THE EFFECT OF LUMINANCE ON HUMAN SMOOTH PURSUIT OF PERIFoveAL AND FOVEAL 'TARGeTS'

BARBARA J. WINTERS1 and ROBERT M. STEINMAN
Department of Psychology, University of Maryland. College Park, MD 20742, U.S.A.

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ABSTRACT—Ten subjects tracked targets located in the periphery (5° below the line of sight) while ocular movement performance was recorded with an infrared contact lens. A pursuit target was either a 1.65 log unit area above foveal threshold (photositic) or a 0.5 log unit area above scotopic threshold. Transfer characteristics of smooth pursuit of a sinusoidal motion target (τ = 2.18 s, frequency = 0.13 ± 0.03 Hz) were measured. It was found that (1) smooth pursuit is easily accomplished with no practice, (2) smooth pursuit characteristics were largely determined by target luminance, (3) the phase of smooth pursuit showed greater lag with the scotopic target than with photositic 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 was spread over a larger region in the fovea since overall smooth pursuit gain was lower than in the fovea where luminance 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 photositic. These data also suggested a fundamental difference between photositic and scotopic ocular motor control. But the luminance condition of this study was confounded by another factor. The tracking target was not equally visible to the subjects under all luminance conditions. When the target luminance was scotopic, and thus below foveal threshold, the target was invisible at least partly, 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 experiment using a target luminance that was always clearly visible during smooth pursuit. This was accomplished by presenting photositically effective and scotopically effective targets on three different retinas where both cone and rod receptors are numerous (Polyak, 1914, 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 characteristic 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

INTRODUCTION

The ocular motor 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 condition of a stimulus that causes 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, 1971). The size of a fixed stimulus usually affects on effects on the control of the line of sight (Steinman, 1965; Rattie, 1969), as does spectral distribution and luminance above foveal threshold (Steinman, 1967, Boyce, 1967).

However, ocular 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 unsteady eye movement pattern which brought the stimulus image onto the fovea where it would then elicit a photositic stimulus with a luminance that made its appearance and disappearance as equally likely as that of the scotopic stimulus did not allow the stereotyped and counter-progressive eye movement pattern even when it fell on the same part of the extra-foveal retina (Steinman and Conitsa, 1969). This difference in ocular control suggested the possibility that ocular motor 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 (Wise et al., 1972). 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 photositic. These data also suggested a fundamental difference between photositic and scotopic ocular motor control. But the luminance condition of this study was confounded by another factor. The tracking target was not equally visible to the subjects under all luminance conditions. When the target luminance was scotopic, and thus below foveal threshold, the target was invisible at least partly, 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 experiment using a target luminance that was always clearly visible during smooth pursuit. This was accomplished by presenting photositically effective and scotopically effective targets on three different retinas where both cone and rod receptors are numerous (Polyak, 1914, 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 characteristic 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

1 The research was supported by Grant No. 0023 from the National Eye Institute.
2 Present address: Department of Psychology, Erasmus University, Postbus 1738, Rotterdam, The Netherlands.

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

Having found that luminance did not have powerful oculomotor influences on smooth pursuit gain in the periphery, where this variable could be manipulated over a wide range, the measurements were repeated with visually presented targets with the result that, namely, (1) overall characteristics of smooth pursuit were unaffected by a more than a 1:5 ratio change in luminance—this was true even when overall gain was a significant factor. The data were not eliminated before analysis, (2) lag tended to be greater with low luminance targets, and (3) predictive smooth pursuit was observed. It was also found, as might be expected, that overall smooth pursuit gain was higher in the fovea than in the periphery.

**Experimental protocol**

Two experimental eye movements—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 possible illumination. They continued dark adapting for 5 min before data were collected. Each recording session began with photopic effective targets. Recording with such targets was followed by trials with scotopic target stimuli. Each subject's data with photopic targets were obtained at the beginning of each session with eccentric stimuli. The eccentric portion of the data were obtained at the end of each session—after all scotopic recordings had been made. Systematic changes in the photopic stimulus presentations were noted when obvious daily-day variations. There were no significant epochs during which the photopic stimulus conditions were measured and the recording system aligned in a single condition.

At the beginning of each trial the subject faced a red light of light and small black point against a black background. The subject was required to track this target by moving the eye. When the subject felt ready to track this 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. This was followed by target stimuli were presented in random order and were moved in one of three horizontal eye, vertical eye, and stimulus presentation were obtained for each subject. The results showed that vertical eye motions were consistently pursued in the eccentric position presentation. The results showed that vertical eye motions were consistently pursued in the eccentric position.

**Motion and analysis**

The tape-recorded stimulus position and eye position analog voltage data were digitized. After all of the data were collected, a 24-bit A/D converter was used to simulate the stimuli position analog voltage data. The data were analyzed for each subject and the velocities were averaged. The vertical eye motion was used only to determine whether horizontal eye and stimulus position were consistent with the eccentric position. The results showed that horizontal eye and stimulus position were consistent with the eccentric position. The results showed that horizontal eye and stimulus position were consistent with the eccentric position. The results showed that horizontal eye and stimulus position were consistent with the eccentric position. The results showed that horizontal eye and stimulus position were consistent with the eccentric position.
Effect of luminance on human smooth pursuit

Fig. 1. An analog record of subject BW’s first attempt at smooth pursuit of a target moving sinusoidally at frequency 0.26 Hz, amplitude 2.18° in her periphery. Target luminance was 0.5 log units above absolute scotopic threshold. The complete horizontal eye movement pattern is shown on the right. The oscillatory stimulus pattern is shown on the left. The center trace (DFS) 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 0.15 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. 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 the pursuit 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,

3The choice of systems analysis for the present experiments is dictated primarily by the desire to examine the effects of luminance on tracking with a method that would permit comparisons with the prior study (Wheeler et al., 1967). It has been known since this method was first employed in studies of the ocularmotor system that the behavior of the ocularmotor 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 Wheeler et al., will not attempt to model details of the control system.

however, were small. For example, maximum gains differed by 0.23 for BW and by 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 2 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. 2. Subject BW’s smooth pursuit gain as a function of the frequency of sinusoidally moving targets. The photopic target (0.85 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.

Fig. 3. Subject RS’s smooth pursuit gain as a function of the frequency of sinusoidally moving targets. The photopic target (0.85 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.
Fig. 4. Smooth pursuit gain of subject BW (top graph) and RS (bottom graph) as a function of luminance while tracking a 0.5 Hz sinusoidal target motion. Luminance is shown as filter transmission.

Reduced. Note, however, that the 1000-fold reduction in luminance resulted in only a 30% reduction in gain for this subject. A 300-fold reduction in target luminance led to a 15% increase in gain for subject KS.

Luminance, however, had a systematic effect on phase as is shown in Fig. 5. Both subjects' scotopic smooth pursuit lags their photopic smooth pursuits. Also note that both subjects showed "predictive tracking", i.e. the smooth pursuit led the stimulus at one photopic frequency (0.22 Hz) for BW and for frequencies 0.3 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; Ständerhauf, 1960; Sirk, Vosius and Young, 1962; Bornemann, Drischel and Nicolai, 1964).

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

The present results differ from those of Wheelers 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 peripheral 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 Wheelers 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 0.6 whereas the prior report found gain at this frequency reduced from 2 to almost half (0.56) when target luminance was reduced only by a factor of 40. Not only was the magnitude of the effect of luminance much smaller than in the report of Wheelers 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 the 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 succoate 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 ocular motor 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? Extrafovea! tracking has, in higher primates, at least one obvious function. It permits ocularly coordinating under scotopic conditions when the
Effect of luminance on smooth pursuit pursuit could become with practice, particularly under pressure by damage to the fovea or its central projections. The present results suggest an optimistic outcome.

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

Smooth pursuit of sinusoidal target motions in the periphery

The periphery 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 (Pockett and Steinman, 1969) They were given these instructions to encourage the best possible performance.

Luminance did not have large or systematic effects 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 much brighter. Foveal gain was higher than gain in the periphery, as might be expected. There was an effect of luminance on phase, 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 periphery

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.

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 fixational error while tracking the target. High luminance performance is shown by triangles, low luminance performance is shown by circles.

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 fit because of the almost complete overlap of the data points.
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 ocular motor characteristic. It was true of "overall system gain" as well as of smooth pursuit gain. 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 effects. For example, BW's mean gains at 0.5 Hz were: high luminance = 1.05, low luminance = 1.00 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 = 0.63, low luminance = 0.68. 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. Luminosity 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. 12. Two analog records of subject BW smoothly pursuing, peripherally, a 0.25 hr. astronomical target motion (amplitude = 2.16°) whose luminance was set to absolute scotopic threshold. The complete horizontal eye movement pattern is shown in the right. The suicide-free computer reconstruction is shown in the middle, and the stimulus is shown on the left. Target and eye scale locations are the same. The grid shows the middle of the tip record is a blank which caused a brief interruption in data acquisition.

Record start at the bottom.

latencies (Wheelless et al., 1967) in which lower luminances produced increased reaction times and latencies Retinal position, unlike latency, affects both temporal and spatial characteristics of smooth pursuit. Foveal pursuit is more closely locked to target motion than peripherally pursuit, that smooth pursuit gain is higher and phase lags 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 area centralis. Pursuit velocities are maximal at the center of the area centralis and fall systematically but not dramatically with eccentricity (Michalski, Kossut and Zrenker, 1977). The effect of retinal position on gain might be due to differences in visual function (e.g., periphery, visual quality 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 similarity affects such spatial visual functions. These visual effects can be profound, particularly when delivered to the periphery. The same target can be made to appear as a colored and sharply focused spot or 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 periphery 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). Visual acuity in the periphery may also be very different. The authors just cited found that there was a 7.4-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 as good as it is 2 kg units higher (Graham, 1965, p. 33S). Movement thresholds change by a factor of 4 under such conditions (Graham, 1965, p. 157). 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 in wish with respect to the prior report in which large systematic effects of luminance on scotopic tracking were described (Wheelless 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 smooth 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 low luminance thresholds are highly reliable, show consistent effects when varied over large ranges—variations that cause the fixation stimulus to look very different. Also realize that such oculo-motor independence serves a useful purpose: it allows us to look at individual track objects of interest which are not effectively rather than blind the properties of the object of choice for us (see Steinman, 1976, for a discussion of the usefulness of oculo-motor independence). The degree to which the oculo-motor 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 invariable persistence of the target moving in the periphery. The reader should have little difficulty recognizing the general 6°-eye movement pattern, when the target was visible and when it was not because targets, when they become visible, engender vigorous smooth pursuit.

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