for BW and by only 0.17 for RS. Corner frequencies were similar at photopic and scotopic luminances for both subjects (BW: photopic = 1.3 Hz; scotopic = 1.2 Hz; RS: photopic = 0.37 Hz; scotopic = 0.45 Hz). Corner frequency was estimated by finding the intersection of the asymptote of the high frequency portion of the function with the horizontal axis where gain is equal to 1.

Figure 4 shows additional measurements of luminance on smooth pursuit in an experiment that examined this parameter systematically. Subjects tracked 0.26 Hz sinusoidal target motion with targets whose luminance fell in the range whose extremes are shown in Figs 2 and 3. Again, BW pursues more briskly at higher luminances and her response falls off in an orderly manner as target luminance is

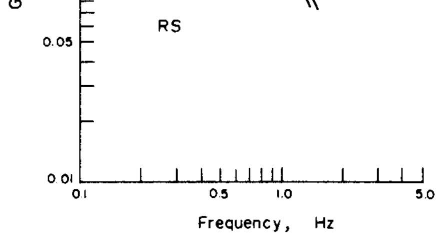

Fig. 3. Subject RS's smooth pursuit gain as a function of the frequency of sinusoidally moving targets. The photopic target (1.85 log units above absolute foveal threshold) is shown by triangles and the scotopic target (0.5 log units above absolute scotopic threshold) is shown by circles.

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[3] The choice of systems analysis for the present experiments was dictated primarily by the desire to examine the effects of luminance on tracking with a method that would permit comparisons with the prior study (Wheeless *et al.*, 1967). It has been known since this method was first employed in studies of the oculomotor system that the behavior of the oculomotor system is non-linear. This limitation, however, did not seem to preclude its use to measure the influence of luminance on smooth pursuit because the present experiments, like those of Wheeless *et al.*, will not attempt to model details of the control system.

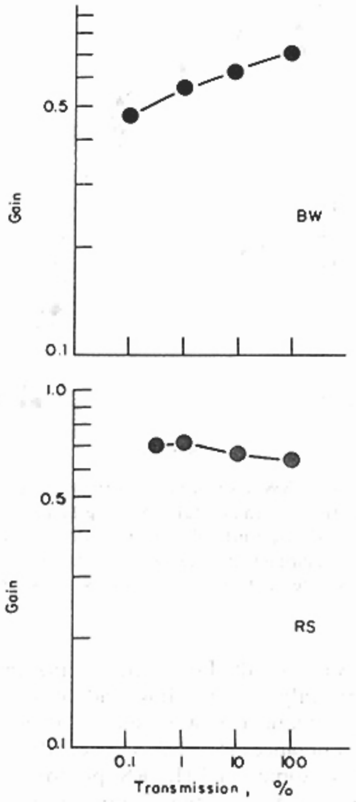

Fig. 4. Smooth pursuit gain of subject BW (top graph) and RS (bottom graph) as a function of luminance while tracking a 0.26 Hz sinusoidal target motion. Luminance is shown as filter transmission.

reduced. Note, however, that the 1000-fold reduction in luminance resulted in only a 35% reduction in gain for this subject. A 300-fold reduction in target luminance led to a 15% increase in gain for subject RS.

Luminance, however, had a systematic effect on phase, as is shown in Fig. 5. Both subjects' scotopic smooth pursuits lagged their photopic smooth pursuits. Also note that both subjects showed "predictive tracking", i.e. the smooth pursuit led the stimulus at one photopic frequency (0.25 Hz) for BW and for frequencies 0.5 Hz and below under both luminance conditions for RS. Such predictive tracking has been reported a number of times for single sine-waves (Drischel, 1958; Sünderhauf, 1960; Stark, Vossius and Young, 1962; Bornemann, Drischel and Niedergesäss, 1964).

Comparison of the present experiment with Wheeless et al. (1967)

The present results differ from those of Wheeless *et al.* (1967) in two respects. First, under both luminance conditions overall gain in the prior report was higher than those obtained in our measurements. This difference was not unexpected and, as we shall see, is probably due to the difference between foveal and perifoveal tracking. The other difference between our results and those of the prior report was that the magnitude of the effect of luminance on smooth pursuit gain was surprisingly small when compared to that of Wheeless *et al.* (1967). For example, when luminance was varied over 1000-fold for the subject that showed detrimental effect of luminance (BW), the change in gain at 0.5 Hz was only a factor of 0.10 whereas the prior report found gain at the same frequency reduced from 1 to almost half (0.56) when target luminance was reduced only by a factor of 180. Not only was the magnitude of the effect of luminance much smaller than in the report of Wheeless *et al.*, but there was a qualitative difference as well. They report a systematic influence of luminance on tracking performance whereas our subjects showed opposite effects. The subject whose maximum gain was highest in the present experiment (see Fig. 3) showed this gain with a scotopic target. In general, his scotopic gains were higher than his photopic gains when luminance was varied systematically (see Fig. 5). RS's gain went up as luminance went down!

Implications

Smooth pursuit is not only a foveal function. It is popular to describe smooth pursuit as the foveal fixation of a smoothly moving target (Robinson, 1976). This description is reasonable because humans and other foveate animals will use saccades to bring the image of the moving target to the fovea and then proceed to pursue. Foveate animals prefer to look directly at objects while they follow them about in visual space. The present experiments show that such typical performance is a preference and is not the result of a deficiency in the oculomotor machinery. Targets moving outside of the fovea provide effective input for smooth pursuit (maximum gain, BW photopic = 0.79, scotopic = 0.61; RS photopic = 0.76, scotopic = 0.92).

What is the functional significance of extrafoveal smooth pursuit? Extrafoveal tracking has, in higher primates, at least one obvious function. It permits oculomotoring under scotopic conditions when the

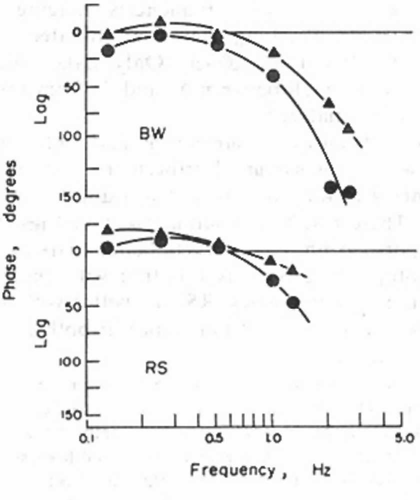

Fig. 5. Phase as a function of frequency for subject BW (top graph) and subject RS (bottom graph) while smoothly pursuing photopic (triangles) and scotopic (circles) sinusoidal target motions. Lags of the eye are represented by values below the horizontal line (zero) in each graph and leads of the eye by values above zero.

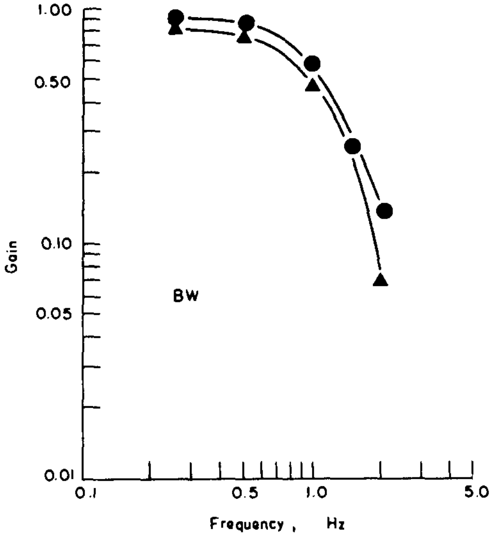

Fig. 6. Subject BW's smooth pursuit gain as a function of the frequency of sinusoidally moving targets tracked with the fovea. The subject was instructed to smoothly pursue the target as best she could. High luminance performance is shown by triangles, low luminance performance is shown by circles.

fovea is unable to see. Such needs have become less pressing in recent years, for humans at least, since artificial sources of illumination have come into widespread use. But man, through most of his evolutionary development, has been forced to use his peripheral oculomotor skills to move about at night. Perhaps, then, it is not surprising that unpracticed subject could demonstrate such capacity when first asked to do so. The demonstration of effective extrafoveal smooth pursuit raises the question of how good such pursuit could become with practice, particularly under pressure by damage to the fovea or its central projections. The present results suggest an optimistic outcome.

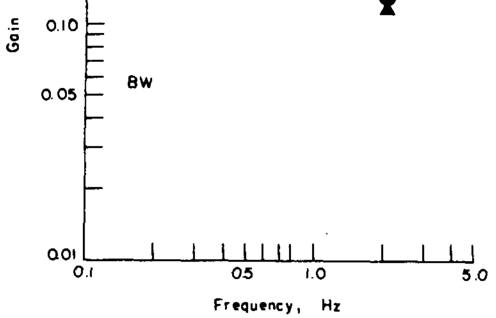

Fig. 7. Subject BW's smooth pursuit gain as a function of the frequency of sinusoidally moving targets tracked with the fovea. The subject was instructed to use saccades freely to allow no fixation error while tracking the target. High luminance performance is shown by triangles, low luminance performance is shown by circles.

The failure to find large effects of luminance on smooth pursuit gain in the perifovea encouraged us to re-examine the effects of luminance on foveal tracking as reported by Wheeless *et al.* (1967).

Smooth pursuit of sinusoidal target motions in the fovea

The perifoveal experiment was repeated with only two differences. First, the moving target was fixated and its luminance set near (0.5 log units) or well above (1.5 log units for BW and 2 log units for RS) absolute foveal threshold. Second, subjects were asked to use two different tracking strategies. They were encouraged in half of the trials to smoothly pursue as well as they could and in the other half of the trials they were encouraged to use saccades as frequently as possible to keep the line of sight dead on target. Such differences in instructions have been shown to affect tracking performance (Puckett and Steinman, 1969). They were given these instructions to encourage the best possible performance.

Luminance did not have large or systematic effect on tracking gain under either instruction. This result is summarized in Figs 6–9. RS showed no effects of luminance and BW tended to track better when the foveal target was near absolute threshold than when it was very mich brighter. Foveal gain was higher than gain in the perifovea, as might be expected. There was an effect of luminance on phase where, although not as dramatic, lower luminance targets tended to produce greater lags (see Figs 10 and 11). Predictive tracking was observed at both luminance levels in the fovea in both subjects. In the perifovea

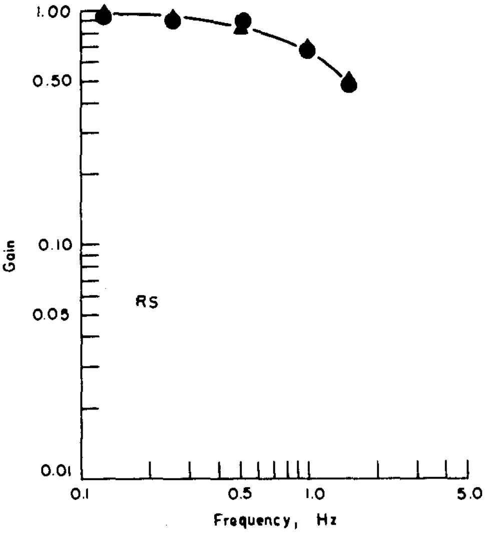

Fig. 8. Subject RS's smooth pursuit gain as a function of the frequency of sinusoidally moving targets tracked with the fovea. The subject was instructed to smoothly pursue the target as best he could. High luminance performance is shown by triangles, low luminance performance is shown by circles. Data were obtained for both luminances. A single function was fitted because of the almost complete overlap of the data points.

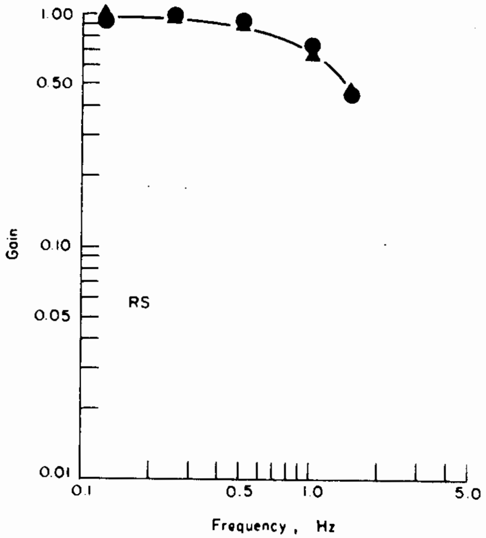

Fig. 9. Subject RS's smooth pursuit gain as a function of the frequency of sinusoidally moving targets with the fovea. The subject was instructed to use saccades freely to allow no fixation error while tracking the target. High luminance performance is shown by triangles, low luminance performance is shown by circles. Data were obtained for both luminances. A single function was fitted because of the almost complete overlap of the data points.

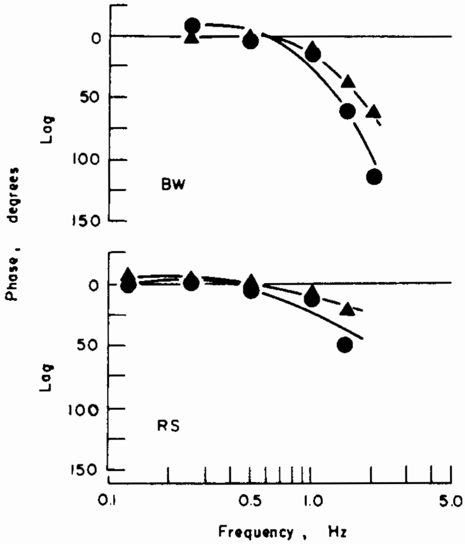

Fig. 10. Phase as a function of frequency for subject BW (top graph) and subject RS (bottom graph) while smoothly pursuing high luminance (triangles) and low luminance (circles) sinusoidal target motions tracked with the fovea. Subjects were instructed to smoothly pursue as best they could. Lags of the eye are represented by values below the horizontal line (zero) in each graph and leads of the eye by values above zero.

BW only predicted with the photopic target—RS with both targets (see Fig. 6).

The failure to find an effect of luminance on smooth pursuit gain was a general oculomotor characteristic. It was true of "overall system gain" as well as of smooth pursuit gain.[4] In this analysis saccades were not removed and gains were computed from those trials in which the subject had been instructed to keep the line of sight dead on target using saccades as frequently as possible. The analysis of "overall system response" did not suggest that luminance had large or systematic effect. For example, BW's mean gains at 0.5 Hz were: high luminance = 1.05, low luminance = 1.09; at 1.0 Hz: high luminance = 0.76, low luminance = 0.88. RS's means gains at 0.5 Hz were: high luminance = 0.89, low luminance = 0.95; at 1.0 Hz: high luminance = 0.83, low luminance = 0.86. The main effect of leaving saccades in the analysis was to increase gain measured at these frequencies. The only other tendency observed was that the highest gains were measured at the lower luminance!

DISCUSSION

Our results show that both luminance and retinal position have effects on human smooth pursuit. Luminance had an entirely expected effect on smooth pursuit performance in that smooth pursuit to lower luminance targets almost without exception showed greater lags than smooth pursuit to higher luminance targets. This systematic effect on phase lag is consistent with known effects of luminance on simple reaction times (e.g. Dwyer and White, 1974) and saccadic

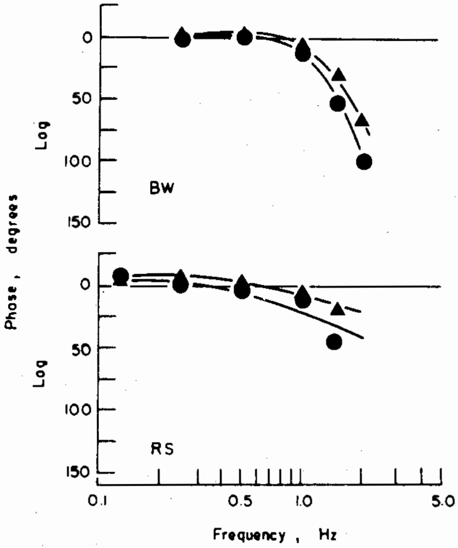

Fig. 11. Phase as a function of frequency for subject BW (top graph) and subject RS (bottom graph) while smoothly pursuing high luminance (triangles) and low luminance (circles) sinusoidal target motions tracked with the fovea. Subjects were instructed to use saccades freely to allow no fixation error while tracking the target. Lags of the eye are represented by values below the horizontal line (zero) in each graph and leads of the eye by values above zero.

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[4] It was not clear from Wheeless *et al.* (1967) precisely how "overall system response" was measured. Wheeless (1965), as well as a personal discussion with Wheeless, suggests that sections of records that were free, or relatively free, from saccades were used to compute tracking characteristics with sinusoidal target motions.

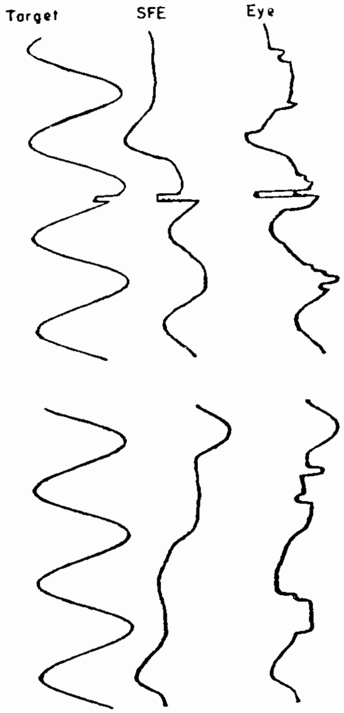

Fig. 12. Two analog records of subject BW smoothly pursuing, perifoveally, a 0.26 Hz sinusoidal target motion (amplitude = 2.18°) whose luminance was set to absolute scotopic threshold. The complete horizontal eye movement pattern is shown on the right. The saccade-free computer reconstruction is shown in the middle, and the stimulus is shown on the left. Target and eye scale factors are the same. The glitch near the middle of the top record is a blink which caused a brief interruption in data acquisition. Records start at the bottom.

latencies (Wheeless *et al.*, 1967) in which lower luminances produced increased reaction times and latencies. Retinal position, unlike luminance, affects both temporal and spatial characteristics of smooth pursuit. Foveal pursuit is more closely locked to target motion than perifoveal pursuit, in that smooth pursuit gain is higher and phase lags and leads are smaller when the pursued target is tracked with the fovea.

Our results that foveal pursuit is more effective than eccentric pursuit have been recently corroborated in another species—the cat—where surgical interruption of anatomical pathways controlling horizontal eye movements prevented cats from looking directly at the targets that they pursued. Cats with such lesions can pursue relatively small (1° × 4°) targets that fall on their peripheral retinae as much as 40° from the center of the areae centralis. Pursuit velocities are maximal at the center of the areae centralis and fall systematically but not dramatically with eccentricity (Michalski, Kossut and Żernicki, 1977). The effect of retinal position on gain might be due to differences in visual function (e.g. perceived extent, visual acuity and movement sensitivity) known to vary across the highly heterogeneous retina. But, we consider a visual explanation unlikely because luminance, despite its expected effect on lag, had little or no effect on gain, even though luminance similarly affects such spatial visual functions. These visual effects can be profound, particularly when delivered to the perifovea. The same target can be made to appear as a colored and sharply focused spot or as an achromatic fuzzy mass simply by changing its luminance. Other visual functions show similar profound effects of luminance—effects that would intuitively seem likely to have considerable impact upon smooth pursuit. For example, visual acuity in the perifovea 6° away from the center of the fovea is 6 times better at the photopic level used (photopic MAR = 6′, scotopic = 36′) according to Klein (1942) and Gordon (1947). Movement thresholds are also very different. The authors just cited found that there was a 7-fold difference in movement thresholds (photopic = 6′/sec, scotopic = 40′/sec). The effects of luminance on smooth pursuit gain in subject BW, who showed detrimental effects of low luminance on her perifoveal performance, were far from this magnitude—the largest factor was less than 0.5.

The situation is similar in the fovea. For example, visual acuity, 0.5 log unit above absolute foveal threshold, is about $\frac{1}{6}$ as good as it is 2 log units higher (Graham, 1965, p. 335). Movement thresholds change by a factor of 4 under such conditions (Graham, 1965, p. 576). Smooth pursuit and overall tracking does not show such influences. This seems to be the case with respect to the present experiment. It certainly is not with respect to the prior report in which large systematic effects of luminance on sinusoidal tracking were described (Wheeless *et al.*, 1967). The differences between the present and prior report cannot be reconciled in any obvious way. The reader may be encouraged, like ourselves, to accept the conclusion that luminance has only modest influences on sinusoidal tracking rather than the conclusion of the prior authors because the present results, unlike the prior report, are consistent with a number of studies of maintained fixation which have shown that luminance, and other stimulus variables, have modest effects when varied over large ranges—variations that cause the fixation stimulus to look very different.

Also realize that such oculomotor independence serves a useful purpose: it allows us to look at and track objects of our choice effectively rather than having properties of the object choose for us (see Steinman, 1976, for a discussion of the usefulness of oculomotor independence). The degree to which the oculomotor system is independent in the sense that it can function effectively when a stimulus parameter assumes an extreme value is illustrated in Fig. 12. This figure reproduces smooth pursuit records obtained at absolute scotopic threshold when the subject reported intermittent visibility of the target moving in the perifovea. The reader should have little difficulty deciding, on the basis of the eye movement pattern, when the target was visibile and when it was not because targets, when they become visible, engender vigorous smooth pursuit.

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