RELATIONSHIP BETWEEN SLOW DRIFT
AND SMOOTH PURSUIT EYE MOVEMENTS

by Robert J. Cunitz

Ph.D. Dissertation

ABSTRACT

Title of Thesis: Relationship Between Slow Drift and Smooth Pursuit Eye Movements

Robert Jesse Cunitz, Doctor of Philosophy, 1970

Thesis directed by: Robert M. Steinman
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The present research examined the relationship between noisy drift, corrective drift and smooth pursuit eye movements. Nachmias (1961) suggested that smooth pursuit of a moving target is controlled by the same low velocity system that corrects position errors produced by noisy drifts during fixation of a stationary target. The present study examined this suggestion by recording two-dimensional eye movements with a contact lens-optical lever while 2 experienced subjects fixated and subsequently tracked a point target suddenly set into motion in 8 unpredictable directions at 6 constant velocities (0.5 to 64 min arc/sec). A correlational technique was used to determine the degree to which drifts corrected position errors during fixation of a stationary target. A vector averaging procedure was used to determine the direction and velocity of smooth pursuits.

It was found: firstly, slow drifts could be an appreciable source of compensation for position errors along all retinal meridians during the fixation of a stationary target. This finding is new, because prior research had shown that drifts corrected position errors only parallel to a few idiosyncratic directions. Another new result was the finding that 0.3 sec drifts could be as effective as saccades in correcting fixation position errors. Secondly, when targets moved

faster than 8-16 arc/sec, slow drifts became directionally uniform, moving the eye in the direction of the target at slightly less than target velocity. When the target moved more slowly than 8-16 min arc/sec, the eye drifted much faster than the target moved, and drift direction was not influenced by the direction of target motion. The changes in drift direction and velocity, which occurred when the target moved faster than 8-16 min arc/sec, were interpreted as evidence for a velocity threshold for smooth pursuit. The velocity threshold lay within the range of drift velocities observed during fixation of a stationary target. This finding supports Nachmias' suggestion that a single low velocity control system is responsible for both corrective drifts and smooth pursuits.

A servomechanical model of low velocity eye movement control was developed to summarize the present results. The model incorporates all low velocity eye movements (noisy and corrective drifts as well as smooth pursuits) within a single descriptive framework. The main features of the model include: 1) a source of noisy drifts, which, when fast enough, initiate corrective drifts during fixation of a stationary target, 2) time-delay and low-pass components to simulate the response latency of the smooth eye movement system and the inability of the smooth system to follow very rapid changes in target position, 3) a differentiator to simulate the smooth pursuit velocity threshold and convert changes in target image position to velocity signals which guide low velocity corrective eye movements and 4) a Type "0" servo whose output velocity is always less than its input velocity.

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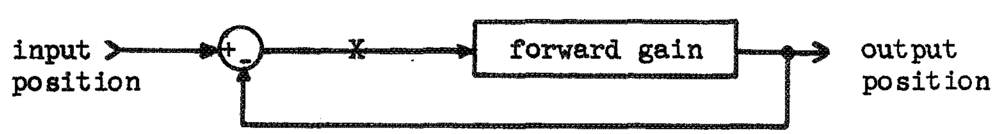
INTRODUCTION

The oculomotor system that controls human eye position has many of the characteristics of a closed-loop position control servomechanism. This type of servomechanism, in its simplest formulation, consists of a summing input terminal, some device exhibiting forward transfer characteristics and a unitary gain feedback loop. In the example shown in Fig. 1, the actuating signal, X, is the difference between the input and output positions. The output motion of the system serves to reduce this difference signal because the feedback loop transmits the output position back to the summing point. In time, the signal, X, approaches zero and no further output motion is necessary. The usefulness of this analogy between the eye and a simple position control servo will become apparent when the input-output (stimulus-eye rotation) relationships of the oculomotor system are described.

Fig. 1. A SIMPLIFIED POSITION CONTROL SERVOMECHANISM.



The outputs of the oculomotor system are spherical rotations of the eyeball. Eye rotations are produced by contractions of three pairs of opposing reciprocally innervated muscles attached to the outside surface of the globe. These extra-ocular muscles rotate the eye so as to position the retinal image of a relatively bright target on a small (less than 20 min arc diameter) portion of the fovea, the region of best detail vision. Once a target image is located within this "optimal" locus ("fixated"), the eye's external musculature provides the small amount of image motion which is known to be necessary for the maintenance of target visibility.[1] Two distinct types of eye movements, saccades and slow drifts, are found during maintained fixation of a stationary target object.

Saccades are small, fast (5-10 deg arc/sec) rotations that typically occur twice each second and move the eye through an angle of about 5 min arc (Zuber, Stark and Cook, 1965; Ditchburn and Foley-Fisher, 1967). Saccades are "corrective", i.e. a statistically significant number return the retinal image of the fixation target toward the optimal locus (Cornsweet, 1956; Nachmias, 1959). The direction and magnitude of a saccade depends upon the retinal position of the attended portion of the visual array relative to the optimal locus (the fixation error).[2] Saccades are initiated either by the size of the fixation error (Cornsweet, 1956) or by the time that has elapsed since the last saccade (Nachmias, 1959).

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[1] "Stabilized" target images disappear. Numerous experiments have shown that small eye movements prevent target disappearance by continuously placing fresh retina under the target. An extensive discussion of this phenomenon is beyond the scope of the present paper. The interested reader is directed to a review by Heckenmueller (1965).

[2] Fixation saccades may not be position "corrective" movements elicited by fixation errors but rather, small scanning movements which indicate a slight shift in attention within a circumscribed portion of the visual field. See Cunitz and Steinman (1969) for a discussion of this interpretation of the function of small fixation saccades.

Intersaccadic drifts are slow (3-8 min arc/sec) eye movements that occur in the intervals between saccades (Ditchburn and Foley-Fisher, 1967). When the eye drifts, two kinds of slow movements have been described: "noisy" drifts that allow the target image to wander away from the optimal locus, and "corrective" drifts that move the displaced target image back toward this position. Errors produced by noisy drifts during fixation are corrected mainly by saccades (Nachmias, 1959). Corrective drifts have been demonstrated only along a few idiosyncratic meridians where saccadic correction was minimal (Nachmias, 1959; Fiorentini and Ercoles, 1966). Recently it has been inferred, but not shown quantitatively, that corrective drifts can effectively take over control of eye position when saccades are suppressed by experienced subjects who explicitly avoid making saccades during fixation (Steinman, Cunitz, Timberlake and Herman, 1967).

The third major kind of eye movement, smooth pursuit, is observed when subjects track a moving target. Smooth pursuits are slow eye movements in the direction of target motion. These movements have been studied for target velocities as low as 10 min arc/sec (Yarbus, 1967) and as high as 30 deg arc/sec (Westheimer, 1954). Most quantitative studies of smooth pursuit have been confined to target velocities between 0.5 deg arc/sec and 15 deg arc/sec. Saccades occur from time to time during smooth pursuit (Dodge, 1907) and serve to correct position errors created by the subject's inability to exactly match the velocity of the target (Puckett and Steinman, 1969) and by the latency between the onset of target motion and the activation of the smooth pursuit system (Westheimer, 1954; Rashbass, 1961; Robinson, 1965). Smooth pursuits keep the image of a moving target relatively stationary on the retina.

There are, then, three corrective oculomotor outputs (saccades, corrective drifts and smooth pursuits) and one non-corrective output (noisy drifts). Because there are four kinds of system outputs, any servomechanism analogue to eye position control must be complicated. The descriptive problems would be simplified if it were possible to demonstrate that all outputs were independent of one another: they could then be modeled separately. The description would also be simplified if some of these distinctions were not warranted, and a smaller set of qualitatively different outputs were sufficient to describe the system. For example, if corrective drifts and smooth pursuits are the same output (one responding to a stationary target; the other responding to a moving target), a single low velocity control system could be a sufficient description.

At present, one important simplification can be justified experimentally, i.e. saccades and smooth pursuits are independently controlled. Rashbass (1961) demonstrated this independence in two ways. First, subjects were asked to track a target that moved with a step displacement immediately followed by a constant velocity displacement in the direction opposite to the step. Subjects tracked by first smoothly pursuing the constant velocity target and only later made a saccade backward to cancel the fixation error produced by the step. Rashbass, also showed differential effects of barbiturates on high and low velocity tracking. Large doses of these drugs completely eliminated smooth pursuit without influencing saccadic tracking. Rashbass concluded that saccades and smooth pursuits are generated independently of one another: saccades are caused by, and reduce, retinal position errors. Smooth pursuits are caused by movement of the target image and they prevent the image from being swept across the retinal surface.

Robinson (1965) presented further evidence for the independence of the smooth and saccadic systems by showing that the two systems have different response latencies (200-250 msec for saccades and 125 msec for smooth pursuits) and execution times, eg. saccades require 45 msec and smooth pursuits require 133 msec to negotiate comparable 10 deg arc transitions. Robinson, also, showed that the systems have different oscillation frequencies under negative feedback (2-2.5 Hz for the saccadic system and 3.3 Hz for the smooth system) and require different feedback gains to sustain such oscillations (-5 for the saccadic system and -8 for the smooth system).

The relationship among the three low velocity outputs (noisy drifts, corrective drifts and smooth pursuits) is not well established. All three might be independent, responding to different stimulus parameters, or, as was originally proposed by Nachmias (1961), corrective drifts during fixation of a stationary target might be controlled by the same system that controls smooth pursuit of a moving target.

The present research examined Nachmias' (1961) suggestion by requiring subjects to fixate a stationary target that was set in motion at one of six velocities between 0.5 and 64 min arc/sec (from below the velocity of fixation drifts into the range where smooth pursuits are known to occur). If the same system controls corrective drifts and smooth pursuits the directional characteristics of slow drifts should gradually shift from the irregular pattern typical of the fixation of a stationary target to the directionally regular pattern typical of smooth pursuit. In other words, corrective drifts should be indistinguishable from smooth pursuits except that in the former case, the direction required for drift correction would be determined, exclusively, by error producing movements of the eye, whereas in the latter, the low velocity corrective system must follow movements of the target as well.

Experimentally, it should be possible to predict smooth pursuit characteristics from a knowledge of the particular directional errors which are nulled by corrective drifts for any single subject. For example, the lowest pursuit velocity threshold would be expected parallel to the meridian along which drift correction is most effective. The low velocity control system responds in a corrective fashion to many noisy drifts on this meridian when the target is stationary and should, therefore, respond to a target moving at noisy drift velocity in this direction. Pursuit velocity threshold would be higher for target motion along other meridians where drift correction is less effective in the control of retinal image position. It should be possible to rank the measurements of drift correction a subject shows on each retinal meridian and to correlate these rankings with smooth pursuit velocity thresholds found on the same meridians. Clearly, then, it is necessary to examine pursuit of targets moving in a number of different directions to determine whether a single system controls corrective drifts and smooth pursuits. Accordingly, subjects were asked to track a target which was set in motion in one of eight directions spaced at 45 deg arc intervals. Trials during which the fixation target did not move were also recorded in order to determine the degree of corrective drift compensation along each meridian for each subject. Because the long term stability of the idiosyncratic corrective drift pattern was not known, trials during which the target did not move were randomly intermixed with trials with moving targets, making it possible to determine each subject's corrective drift pattern at the same time as his smooth pursuit characteristics.

METHODS

Apparatus. Two experienced subjects (RS and AS) viewed, from a distance of 1.0 m, a small point displayed on the face of a Tektronix Model 503 oscilloscope (P-2 phosphor). The oscilloscope graticule was replaced by a filter (Kodak Wratten #25) which made the target appear red and eliminated all afterglow. The target's location and velocity were controlled (± 0.5%) by a modified Electronic Associates analog computer and solid-state RC timers. The luminance of the target was set 1.31 log units above absolute foveal threshold (8.5 mL for RS and 14.1 mL for AS). (See Appendix A for a description of the stimulus generation procedure and Appendix B for calibration procedures.)

Two-dimensional eye movements of the right eye were recorded on 35mm infrared film by means of a contact lens-optical lever that resolved horizontal and vertical rotations in Listings's plane as small as 10 sec arc without contamination by torsions of the eye or translations of the head. S steadied his head on a plastic dental bite-board while viewing the target with his right eye. The left eye was occluded by a light-tight eye patch. (See Appendix C for description of the recording technique.)

Procedure. Trials initiated by S, typically began with 10.2 sec fixation of a stationary centered target which then moved 45.0

min arc in 1 of 8 directions spaced at 45 deg arc intervals. Target velocities were 0.5, 2.0, 8.0, 16.0, 32.0 or 64.0 min arc/sec. The trial ended with 10.2 sec fixation of the stationary target in its new position.[1] Trials were presented in blocks of 8 at each velocity. Each 8 -trial block contained 1 randomly inserted trial during which the target remained stationary. The directions of target motion were randomized within each block. Target velocity was counterbalanced as the conditions were replicated. (See Appendix D for details.)

Film measurement and measurement error. Two people (not familiar with the eye movement literature) measured records on a projection film reader. To determine the optimal locus, eye position was measured for each record at randomly sampled times within successive 0.5 sec of the 3 sec period just prior to target movement (shown by a strobe stripe on the film), and during the second, third and fourth seconds after the target stopped moving (also shown by a strobe stripe). To determine direction and magnitude of pursuits, eye position was measured each 0.1 sec during the first second after the onset of target motion. Similar samples, obtained at 0.1 sec intervals during

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[1]The fixation periods before and after target motion were shortened to 4.5 and 4.0 sec for a number of high-velocity trials. This was done to increase the number of short duration trials that could be efficiently recorded. For similar reasons, the movement period of all 0.5 min arc/sec trials was shortened to 45.0 sec, allowing an angle of 22.5 min arc for target movement.

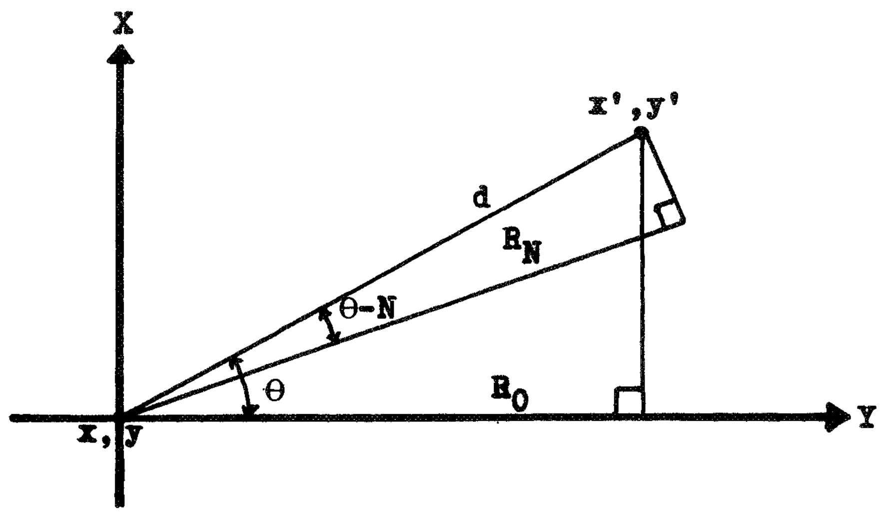
trials with the stationary target were pooled with the pre- and post-movement samples to improve the estimate of the optimal locus. All saccades were counted and their onset times relative to the beginning of target motion were measured. A random sample (9%) of the records was remeasured. Standard errors of measurement were calculated for two of the more important statistics used to describe the eye movement data. The standard errors of measurement of these statistics were: 4.6 deg arc for drift direction and 0.32 min arc for 0.1 sec drift magnitude.

Measures. The statistical procedures used in the present experiment were, for the most part, straight-forward and will be defined when results are presented. One procedure, the Directed Magnitude of Components of Eye Motion (DMCEM), however, is unusual and its derivation and interpretation are discussed in the following section.

The DMCEM is a procedure for summing vectors in two-dimensional space that can be used to calculate the size and direction of eye movements. This procedure was first used in eye movement research by Nachmias (1959) for describing maintained fixation of a stationary target. The procedure was modified to calculate mean eye movement direction to the nearest 0.5 deg arc and was used to describe both the fixation of a stationary target and pursuit of moving targets.

In the DMCEM procedure an individual eye movement vector is defined by referencing the beginning of the eye movement to an arbitrary zero and determining the distance and direction (in polar coordinates) of the end-point of the eye movement. The mean directed magnitude of components of motion parallel to each of 360 equispaced meridians can then be obtained by calculating the sum of the normal reflections on each meridian for every eye movement vector and dividing each of the 360 sums by the number of vectors. Fig. 2 illustrates the procedure for computing the directed magnitude of components of motion (R_N) for one eye movement vector (x,y to x',y') in the first quadrant.

Fig. 2. DIRECTED MAGNITUDE OF COMPONENTS OF MOTION PROCEDURE FOR EYE MOVEMENT VECTOR x,y to x',y'.



$$R_{N \atop 1 \rightarrow 360^\circ} = d \cdot \cos(|\theta - N|), \text{ for positive values of } R_N \text{ only, in increments of } 1^\circ.$$

where $\theta = \tan^{-1}(y - y'/x - x')$,

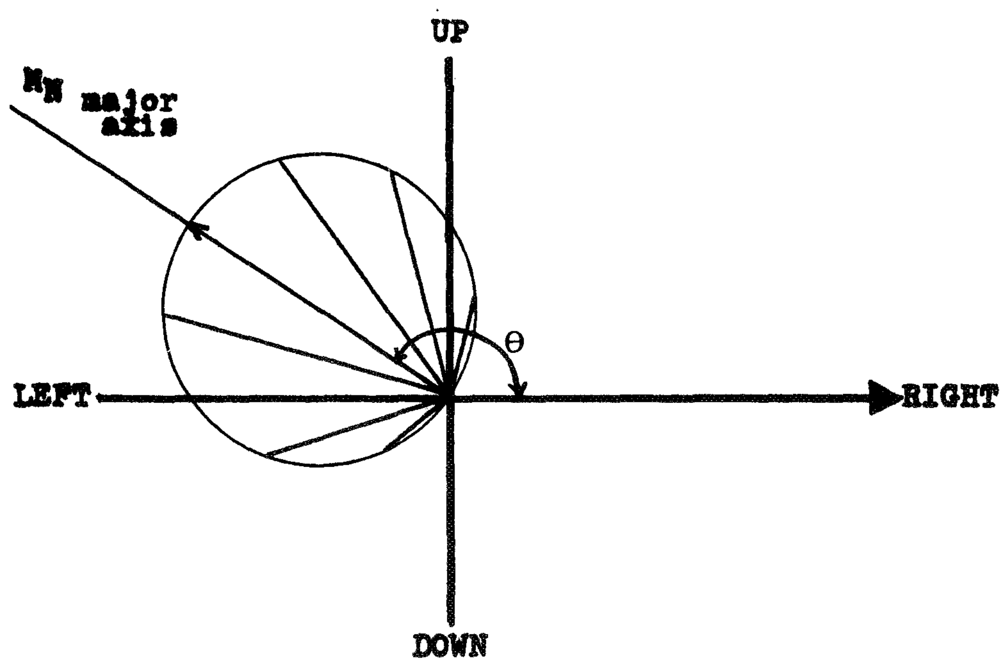
$d = \left[(x - x')^2 + (y - y')^2\right]^{\frac{1}{2}}$

and N = one of 360 meridians

The values of R_N for each vector are then summed and divided by the number of vectors contributing to the total. The mean values of the components on each meridian may be plotted as in the example of

Fig. 3. The meridian (M_N) containing the largest mean vector is the meridian of interest. Its angle and length represent the mean direction to the nearest 0.5 deg arc and size of the eye movement vectors contributing to the calculations. Note that the mean vectors trace out a perfect circle and that the circle is traced out twice because meridians outside the range $M_N \pm 90^o$ have negative vector lengths. (A Fortran V program for calculating M_N is given in Appendix E.)

Fig. 3. MEAN MAGNITUDE AND DIRECTION (M_N) OF AVERAGED EYE MOVEMENT VECTORS. THE ARROW SHOWS THE DIRECTION OF TARGET MOTION.



RESULTS

Drift Correction During Fixation of a Stationary Target

Drifts as well as saccades were corrective along all meridians. Drift and saccade characteristics during fixation were examined by means of a correlational analysis of trials during which the target remained stationary (19 trials for AS and 18 for RS). The technique, developed by Nachmias (1959), determines the degree to which eye movements correct fixation errors along a number of different retinal meridians (Nachmias examined 8 spaced at 22.5 deg arc intervals). In the present analysis correlations were calculated for 180 meridians spaced at 1 deg arc intervals.[1] Two vector magnitudes were determined for each saccade and 0.1 sec drift. The initial error vector was defined by the line connecting the position of the eye at the beginning of each saccade or 0.1 sec drift to the trial mean fixation position. The movement vector was defined by the line connecting the position of the eye at the beginning of a saccade or 0.1 sec drift to the position at the end of the movement. Reflected magnitudes of both vectors were calculated on 180 meridians. On each meridian, the Pearson Product-Moment Correlation was then calculated for the set of

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[1] 180-0 deg arc is one such meridian and 360-180 deg arc is the same meridian. In this example, movements to the right and to the left will be described. The origin in this polar coordinate system is the optimal locus which is estimated from the mean fixation position, generally assumed to locate the target image in the foveal bouquet.

paired (error-movement) reflected magnitudes.[1] A negative correlation coefficient on a meridian indicates that the mean eye movement on that meridian was corrective: it reduced the mean initial fixation error on that meridian.

Fig. 4 shows the degree of drift and saccadic correction. Saccades, and drifts were statistically significant sources of position error compensation parallel to all meridians, *i.e.*, all correlations were negative and significantly different from zero ($p < .01$). One-tenth sec drifts were not, however, as effective as saccades in correcting position errors (the drift correlations were smaller) but drifts did correct position errors, and they did so along all meridians. This result is at variance with the earlier study by Nachmias (1959) who found drift correction parallel to only a few meridians.[2] Because intersaccadic drifts often change direction, Nachmias' 0.2 sec drift samples may have included more drifts that changed direction than the shorter 0.1 sec drift samples analyzed in the present experiment. This possibility was examined by computing drift correlations on the present data for 0.2, 0.3 and 0.4 sec drifts in addition to the 0.1 sec drifts shown in Fig. 4. The results of this analysis are plotted in Fig. 5. Both *Ss* showed relatively uniform correction along all

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[1]The correlation coefficients repeat every 180 deg arc because the reflected magnitudes of a vector on any two axes 180 deg arc apart are equal in magnitude and opposite in sign.

[2]It is more difficult to interpret the Fiorentini and Ercoles (1966) experiment because these investigators inferred the presence of drift correction from frequency distributions of drift directions for drifts that were not of uniform durations.

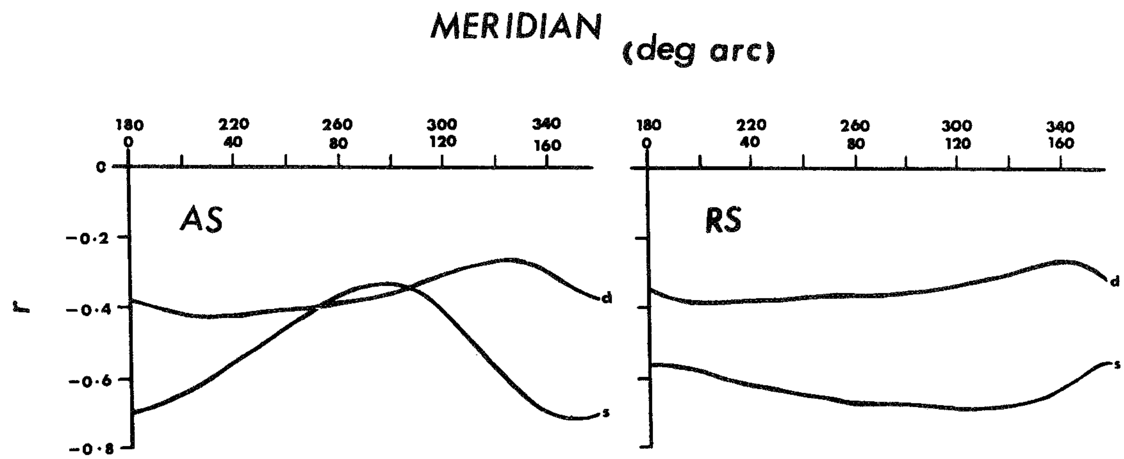

Fig. 4. Pearson Product-Moment Correlations (r) between fixation error and eye movement vectors computed on 360 meridians. Correlations of 0.1 sec drifts (d) and microsaccades (s) are plotted separately for each subject (AS and RS). Microsaccade correlations are based on 44 paired error-movement vectors for AS and 54 paired vectors for RS. One-tenth sec drift correlations are based on 264 paired error-movement vectors for AS and 245 paired vectors for RS. All correlations were significantly different from zero ($p < 0.01$).

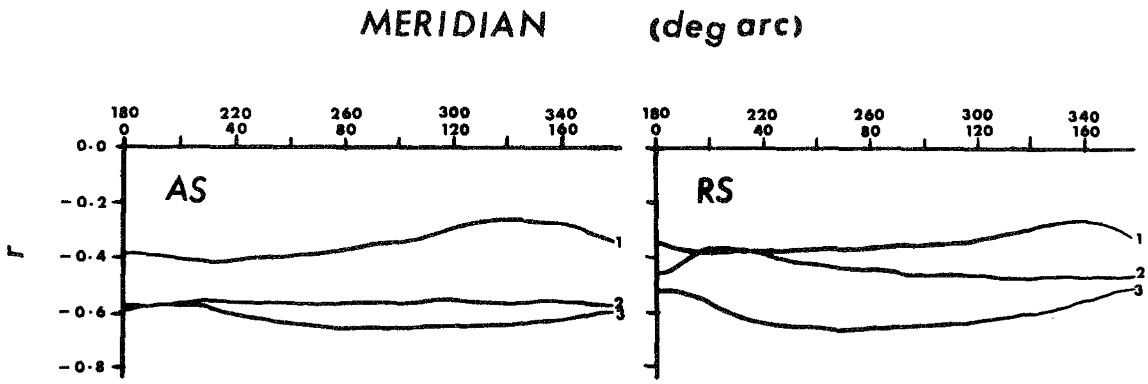

Fig. 5. Pearson Product-Moment Correlations (r) between fixation error and 1, 2 and 3-tenth sec drift vectors computed on 360 meridians. The 0.1 sec correlations are based on 264 paired error-drift vectors for AS and 245 vectors for RS; the 0.2 sec correlations are based on 117 for AS and 105 for RS; and the 0.3 sec correlations are based on 68 for AS and 53 for RS. All correlations were significantly different from zero ($p < 0.01$).

meridians regardless of the duration of the drift sample.[1] The magnitude of the correlations increased with longer sampling intervals which means that drifts became more corrective as time passed. In fact, the 0.3 sec drifts of both Ss were as corrective as their saccades (0.3 sec drift correlations and saccade correlations were both about -0.6).

The finding that the present Ss used low velocity eye movements to keep their eyes in place along all meridians is not surprising in light of the subsequent[2] finding that these Ss' drift eye movements, in the absence of saccades, did not allow the eye to wander from the "optimal" locus (Steinman, *et al.*, 1967). In this prior report, however, low velocity position control was inferred from the stability of the eye in the absence of saccades: drift characteristics were not analyzed. The present research reports a quantitative analysis of drift characteristics of these Ss and shows that they actually do employ corrective drifts on all meridians.

There has been only one prior correlational analysis of the two-dimensional fixation eye movement pattern which provided a detailed description of the relative contribution of saccades and drifts to the control of eye position (Nachmias, 1959). There have, however, been numerous studies of other features of oculomotor control under conditions comparable to those in the present experiment. A

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[1]The correlations for 0.4 sec drifts overlapped the 0.3 sec drift correlations. Since, the number of 0.4 sec drifts was small, 0.4 sec drift correlations were not plotted in Fig. 5.

[2]The present recordings were made 1 year before Ss knew they were able to voluntarily suppress saccades while viewing a stationary fixation target (Steinman, *et al.*, 1967).

comparison of the present Ss' performance with these earlier reports showed that their fixation of the stationary target was quite similar to performance of other contact lens Ss. The median saccade rate of 30 Ss in 14 different experiments (Ditchburn and Foley-Figher, 1967) was 1.7 saccades/sec (Q_1 = 1.4, Q_3 = 3.3); AS's rate was 1.2 saccades/sec and RS's rate was 1.9 saccades/sec. The median absolute saccade magnitude for the same group of Ss was 4.5 min arc (Q_1 = 3.0, Q_3 =6.0); AS's **mean** absolute saccade magnitude was 4.6 min arc and RS's mean absolute saccade magnitude was 3.6 min arc. The mean intersaccadic drift velocity for the same large group of contact lens Ss was 6.0 min arc/sec; AS's mean estimated intersaccadic drift velocity was 6 min arc/sec and RS's was 8 min arc/sec. Fixation stability was described in the present experiment by the area of a bivariate contour ellipse (68.3% of eye positions) (Nachmias, 1959; Steinman, 1965). Contour ellipse areas were 85.5 min arc^2 for AS and 48.2 min arc^2 for RS. These values indicate very stable two-dimensional fixation and compare favorably with earlier reports of these and other Ss. (See Appendix F for a more detailed comparison fixation characteristics and the assumptions required to make some of these comparisons.

Implications. The good agreement between many features of the fixation patterns of the present and previous contact lens Ss indicates that the present results are reasonably representative of fixation patterns observed whenever experienced subjects fixate a stationary target. The finding that the present Ss used drift correction along all meridians was unexpected and ruled out the planned analyses of smooth pursuits along differentially corrective drift meridians. If drift correction had been more or less prominent along different meridians, it would have been possible to see whether smooth pursuit characteristics varied in the same manner when the target was moved in different directions.[1]

The fact that there was a good deal of drift correction has important consequences for estimating fixation drift velocity, particularly for the examination of the relationship of fixation drifts to smooth pursuits. If the same low velocity system controls corrective drifts and smooth pursuits, it should be possible to activate this system with targets moving at fixation drift velocities. The appropriate estimate of fixation drift velocity is, therefore, very important. It should be based on sampling intervals sufficiently brief to exclude changes in drift direction. Long sampling intervals would lead to low estimates of fixation drift velocity because long drifts include movements towards and away from the optimal locus. The best estimate of fixation drift velocity will be based, then, on the shortest available drift sample (0.1 sec). Mean 0.1 sec drift velocity of AS was 15 min arc/sec (S.D. = 9.6). RS's mean 0.1 sec drift velocity was also 15 min arc/sec (S.D. = 7.3). Both Ss' mean 0.1 sec drift velocity was about twice as fast as their intersaccadic drifts which lasted 0.5 - 0.8 sec. The difference between 0.1 sec and intersaccadic drift velocities can best be explained by assuming that intersaccadic drifts move the eye over a curved path. This was the case. The fixation records show many intersaccadic drifts that curved back slowly on their own track. Most drifts appeared to be linear during 0.1 sec periods during which time the eye moved at 15 min arc/sec.

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[1]This strategy remains potentially useful, provided Ss can be found whose corrective drift pattern is not uniform.

Smooth Pursuit of Moving Targets

There was a velocity threshold for smooth pursuit. The degree to which low velocity eye movements rotated the eye in the same direction as the target moved (smoothly pursued) can be estimated from the mean error angle, which is defined as the mean absolute value of the difference (in deg arc) between the direction of target motion (θ) and the major axis (M_N) of the DMCEM analysis of smooth pursuit (described above in the last portion of the MEASUREMENTS section). In other words, the mean error angle is the angular difference between the direction the eye moved and the direction the target moved. Mean error angles were computed from successive 0.1 sec measurements of eye position starting 0.3 sec after the target was set in motion. (Measurements made during the first 0.3 sec of target motion were not included in this analysis because a description of "steady-state" smooth pursuit was desired.)[1]

Slow eye movements in the direction of the target motion (smooth pursuits) became more frequent as target velocity was increased. Mean error angles and their standard deviations are plotted in Fig. 6. At the highest target velocity (64 min arc/sec) both Ss made almost all of their low velocity eye movements in the direction of target motion (Overall mean error angle = 7.8 deg arc, S.D. = 3.9 deg arc for AS; overall mean error angle = 5.7 deg arc, S.D. = 5.1 deg arc for RS.)

The appropriate criterion for smooth pursuit is a mean error angle significantly less than 90 deg arc because 90 deg arc is the error angle which would be expected if target motion had no influence

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[1] See Appendix G for a description of the magnitude of fixation errors as a function of time from the onset of target motion.

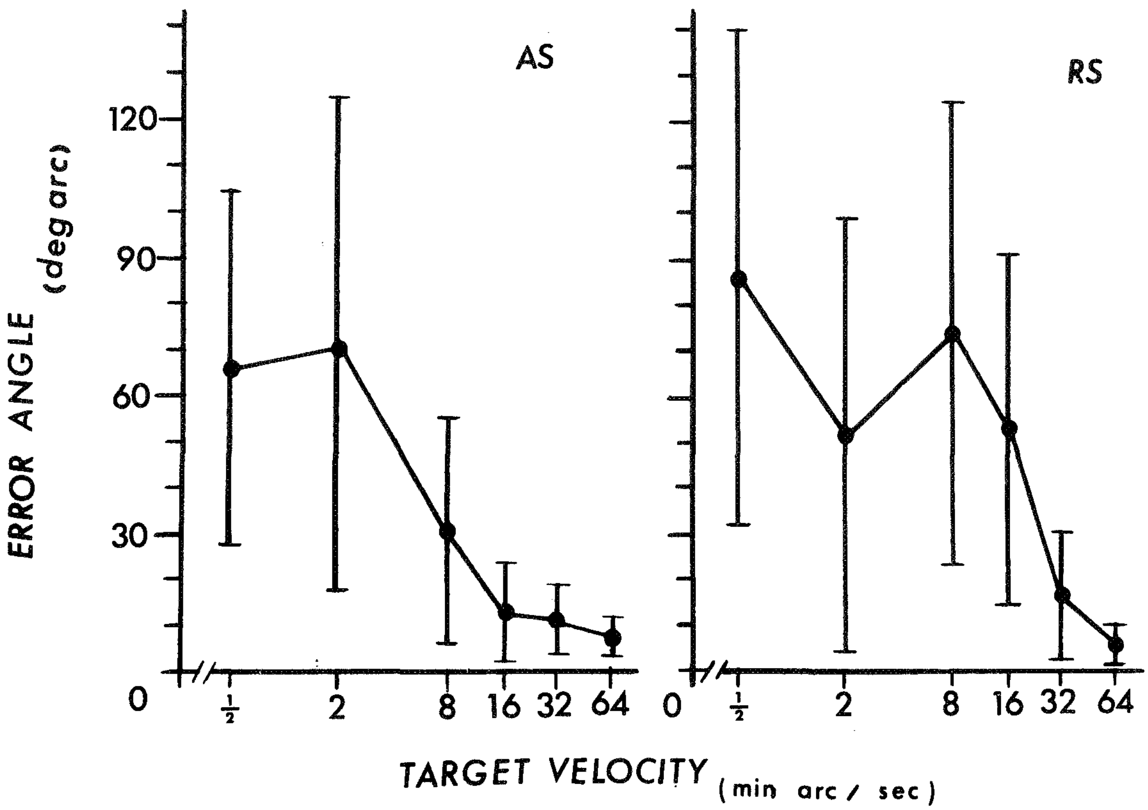

Fig. 6. Mean smooth error angle and standard deviations as a function of target velocity.

over eye movement direction (as much movement toward as away from the direction of the target). By this criterion (estimated with a 95% confidence interval around the mean error angle) both Ss' low velocity eye movements at the highest target velocity were smooth pursuits.

Both AS and RS also smoothly pursued targets moving at 32 and 16 min arc/sec and AS continued to smoothly pursue targets moving as slowly as 8 min arc/sec. RS did not: his mean error angle at the 8 min arc/sec target velocity was 74.5 deg arc (S.D. = 50.5 deg arc). AS smoothly pursued targets moving at 8 min arc/sec but not at and below 2 min arc/sec. AS's mean error angle with the 2 min arc/sec target was 70.5 deg arc (S.D. = 53.5 deg arc). (See Appendix H for tabled mean error angles, standard deviations and the number of eye movements averaged at each target velocity.)

The mean velocity (min arc/sec) of slow eye movements was calculated from the magnitude (M_N) of 0.1 sec drifts obtained by the DMCEM procedure described in the last portion of the MEASUREMENTS section. Mean eye velocity (averaged over the eight target directions) is plotted as a function of target velocity in Fig. 7. The marked change in the slopes of the functions shown in this figure (from a slope of about zero to about one) can be interpreted as evidence for a smooth pursuit velocity threshold. This threshold was found at 8 min arc/sec for AS and at 16 min arc/sec for RS. Target motion had no effect on smooth eye velocity below threshold (drifts were considerably faster than the target velocity below threshold and pursuits were slightly slower than the target velocity above threshold). The eye did not match velocity with the target at all of the target velocities studied.

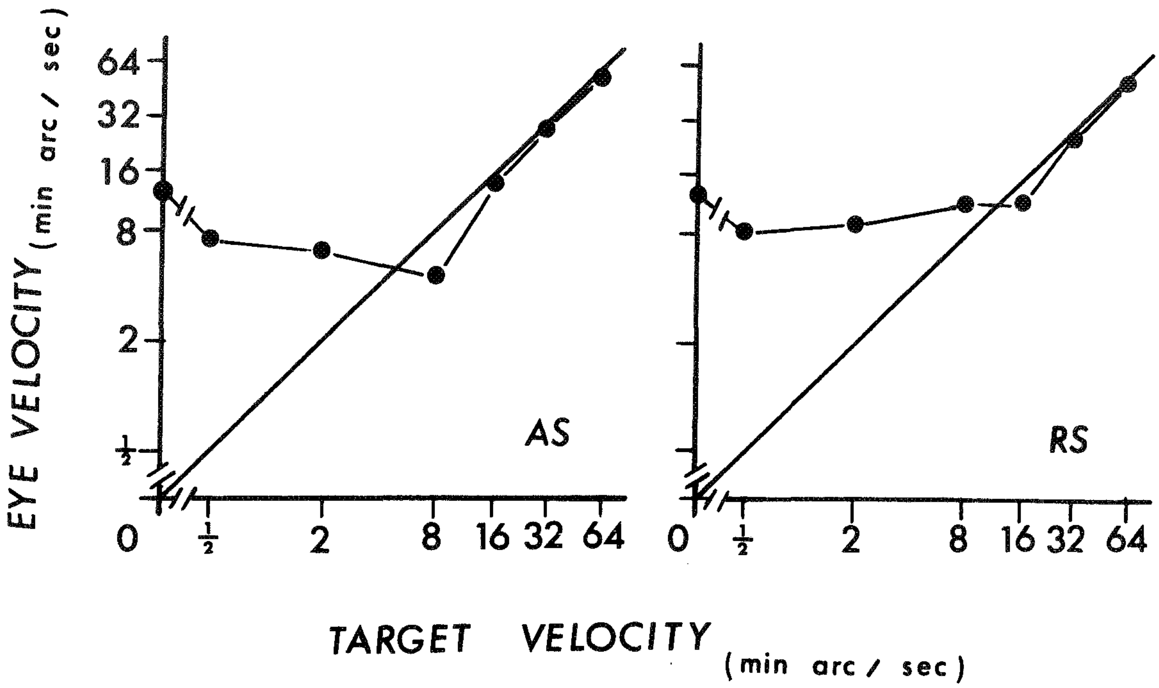

Fig. 7. Mean smooth eye velocity as a function of target velocity. The standard deviations of eye velocity did not vary in a systematic manner with target velocity (S.D.s ranged from 2.7 - 7.2 min arc/sec for AS and from 2.8 - 13.5 min arc/sec for RS).

(The eye would have exactly matched target velocity if the data points had fallen on the solid diagonal line in this log-log plot.) The best velocity matching (96.9%) observed for AS was in response to the target moving at 32 min arc/sec. RS most closely matched (94.8%) the 64 min arc/sec target. (See Appendix I for tabled mean eye velocities and standard deviations, the number of eye movements measured and velocity-matching percentages.)

The smooth pursuit velocity threshold can be described in the servo metaphor by plotting the eye movement velocity data as a velocity gain (output velocity/input velocity) *vs.* target velocity function. Fig. 8 shows this function. Data from an experiment by Steinman, *et al.* (1969) are included in these graphs. In that experiment the same subjects (AS and RS) tracked targets moving horizontally at 34, 69, 172, 344 and 687 min arc/sec. There was a corner in the system's gain function at 8 min arc/sec for AS and at 16 min arc/sec for RS. At target velocities below the corner velocity, gain was high (the eye moved considerably faster than the target) indicating that the system was operating in open-loop conditions, i.e. without stable feedback. Above corner velocity, target velocity had control over low velocity eye movements (the feedback loop had stabilized) and the system's gain was relatively stable at somewhat less than 0.0 dB. The data points obtained in the subsequent experiment (points joined by dashed lines) show that the slope of the gain function remains similar at much higher target velocities. (See Appendix J for tabled gain functions.)

The velocity threshold for smooth pursuit was the same when it was estimated by velocity or error angle criteria. The error angle criterion for smooth pursuit (error angle less than 90 deg arc)

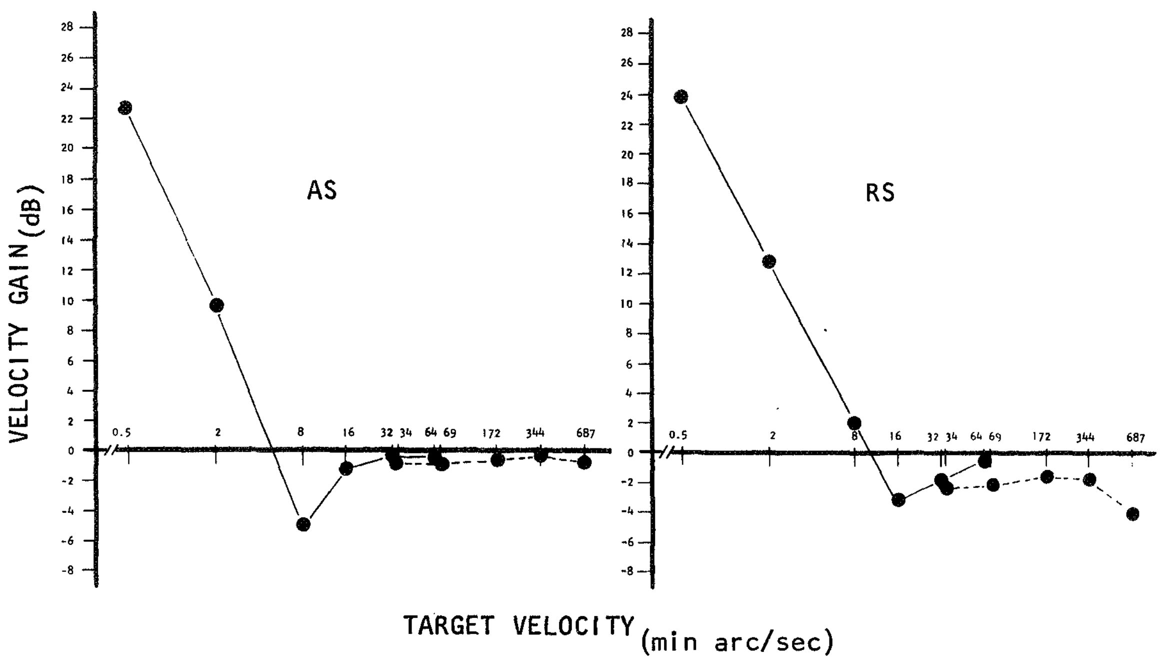

Fig. 8. Gain (eye velocity/target velocity in decibels) as a function of target velocity. The gain of subject AS's low velocity system is shown in the graph on the left and the gain of subject RS's low velocity system is shown in the graph on the right. Solid lines connect data points obtained in the present experiment. Dashed lines connect data points (for the same Ss) reported by Steinman, Skavenski and Sansbury (1969).

and the velocity criterion described above (corner velocity followed by a zero slope gain function) both show that AS's smooth pursuit velocity threshold was 8 min arc/sec and that RS's smooth pursuit velocity threshold was 16 min arc/sec. The fact that both criteria suggest the same velocity threshold makes it possible to modify the definition of smooth pursuit (smooth movements in the direction of the target) to include a requirement that eye velocity must not be greater than target velocity. This modification is necessary because, at very low target velocities, the eye may move in the target's direction at velocities so high as to create, rather than prevent, fixation errors. To illustrate, mean error angles for each direction of target motion were examined to determine whether the present Ss made smooth movements in the target's direction at very low target velocities. Two directions of target motion were found for AS in which mean error angles were quite small at the two lowest target velocities. AS's pursuit velocities in these two directions, however, were 10-20 times greater than the 0.5 min arc/sec target and about 3 times greater than the 2 min arc/sec target. Even though AS frequently went in the "correct" direction, large fixation errors occurred because his drifts were much too fast. The use of both direction and velocity criteria is useful to define smooth pursuit because such usage would prevent classification of gross error-producing low velocity eye movements as smooth pursuits.

Comparison of the present with prior results. Only two prior studies examined eye tracking of constant velocity targets moving slower than 1 deg arc/sec (Yarbus, 1967; Steinman, et al., 1969). The present findings confirmed Yarbus' (1967, p. 162) report that "smooth pursuit begins when the speed of the object equals the speed of the irregular drift of the eye . . ." and that smooth pursuits were readily observed at target velocities greater than 10 - 15 min arc/sec. Similar characteristics were observed in the present recordings. In the second study, Steinman, et al. (1969), using the same Ss as the present experiment, presented only one target velocity below 1 deg arc/sec (34 min arc/sec). Their results were quite similar to the present results.

When the target moved faster than 1 deg arc/sec, the eye's two-dimensional pursuit characteristics were, for the most part, similar to those reported by previous investigators for one-dimensional records of horizontal tracking (see Alpern, 1962 for a summary of the eye's horizontal tracking characteristics). The major exception noted was that smooth pursuit velocity was generally less than target velocity. This failure to match target velocity has been reported and discussed in detail by Puckett and Steinman (1969) who suggested that velocity undershooting is probably a general characteristic of smooth pursuit. This suggestion was based on the experience of their Ss, the sensitivity of the recording method and the demonstration of velocity undershooting in a large sample of smooth pursuits. The present results were obtained with the same Ss and recording method. These results show that velocity undershooting occurs even when the target is very slow. It seems reasonable to ask whether there might be something "abnormal" about AS and RS and whether "velocity undershooting" is really a general characteristic of the low velocity control system.[1] Some evidence in the present experiment suggests that AS and RS are "abnormal": these subjects are the first to show uniform patterns of drift "correction" parallel to all meridians. However, the drift "correction" pattern has been analyzed in detail for only four subjects to date (the present two and Nachmias' (1959) two Ss who did not have uniform drift "correction" patterns). Any populational statement based on this sample would be unwarranted. Also, even if AS and RS turn out to be exceptions with respect to the uniformity of their "corrective" drift pattern, there is no reason to assume that their ability to smoothly "correct" position errors along all meridians (a useful skill) is in any way related to their inability to smoothly pursue as fast as the target moves (probably also a useful skill, because if Ss actually match target velocity, the target image would be "stabilized" and would disappear from view).

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[1]Amplitude gains of less than 0.0 db (velocity undershooting) have been reported for sinusoidally moving targets on the horizontal axis (Fender, 1964) and also for "unpredictable" sinusoidally moving targets on the horizontal axis (Stark, et al., 1962). These researchers, however, did not choose to emphasize this particular result, although it has considerable significance for the operation of the low velocity pursuit system.

DISCUSSION

A Single System Controls All Low Velocity Eye Movements

The purpose of the present research was to clarify the relationship between noisy drifts, corrective drifts and smooth pursuits by examining Nachmias' (1961) suggestion that corrective drifts and smooth pursuits are controlled by a single system, i.e. smooth pursuit of a moving target is controlled by the same low velocity system that corrects position errors introduced by noisy drifts during maintained fixation of a stationary target. The results did not provide entirely convincing support of Nachmias' suggestion. This might not have been the case if AS and RS had shown some retinal meridians where drift correction was not an effective means of retinal position control. Had they performed in this manner, it would have been possible to analyze low velocity tracking along corrective and non-corrective meridians looking for different smooth pursuit characteristics parallel to each type.

The results seem to support Nachmias' suggestion that a single system controls all smooth corrective movements. This conclusion is based on the following two considerations:

1) If there are two low velocity control systems, one that corrects position errors produced by noisy drifts during fixation of a stationary target and a second that smoothly pursues a moving target, as target velocity increases control must shift from the corrective

drift position system to the smooth pursuit velocity system. The analyses performed on the present eye movement records failed to show any sign of a shift from one system to a qualitatively different one. It is possible, however, that the velocity at which the smooth pursuit system took over control from the corrective drift system was in the range of fixation drift velocity and that the transfer of system control was, therefore, unobservable. The changes in the error angle *vs.* target velocity functions were very gradual and it seems unlikely that low velocity control shifted from one system to a qualitatively different one. The present results are more easily explained by assuming that there is a single low velocity control system whose characteristics can account for the present data.

2) A dual system model of low velocity control is unnecessary because it can be shown that a single low velocity control system can not only follow moving targets but can correct position errors when stationary targets are fixated. There are two input signals to such a system. The first is the retinal position of the target image and the second is the low velocity changes in position generated by instabilities in the oculomotor system (noisy drifts continually change the velocity and direction of the eye). This single low velocity control system has a response threshold for low velocity errors somewhere in the range of noisy drift velocities. When the fixation target is objectively stationary, the low velocity control system will pursue all noisy drifts that are fast enough to exceed velocity threshold. These pursuits will move the eye in a direction opposite to the direction of drift displacement. In other words, the system moves the eye so as to null the velocity error signal which, in this case, was

produced by instability within the system itself. Once the eye starts to follow a displacement of the target image produced by a suprathreshold noisy drift, the magnitude of the velocity error will be reduced and eventually fall below threshold for the control system. At this point, the eye will begin to wander in a pattern determined solely by parameters of the system's own instabilities.

When the fixation target is objectively moving, the motion of the target provides a velocity error signal which is the same as that produced by oculomotor instability when the target is stationary. If the target moves fast enough, the low velocity control system will be activated and will try to null the suprathreshold velocity error. Such eye movements are called smooth pursuits.. During smooth pursuit, the velocity of the target motion will add algebraically to the velocity of the noisy drifts and the net image velocity must be sufficient to exceed the system's threshold before pursuit of a very slowly moving target can occur. The velocity threshold is less important when the target is moved rapidly because noisy drifts contribute only a small percentage of the total movement of the target image under such conditions.

When the eye begins to match target velocity, the velocity error (difference between eye and target velocity) decreases. When the error falls below velocity threshold, pursuit is no longer signalled and the eye starts to slow down. Once pursuit has slowed down, the velocity error signal increases as long as the target continues to move, exceeds threshold and once again provides a signal for the system to continue pursuing. Noisy drifts and the eye's inertial characteristics (Robinson, 1965) may occasionally combine with the low velocity control system's pursuit to allow the eye to move faster than the target for short periods of time. The eye's average velocity, however, must always be less than the target's because pursuit, itself, reduces the stimulus which activates pursuit.

Two other characteristics of the proposed single system model of low velocity control can be described:

1) The low velocity system does not respond to position errors. It responds only to velocity errors. The system does not know where the target image is on the retina and maintains whatever position is present until the position of the target image is changed by a saccade or objective movement of the target.

2) Low velocity position control is highly dependent upon the characteristics of the oculomotor system's instabilities. The present Ss showed directionally uniform patterns of drift correction, which makes it possible to predict that these Ss will be able to hold their eyes in place for long periods of time when they suppress fixation saccades. They can do this (Steinman, et al., 1967). Other subjects (such as those reported by Nachmias, 1959, who did not show uniform directional patterns of drift correction) should perform differently. Subjects, who have dominant directions of noisy drifts not compensated by corrective drifts, use saccades, exclusively, to correct errors in these directions. If such Ss suppress fixation saccades, they should drift away from their original fixation position in directions predictable from an analysis of their corrective drift pattern. This prediction has not yet been studied.

These considerations led to the examination of the problem of low velocity control from a servo theory approach in order to provide a more precise description of a control system which had such characteristics. First, I reviewed existing servomechanical models of eye position control in order to determine whether prior applications of the feedback control system approach could be used to describe my data. They could not.

What is wrong with existing servo models of eye position control? There have been a number of attempts to apply the mathematical and analytical tools of servo-mechanics to the entire or portions of the eye position control system. Among the many stimuli which have been used are: ramps (Westheimer, 1954; Rashbass, 1961); pulse-steps (Young and Stark, 1962; Wheeless, et al., 1966), step-ramps (Rashbass, 1961; Young and Stark, 1962; Stark, et al., 1962; Robinson, 1965), pure sinusoids (Fender and Nye, 1961; Stark, et al., 1962; Dallos and Jones, 1963; Robinson, 1964, 1965), motion consisting of the sums of several sinusoids (Stark, et al., 1962; St.Cyr and Fender, 1969b, c), and bandwidth-limited Gaussian random motion (Dallos and Jones, 1963; St.Cyr and Fender, 1969b, c). No researcher to date, however, has examined the smooth response of the eye to both stationary targets and targets moving slowly in a single unpredictable direction (very low velocity ramp stimuli).[1] Nevertheless, at least one of the many existing servo models should be able to describe the eye's response to both of these simple stimulus conditions.

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[1] This omission is not surprising because cyclical stimulus motions are more appropriate for the derivation of the mathematical describing functions used in feedback control theory.

Unfortunately, this is not the case. For example, one model (Boyce, 1967), is concerned primarily with the role of saccades in establishing a series of short-term fixation loci within the retinal "dead-zone" (a retinal area which does not provide image position information). This model ignores drift correction of stationary-target image position errors and predicts target velocity matching. Both corrective drifts and smooth pursuit velocity undershooting were observed in the present experiment.

Another model (Fender and Nye, 1961) also makes use of a retinal "dead-zone" and provides that when "the image returns to the insensitive zone no retinal feedback is generated, and the feedback system that remains, being only marginally stable, will perform the oscillations which have been described as the flick (saccade), drift, and tremor . . .". Therefore, this model fails to predict drift and saccadic correction observed in the present data because it ascribes all drifts and saccades to oculomotor system instability. A subsequent modification of this model (St.Cyr and Fender, 1969b, c) continues to overlook corrective smooth eye movements described in the present and and earlier papers (Nachmias, 1959, 1961; Steinman, 1964, 1965; Steinman, et al., 1967). Furthermore, the St.Cyr and Fender model, as did its predecessor, fails to take into account the demonstrated independence of the smooth and saccadic systems (Rashbass, 1961; Robinson, 1965) and treats both smooth and saccadic eye movements as if they were outputs of a single system.

Other models of the eye movement control system have been proposed which do not suffer these faults. Unfortunately they too are unable to predict certain aspects of the sensori-motor system's response to simple stimuli. For example, Young and Stark (1962) presented separate sampled-data models for smooth and saccadic eye movement systems. The primary assumption of both models is that each eye movement system obtains a brief sample of retinal image position every 100-200 msec and is then refractory for a period of the same duration during which changes in stimulation are not processed by either system. Although this may be a viable hypothesis to explain the action of the saccadic system, it seems unlikely to apply to smooth eye movement control for two reasons. First, the smooth system appears to act in a continuous fashion. Gradual smooth accelerations and decelerations of the eye, which are not dependent upon the kinematics of the globe and its supporting tissue (Robinson, 1964, 1965), are almost always observed in the records of subjects fixating a target suddenly set in motion. More importantly, Robinson (1965) has shown that the eye's response to two successive ramp stimuli temporally spaced either 150, 100 or 75 msec apart is (although delayed by a response latency) two smooth eye movements temporally separated from each other by 150, 100 and 75 msec, respectively. Thus, if there is a refractory or intersampling period, it must be shorter than 75 msec. If the intersample interval is less than the response time of the mechanical apparatus being controlled, the "sampled-data" model is indistinguishable from a continuous system (Rashbass, 1961). A continuous system recommends itself on the basis of simplicity (Robinson, 1965).

In summary, existing servo models of the eye movement control system cannot describe the performance of Ss in the present as well as many prior experiments. This discouraging fact led me to try to sketch out the qualitative features of a potentially satisfactory model. This model will now be discussed.

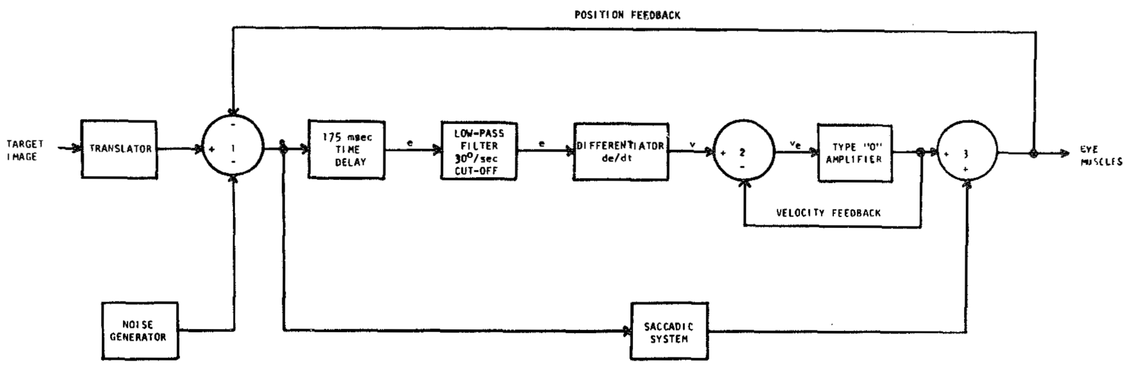

Fig. 9. The proposed model of low velocity eye movement control.

Servo Model of Low Velocity Eye Movement Control

The proposed model of the low velocity control system is illustrated in block diagram form in Fig. 9. The saccadic system is represented only by a single block and will not be discussed because this system has been shown to be independent of the smooth system and the present experiments do not add any information to what is already known about its operation. The main features of the model include a signalling grid (translator) and "noise" generator which provide the input to the system; a low-pass filter which limits the system's response to very fast target motions; a differentiator to transform position error signals into velocity error signals; and a servomechanism whose output velocity is always less than its input velocity, *i.e.* a Type "O" servo.

Translator. When subjects fixate a target, the target is imaged on the retinal surface and is converted into a position signal which defines the retinal location of the target image with respect to the functional center ("optimal" locus) of the retinal signalling grid. The image position signal serves as the input to Summing Point 1 in the proposed model. Steinman's (1965) evidence makes it plausible to maintain that retinal image position is signalled by the stimulation of concentrically arranged retinal elements which provide distance and direction signals which locate the retinal image relative to the optimal locus. The proposed *Translator* has similar characteristics.

The Translator provides a position signal to the low velocity control system only when it is presented with a target. Skavenski and Steinman (1969) have shown that there is no low velocity control of eye position when subjects attempt to maintain their eyes in place in the dark. The eye drifts rapidly away from the previously defined fixation position when a visible target is removed from view if saccades are suppressed. Some control of eye position in the dark remains, however, when saccades are permitted but such control is exclusively saccadic and much less precise than when a target is visible and low velocity correction is signalled (the variability of eye position on an average meridian increased from approximately 5 min arc when the target was visible to about 30 min arc when Ss tried to keep in place in total darkness).

Noise Generator. This element in the model produces noisy drifts. Direction and velocity signals produced by noisy drifts in the presence of a target are introduced at Summing Point 1 in the proposed model.[1] The oculomotor system must have a noise generator because the eye is in continual motion even when the target is stationary and the subject tries to keep his eye in place. These noisy movements are important because without them the eye would come to rest, the retinal image would be stabilized and the target would disappear from view. The characteristics of noisy eye movements during fixation of a stationary target have been described and modeled by Cornsweet (1956), Nachimas, (1959, 1961), and Boyce (1967). The proposed model, however, is the

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[1] The characteristics of the Noise Generator output may be determined for any subject by examining the drift pattern of his eye in the absence of a visual stimulus. Such an examination is currently being made for the present Ss by Skavenski (private communication).

first to explicitly include noisy drifts in the description of the pursuit of moving targets. The inclusion of noise in the model of low velocity control permits drift correction during fixation of a stationary target to be described in the same manner as smooth pursuit of a moving target. Under both conditions, low velocity control begins only after target image velocity exceeds some threshold just above the velocity of noise drifts. Noise becomes less important at higher target velocities because noisy drifts contribute little to target image motion when the target moves much faster than the eye drifts (about 15 min arc/sec).

Summing Point 1. The position of the eye at any particular moment is fedback from the output of the eye position control system to Summing Point 1 where it is subtracted from the difference of the image position and "noise" signals. This operation provides the position error signal, e, which is used to actuate the smooth (and saccadic) eye movement sub-systems.

Smooth System. The smooth portion of the eye position control system model consists of five components and one internal feedback loop:

1) The position error signal, e, determined at Summing Point 1, is delayed approximately 175 msec by the first component of the smooth eye movement sub-system. This time-delay element represents the lumping together of all neural transmission delays and is equal to the response latency of the smooth system to step changes in velocity (Robinson, 1968).[1]

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[1] This estimate of the time delay applies only to pursuit of simple linear target motions. St.Cyr and Fender (1969c) present compelling

2) The second element in the smooth system is a low-pass filter which places an upper limit on the velocity of position error changes which can be followed by the system. The forward gain of the low-pass filter is unity at low target velocities and drops to zero at higher target velocities. The "cut-off" (zero gain) velocity is probably about 30 deg arc/sec (Westheimer, 1954).[1]

The low-pass filter serves an important function in that it prevents error position signals that change at very high target velocities (eg. step changes of target position) from overloading the next element in the system, a differentiator. It may be seen that velocity limiting is a necessary feature of any velocity controlled system. A theoretically perfect differentiator will respond with infinite output to any instantaneous (infinitely rapid) change at its input and a practical differentiator will immediately overload (saturate) if

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evidence to show that response latency depends on the class of target motion. They found delays ranging from 129 to 534 msec for monocular fixation of various bandwidth limited, random Gaussian target motions (narrower bandwidths and, therefore, simpler pursuit tasks, yielded the shorter time delays).

[1] A summary of the frequency response characteristics of the human oculomotor system observed in five different sets of experiments may be found in St.Cyr and Fender (1969b). The gain vs. frequency curves they present indicate that the oculomotor system can be approximated by a low-pass network with a corner frequency (frequency at which gain starts to decrease) at roughly 1.5 Hz. St.Cyr and Fender point out, however, that the system gain characteristics are non-linear, i.e. gain decreases with increased stimulus amplitude and also decreases with increasing complexity of target motion. Since the data base for the present model consisted of the eye's smooth response to constant velocity target motion and not to various kinds of sinussoidal target motions, the gain vs. frequency characteristics of the present Ss could not be described.

confronted with such signals. Furthermore, note that this feature is characteristic of the data; the eye does not smoothly respond to step changes in target image position (Robinson, 1965).

3) The third element in the model of the smooth eye movement subsystem is a differentiator which transforms the position error signal, *e*, into a velocity (rate of change in position) signal, *i.e.* it differentiates position error with respect to time ($v = de/dt$). The differentiator simulates the smooth pursuit threshold, a characteristic of low velocity control observed in the present experiment. An electronic differentiator (functionally equivalent to the one proposed) responds similarly to a capacitatively coupled amplifier which cannot respond to very slow changes, *eg*. D.C., at its input. The proposed differentiator will have this characteristic. It will not respond to very slow changes of image position at its input. This failure to respond to slow changes in image position is analogous to a threshold. Furthermore, electronic differentiators, similar to the one proposed, are well known for their tendency to disproportionally amplify small amounts of input noise. Since the output of the proposed differentiator drives the remainder of the smooth eye movement control system, noisy *differentiator* outputs, as well as oculomotor instabilities, may also be expected to serve as a source of noisy drifts.

4) The next two elements and the internal velocity feedback loop comprise a Type "0" servo. The input and output signals of a Type "0" servomechanism are of the same order. In the proposed model, velocity is the relevant signal and a velocity change at its input causes a velocity change in its output (D'Azzo and Houpis, 1966). Furthermore, the output of a Type "0" servomechanism is always less than its input.

This characteristic will cause the eye to smoothly pursue at <u>less</u> than target velocity. In the present experiment, smooth pursuits were slower than the target at target velocities where target motion was a large fraction of the total movement of the eye. Similar velocity undershooting at still higher target velocities was reported for these same subjects by Puckett and Steinman (1969) and Steinman, <u>et al</u>. (1969).

The proposed model represents a significant departure from earlier models in this respect. Earlier models were, without exception, Type "1" servos. A Type "1" servo was proposed because data, obtained with relatively insensitive recording techniques, suggested that the eye "perfectly" matched the velocity of a moving target. If gain is, in fact, unity (input velocity = output velocity), it is appropriate to describe the low velocity control system as a Type "1" servo.[1] Dallos and Jones (1963) discussed the problem of determining the order of the eye movement control servo and pointed out that in their experiments "the system response can only be measured to within some experimental error, say one or two percent, and within this limit it is impossible to say that the gain is precisely unity, and the system Type '1'." The sensitivity of the contact lens-optical lever technique used in the present experiment was an order of magnitude better than most earlier techniques and was sufficient to allow this distinction to be easily made. The average velocity of the eye's smooth component was less than the target's velocity once the system's "noise" levels had been exceeded. Therefore, the closed-loop gains were less than unity and the system is similar to a Type "0" servo.

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[1] The defining feature of a Type "1" servo is an integrating element which permits it to match input velocities (Dallos and Jones, 1963; D'Azzo and Houpis, 1966).

The first component in the velocity servomechanism portion of the smooth system is Summing Point 2 which receives the velocity signal from the differentiator. This element calculates the velocity difference between the input and the output of the servo and transmits this velocity error ($\underline{v_e}$) in the form of an actuating signal to the amplifier.

5) The final component in the smooth eye movement control sub-system is the amplifier. The amplifier represents the smooth motor system's response to the velocity-error actuating signal.

6) The output velocity of the amplifier is negatively fedback to Summing Point 2 in the velocity feedback loop. It is assumed that the gain in this loop is unity since it is, in current practice, unmeasureable and since unity is the most likely value. Fortunately, the exact value of the feedback gain is of relatively little consequence to the general structure of the model; other feedback gains merely alter the time required for the servo to achieve its maximum "steady-state" velocity (D'Azzo and Houpis, 1966).

<u>Summing Point 3</u>. The smooth and saccadic sub-systems share a common outlet, the motor nuclei which innervate the extra-ocular muscles (Robinson, 1968). Summing Point 3 represents the point where the outputs of the smooth and saccadic sub-systems are combined.

<u>Position Feedback Loop</u>. This is a negative feedback loop which transmits the output position of the eye position control system back to its input at Summing Point 1 where it is used to determine the magnitude and direction of the retinal position error. It is assumed that there is unity gain in the position feedback loop.

<u>Implications and limitations</u>. The features which distinguish the proposed model from others are the prediction of noisy and corrective eye movements when stationary targets are fixated and the prediction of velocity undershooting when moving targets are tracked. Several features of the model as it now stands are either open to question or require further elucidation. For example:

1) Relatively little is actually known about the characteristics of the retinal "dead zone" reported by Glezer (1959) and Boyce (1967) who suggested that there is an area of the retinal surface which does not provide <u>position</u> information to the oculomotor system. The present model is based, in part, on a different concept; that there is no "dead zone" for velocity but there is a smooth pursuit velocity threshold. It is possible that there is a retinal "dead zone" for <u>velocity</u> and only when targets move outside this area will the eye begin to smoothly pursue. This possibility can be examined by instructing subjects to smoothly pursue a target which is stepped in one direction and is then set into constant velocity motion in that direction. If the target image position is initially displaced far enough to be outside the limits of a velocity "dead zone", smooth pursuit at lower velocities than were observed in the present experiment will occur. On the other hand, the smooth pursuit velocity threshold will remain unchanged under these conditions if there is no "dead zone" for target velocity. If this proves to be the case, the proposed model is tenable.

2) The location of the noise generator is not specified in the model. Noise has been attributed to instability of the extra-ocular muscles. It seems reasonable to suspect that at least some of the

noise may be due to the differentiating process[1] which determines stimulus velocity. Electro-physiological studies of movement-sensitive ganglion cells may provide a measure of the amount of noise generated by the differentiating process itself.

3) The low-pass filter is schematicized as a single element. It is quite likely that each element in the low velocity control system has its own band-pass characteristics. These characteristics are unknown at the present time, although it is hoped that it will be possible to design experiments to identify the characteristics of each element in the low velocity control system. Such experiments are likely to procede from behavioral attempts to open the velocity and position feedback loops in the intact organism and from neurological studies within the system itself.

4) In its present qualitative state it is not possible to use the proposed model to describe quantitatively the smooth system's response to periodic stimuli. Unfortunately, existing transfer functions reported in earlier models cannot be used for this purpose because their developers did not have sufficiently sensitive recording techniques, a fact shown by their failure to detect velocity undershooting. For quantitative prediction, cyclical stimulus motions with specifiable frequency characteristics (perhaps the two-dimensional sinusoids used by St. Cyr and Fender, 1969b, c) must be coupled with a sensitive recording method in order to establish the functional

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[1] Any differentiator will be noisy because differentiating results in large outputs for small noisy inputs, i.e. differentiators amplify rapidly changing signals (typical of nervous system "noise") more than slowly changing signals.

parameters (gain and phase vs. frequency) of the proposed Type "0" smooth eye movement control system. Establishing these parameters may not be a simple task. St. Cyr and Fender (1969b, c) demonstrated that, when the outputs of the smooth and saccadic systems are treated as a single combined output, the functional parameters of the combined system change with the complexity of the fixation task, eg. bandwidth decreases with increasing task complexity (the combined systems respond to a narrower range of stimulus frequencies) and response latency increases.

In its present form, the proposed model may be used to quantitatively predict the smooth system's response to linear, constant velocity target motions and only qualitatively predict the response to cyclical target motions. Quantitative prediction of the response to periodic stimuli will require only further data gathering (as outlined above) and fitting of the appropriate transfer functions. If, however, the stimulus dependent parameter modifications reported by St. Cyr and Fender turn out to be characteristic of the smooth system the proposed model of the low velocity control system will have to be modified. Such modifications will directly concern the time-delay and low-pass elements and will have strong implications for the investigations described in paragraph 3 above.

5) The present model also does not account for several other non-linear phenomena associated with the tracking of periodic stimuli. For example, Dodge (1907), Westheimer (1954), Stark, et al. (1962) and Dallos and Jones (1963) have shown that when stimuli are periodic and thus predictable, the eye position control system's performance

can improve with practice. Furthermore, Westheimer (1954) demonstrated that when relatively simple periodic stimuli are occasionally obscured from view, tracking performance did not deteriorate. The eye was able to predict the position of the target even though it was not visible at all times. Since such predictive and learning capabilities are probably characteristic of the smooth system alone, the system will be, as Fender (1964) has used the term, an input-adaptive system. Input-adaptation implies that the system can add predictive and short-term memory units to its structure when required by the fixation task. The proposed model does not have this capability and, therefore, will only be applicable to the early stages of a periodic tracking task. Such features could, of course, be added to the input side of the present model in a fashion analogous to that employed by Dallos and Jones (1963) when sufficient descriptive data become available.

6) There is some evidence to suppport the notion of complete voluntary control of the low velocity control system. Steinman, et al. (1969) have shown that subjects are able to smoothly pursue targets at voluntarily chosen fractions of the target's velocity. Their finding implies that the overall gain of the smooth system is adjustable in some voluntarily controlled manner. In its present non-voluntary (reflexive) form, the model does not attempt to, and is not able to, describe voluntarily controlled velocity undershooting. Note, however, that a gain control could be simply added to the present model by varying the amplification of velocity signals in the Type "0" servo. The way in which this amplification factor would be adjusted (in other words, what mechanism operates the control) is certainly open to question and is beyond the scope of the present paper.

7) The evidence presented in support of a single, velocity controlled, smooth pursuit system was of a negative character. A shift from a position controlled system to a velocity controlled system when the stationary target was set in motion is possible. This hypothesis may be examined by studying the directional pursuit movements of subjects who do not show uniform patterns of drift correction.

APPENDIX A

STIMULI

The fixation target, a small (< 1 min arc diam) point of red light, was displayed on the face of a Tektronix Model 503 X-Y Oscilloscope. The oscilloscope face was covered with a red filter (Kodak Wratten #25) located 1.0m from S's eye. Target luminance was adjusted by means of a 10 turn precision potentiometer substituted for the oscilloscope's standard intensity control. The luminance was set at 1.31 log units above the absolute foveal threshold, determined for each S by a descending method of adjustment. The actual luminance of the targets was 8.5 mL for RS and 15.1 mL for AS. (See Appendix B for a description of the absolute calibration procedures.)

The oscilloscope display was driven by a modified Electronic Associates radar computer which was programmed to provide a series of ramp voltages. $\Delta V / \Delta t$ (the rate of increase of the ramp voltages and thus the velocity of the point target) was adjusted by means of two weighted summing integrator circuits. The direction of target motion could be chosen by varying the ratio $\Delta V_x / \Delta V_y$ (x refers to the horizontal and y the vertical input of the oscilloscope). The duration of target motion, and thus its extent, was controlled by locally constructed, highly stable, solid-state RC timers.

Fig. 10 is a block diagram of the computer and associated timer-oscilloscope circuitry. A regulated +100VDC power supply and an inverting amplifier (1) provided a + or - 100 VDC input to the

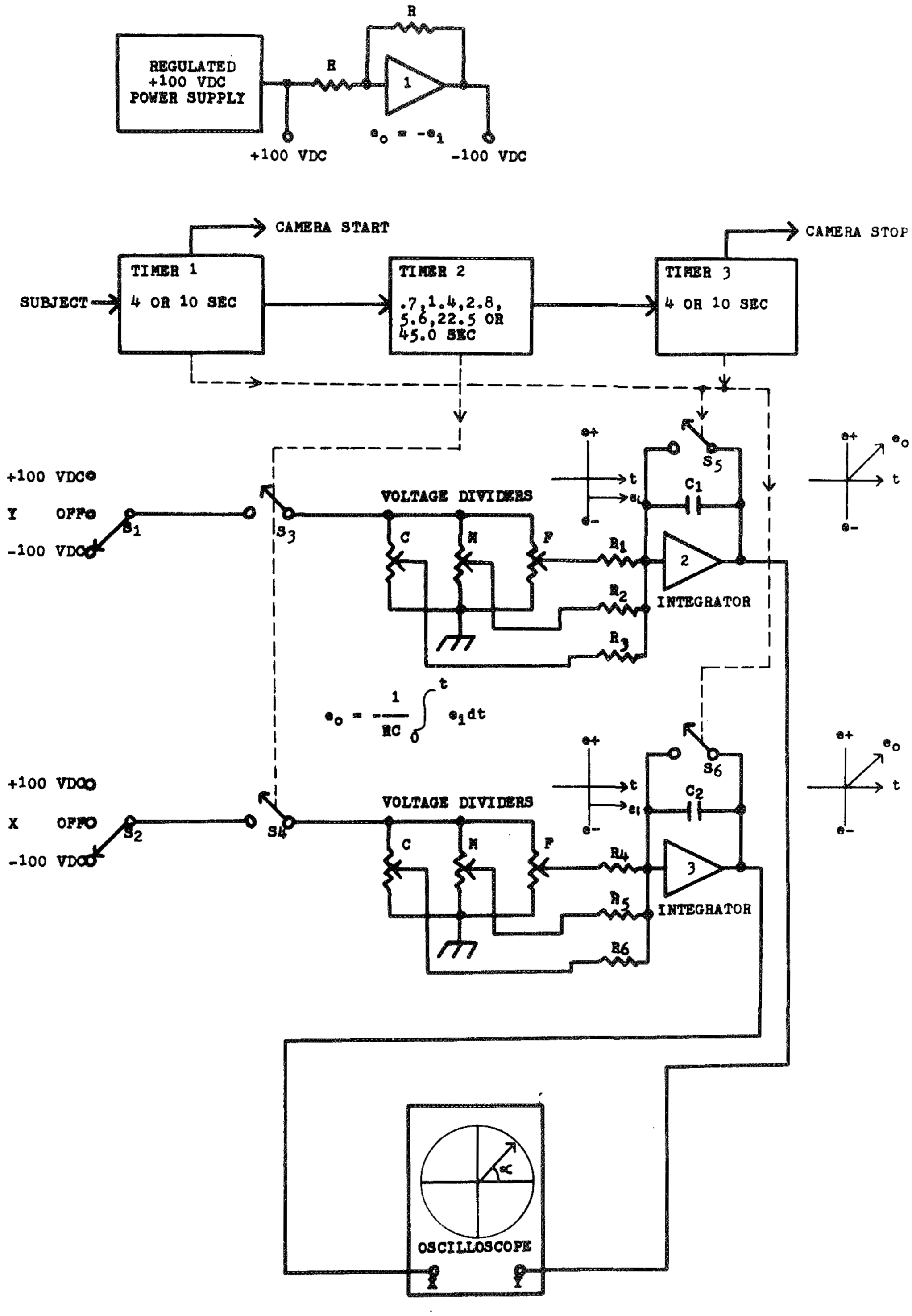


Fig. 10. A block diagram of the electronic apparatus employed for generating and timing stimuli. An example of the switch configurations required to move a point up and to the right on the oscilloscope face is also illustrated.

integrator circuits. E set S_1 and S_2 prior to each trial. These switches determined the direction of the target motion by changing the polarity of the input voltage to the integrators. The "off" position on these switches preset a pure horizontal, pure vertical or zero velocity trial.

Ss initiated a trial by closing a push button which activated Timer 1. This timer started the camera and short-circuited the integrating capacitors. When it had "timed-out", Timer 2 was activated and the short was removed from the integrating capacitors. The second timer operated an infrared strobe tube to mark the beginning of target motion and closed S_3 and S_4 which applied input to the voltage dividers. The voltage dividers and the weighting resistors C, M, and F, effectively divided the 100 VDC input into 90,000 steps of .00111... volts each. Since the transfer function for circuits of this type is $e_{out} = (-1/RC) \int_0^t e_{in}\, dt$, the output voltage was an increasing function of time for a constant voltage input. E preset the input voltages by adjusting the voltage divider to a precalibrated position. The outputs of the integrators (amplifiers 2 and 3) were fed into the oscilloscope during the operation of Timer 2.

Fig. 10 includes an example of the circuit configuration used to move the target point up and to the right at a constant velocity. S_1 is set in the -100VDC position. The voltage dividers in the Y channel apply some portion of this voltage to the input of the integrating amplifier (2) which inverts its polarity. The capacitor (C_1) gradually charges and applies a positively increasing (ramp) voltage to the vertical amplifier circuits of the oscilloscope. This has the effect of moving the point smoothly upward. The X channel, at the same time, is providing a positively increasing (ramp) voltage to the horizontal amplifier circuits of the oscilloscope. This moves the point smoothly to the right on the face. The resultant target motion is up and to the right.

The angle at which the target point moves (α) is determined by the ratio of the voltages produced by the two voltage dividers. For example, if the input to the integrators is equal and negative, the point will move up and to the right at an angle of 45°; a negative input to the Y channel and an equal positive input to the X channel will move the point up and to the left at an angle of 135°; no input (zero voltage) to the X integrator and a positive input to the Y integrator would result in a pure downward movement of the target at an angle of 270°. When Timer 2 "timed-out" the input voltage to both integrators was removed, the infrared strobe tube was again flashed marking the end of target motion and Timer 3 was activated. This had the effect of stopping the target motion completely and leaving the target in the position where it had stopped. "Timing-out" of Timer 3 stopped the camera and discharged the integrating capacitors, thus ending the trial and returning the point target to its initial position.

APPENDIX B

CALIBRATION

<u>Stimulus velocity</u>. An illuminated plexiglass reticule, enscribed with a 45 min arc radius circle and center, was placed in front of the oscilloscope face. The oscilloscope position controls were adjusted so that the stimulus point was occluded by the small reticule center mark. The duration of the 45 min arc target motion was then calculated for each velocity and set on <u>Timer 2</u> (<u>Timer 2</u> controlled the duraction of stimulus motion). Finally, ramp voltage slopes were adjusted on the computer so that the point was occluded by the 45 min arc radius circle when the timer had "timed-out". These values were recorded for target directions of 0, 90, 180 and 270 deg arc and the computer settings for 45, 135, 225 and 315 deg arc were calculated and confirmed in the manner previously described. All "velocity" and "direction" computer settings were determined prior to running the subjects and checked at the middle and end of the experiments.

The duration of <u>Timer 2</u> was continuously monitored throughout the experiments and was always within ± 0.2% of the appropriate durations. The extent of target motion could be determined within 0.5%; this corresponds to approximately ± 0.5 min arc, the width of the scribed circle and the diameter of the point target.

<u>Timer calibration</u>. <u>Timers 1, 2</u> and <u>3</u> were adjusted by means of a 10 turn potentiometer and precision plug-in resistors. All time values were repeatable to within ± 0.2% of their set value and

were calibrated by means of a tuning fork based, ring tube timer which was capable of resolving 1 msec ± 1 msec. The timer durations were as follows:

1) Timer 1: pre-movement fixation period: median duration = 10.160 sec, N = 9 or duration = 4.454 sec, N = 9

2) Timer 2: target motion; monitored continuously throughout experiment; set at 45.000, 22.500, 5.625, 2.812, 1.406 or 0.703 sec for the 0.5, 2.0, 8.0, 16.0, 32.0 and 64.0 min arc/sec target velocities respectively.

3) Timer 3: post-movement fixation period; median duration = 10.187 sec, N = 9 or duration = 4.052 sec, N = 9.

Stimulus intensity. The stimulus intensity was set at 1.31 log units above each S's absolute threshold for a descending method of adjustment. A 1.31 log unit Kodak neutral density filter was placed in front of S's eye and the oscilloscope intensity was slowly lowered by E who rotated the ten-turn oscilloscope intensity control until S reported the disappearance of the target. Eleven descending trials were presented to each S and the median setting of the ten-turn potentiometer was used throughout the experiments. The neutral density filter was calibrated with a Macbeth Quanta-Log Densitometer.

The absolute luminance of the target was determined indirectly. The red Kodak Wratten #25 filter was removed from the oscilloscope face and placed just in front of E's eye. A point sized aperture was then placed in front of a large homogeneous field whose luminance could be varied by means of a calibrated neutral density wedge. This field and the target point were optically placed side by side by means of a beam splitter. E, utilizing the method of adjustment, rotated the circular neutral density wedge until both points appeared equally bright. The wedge was then set at the median value of five ascending and four descending trials. Next, the aperture was removed from in front of the homogeneous field and heterochromatic photometry of the large field with an S.E.I. Photometer, calibrated against a Spectra Regulated Brightness Source, provided the final determination of absolute luminance. The luminance of the point targets, calibrated in this manner, was 8.5 mL for RS and 15.1 mL for AS.

APPENDIX C

RECORDING

The contact lens-optical lever technique is the preferred method of recording very small eye movements. A variant of this procedure, first described by Nachmias (1959), was used. This method permits simultaneous recordings of eye rotations about the vertical axis and the horizontal axis in Listing's Plane uncontaminated by torsions of the eye or translations of the head.

*S*s were tightly fitted scleral contact lenses[1] on the right eye and steadied their heads with plastic dental biting boards. A plane mirror, adjustable so as to be normal to the line of regard, was mounted on a hollow aluminum stalk attached to the temporal side of the corneal bulge of the lens. A projection system imaged a small portion of an automobile headlight lamp filament (*G.E.* 1183) on the contact lens mirror. A wedge shaped aperture, placed in a collimated portion of the recording beam and reflected from the contact lens mirror, was imaged, after passing through a lens and two mirrors, on a narrow horizontal slit. This slit was located directly in front of

---

[1] It is known that, for fixation of stationary targets, the scleral contact lens will follow movements of the eye with quite reasonable fidelity (Riggs and Schick, 1968). The contact lenses used were of a similar type (limbal seat) and will follow low velocity pursuit movements (up to 10 deg arc/sec) for extents under 2 deg arc without appreciable slippage. Pursuit movements in the present experiment were well within these limits so it is felt that this assumption is easily justified for the present findings.

35 mm Kodak High Speed Infrared film moving continuously at 22.2 in/min in a modified Dumont Oscillograph Record Camera (Model No. 321). The image of the wedge aperture was oriented on the camera slit so that rotations about the eye's vertical axis (horizontal movements) displaced the lateral position of the vertical edge of the wedge image on the film. Rotations about the horizontal axis (vertical movements) changed the width of the aperture's image on the film plane. This resulted in a film trace which, referenced to S's visual world, narrowed for upward movements, widened for downward movements and was shifted left and right for left and right movements respectively (see Fig. 11 for a schematic of the apparatus). A modified auto-tuning motor (Collins Type 596A1) was used to insert either a visible red (for alignment purposes) or infrared (Kodak Wratten #87, for recording) filter in front of the recording source lamp (G.E. 1183 run at 5ADC). A brief (5 minute) alignment procedure preceded each experimental session. The point image of the source filament was adjusted to fall in the center of the contact lens mirror by moving the wedge-lens mechanism. The mirror, on the camera side of the recording path, was also adjusted so that the wedge image was centered on the camera slit (see Steinman, 1964) for a detailed description of the mechanics of the alignment procedure). The alignment procedure was critical since the relatively long (and thus sensitive) optical lever and the 35 mm film width used in the experiment limited the range of the recording system to movements within approximately a 50 min arc radius of a central fixation point.

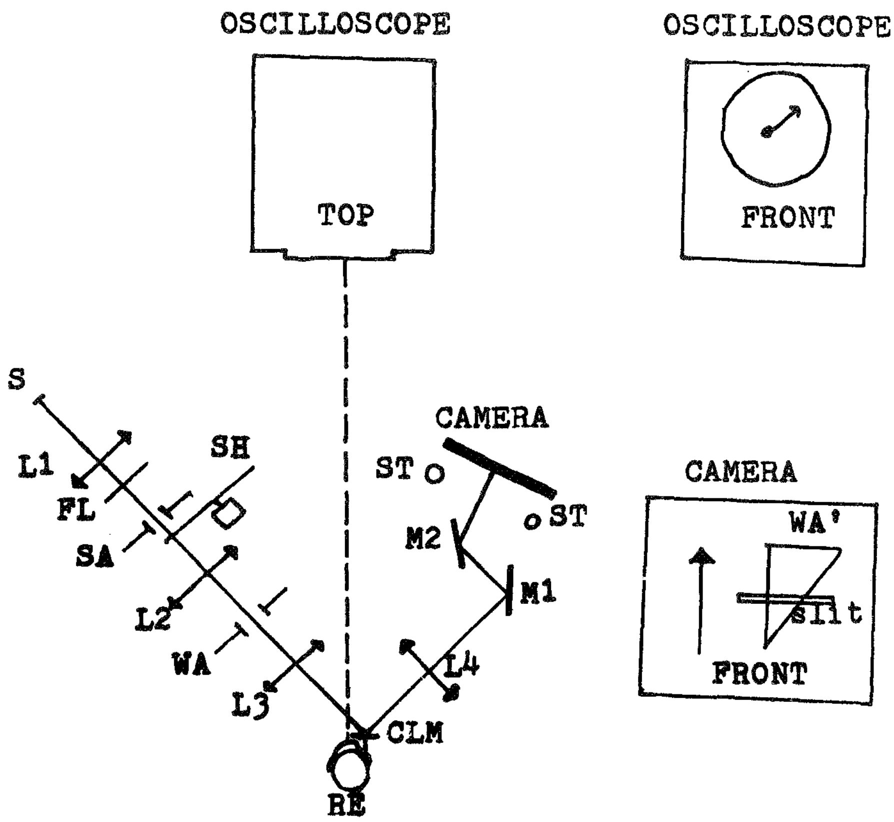


Fig. 11. Schematic diagram of the fixation path (dashed line) and recording apparatus (solid line). S is the recording source (G.E. 1183 automobile lamp); L1, 2, 3, & 4 lenses; SA & WA apertures; FL Kodak #87 infrared filter (recording) or visible red filter (alignment); M1 & 2 first surface mirrors; CLM a small first surface mirror attached to a scleral contact lens worn on the right eye (RE); ST strobe tubes for 1.0 sec time base and for marking onset and offset of target motion; SH 0.1 sec time base shutter. The lower insert shows the image of the wedge aperture on a horizontal slit in front of the film; the arrow indicates the direction of film motion in the camera.

After the alignment procedure was completed, the infrared filter was inserted in the recording path so that stray light from the recording system would not interfere with fixation of the stimuli.

The recording path was briefly interrupted every 0.1 sec and an infrared strobe tube was flashed every 1.0 sec in order to provide a time base on the filmed records. A second infrared strobe tube was operated when the fixation target started and stopped moving.

APPENDIX D

TRIALS SUBJECT AS

Velocity

Direction	0.0	0.5	2.0	8.0	16.0	32.0	64.0	min arc/sec
0°	2	2	3	3	3	2(3)	3(7)	
45°	2	2	2	3	2	3(3)	2(9)	
90°	2	2	2	2	2	2(2)	2(6)	
135°	2	3	2	2	2	2(2)	2(6)	
180°	2	2	3	2	2	2(2)	2(6)	
225°	3	2	3	2	2	2(3)	2(6)	
270°	3	2	3	3	3	2(2)	3(7)	
315°	3	2	3	3	3	2(2)	2(9)	
Extent	0	22.5	45	45	45	45	45	min arc
Duration	var.	45	22.5	5.6	2.8	1.4	0.7	sec

The number of trials under each experimental condition is indicated in the body of the table. Direction is given in degrees in a polar coordinate system. Stationary (0 min arc/sec) trials were randomly inserted in each sequence at a given velocity. The numbers in parentheses refer to trials in which the pre-movement period was 4.5 sec and the post-movement period was 4.0 sec.

Subject **RS**

Velocity

Direction	0.0	0.5	2.0	8.0	16.0	32.0	64.0	min arc/sec
0^o	2	2	2	2	2	2(2)	2(6)	
45^o	3	2	2	3	2	2(2)	3(9)	
90^o	2	2	2	2	2	2(2)	3(6)	
135^o	2	2	2	2	2	2(2)	2(7)	
180^o	2	2	2	2	2	2(2)	2(7)	
225^o	2	3	2	2	3	2(3)	4(6)	
270^o	3	2	2	3	2	2(2)	2(6)	
315^o	2	2	2	2	2	2(2)	2(6)	
Extent	0	22.5	45	45	45	45	45	min arc
Duration	var.	45	22.5	5.6	2.8	1.4	0.7	sec

The number of trials under each experimental condition is indicated in the body of the table. Direction is given in degrees in a polar coordinate system. Stationary (0 min arc/sec) trials were randomly inserted in each sequence at a given velocity. The numbers in parentheses refer to trials in which the pre-movement period was 4.5 sec and the post-movement period was 4.0 sec.

APPENDIX E

PROGRAM FOR CALCULATION OF M_N

This is a Fortran V program for the Univac 1108 which calculates the mean eye movement vector (M_N) of N individual eye movements whose beginning (X,Y) and end (XPRIME, YPRIME) points are known.

```
column
1     7
      DIMENSIØN R(360), RVEC(360)
      DATA PI/3.1415926/
      DATA DEGREE/.017453293/
      DØ 1 L = 1,360
      RVEC(L) = 0.0
    1 CONTINUE
      DØ 100 I = 1,N
      READ(X,Y,XPRIME,YPRIME) @NØTE: PRØPER FØRMAT STATEMENTS MISSING
      IF((X - XPRIME).EQ.0.AND.(Y - YPRIME).EQ.0) GØ TØ 100
      THETA = ATAN2((Y - YPRIME),(XPRIME - X))
      IF(THETA.LT.0) THETA = THETA + 2PI
      D = SQRT((X - XPRIME)**2 + (Y - YPRIME)**2)
      DØ 10 L = 1,360
      R(L) = D*CØS(THETA - L*DEGREE) @ R(L) CØNTAINS 360 CØMPØNENTS
   10 CONTINUE
      DØ 20 L = 1,360
      RVEC(L) = RVEC(L) + R(L)
   20 CØNTINUE
  100 CØNTINUE
      DØ 200 L = 1,360 @FIND MEAN ØF EACH ØF 360 VECTØR CØMPØNENTS
      RVEC(L) = RVEC(L)/FLØAT(N)
  200 CØNTINUE
      IJ = 1 @FIND LARGEST CØMPØNENT
      RMAX = RVEC(1)
  300 IJ = IJ + 1
      RMAX = AMAX1(RMAX,RVEC(IJ)) @RMAX IS THE LENGTH OF M-SUB-N
      IF(IJ.LT.360) GØ TØ 300
      DØ 400 I = 1,360
      IF(RMAX.EQ.RVEC(I)) GØ TØ 500 @FIND MERIDIAN CØNTAINING RMAX
  400 CØNTINUE
  500 IR = I @IR IS THE DIRECTIØN, IN PØLAR CØØRDINATES, ØF M-SUB-N
```

APPENDIX F

COMPARISON OF THE PRESENT Ss' FIXATION OF STATIONARY TARGETS WITH THAT OF OTHER Ss'

An analysis of the randomly interspersed "catch" (no target motion) trials was performed. This analysis permitted the eye movements of the present Ss to be compared with reports of the eye movements of most other contact lens Ss. The descriptive measures (see below) were obtained from the 19 "catch" trials presented to AS and the 18 "catch" trials presented to RS. These trials yielded 54 saccade and 245 tenth sec drift samples in 35.6 sec of fixation for RS and 44 saccade and 264 tenth sec drift samples in 33.9 sec of fixation for AS. The trials were scattered throughout several months' of experimentation.

Ditchburn and Foley-Fisher (1967) reported that 50% of the subjects in their literature survey (comprising 14 different experiments with 30 contact lens subjects) had saccade rates between 1.4 and 3.3 saccades/sec. AS's saccade rate, 1.2 saccades/sec, was just below this range, and RS's rate of 1.9 saccades/sec fell very close to the median of the survey group and was just above the 1.7 saccades/sec rate he had exhibited several years previously while viewing a similar target (Steinman, 1965).

The absolute magnitude of saccadic eye movements was estimated by taking the mean of the angular difference between the beginning and end point measurements of the 0.1 sec intervals that contained saccadic eye movements.[1] The mean absolute magnitude of saccades (4.6 min arc for AS and 3.6 min arc for RS) were well within the 50% range (3.0 to 6.0 min arc) summarized by Ditchburn and Foley-Fisher (1967) and are typical of those usually observed for these Ss in other experiments, eg. Steinman, et al. (1967).

The absolute magnitude of both AS's and RS's mean 0.1 sec drift vector was 1.5 min arc which corresponds to a drift velocity of 15 min arc/sec (10 times the 0.1 sec drift vector). Ditchburn and Foley-Fisher (1967) reported the median magnitude of intersaccadic drifts for their sample from which the mean effective drift velocity can be estimated. However, the estimate (6.0 min arc/sec) cannot be compared with the 15 min arc/sec absolute drift velocities reported above for the present Ss. The difficulty is readily apparent from a casual examination of the fixation records; intersaccadic drifts typically do not follow a linear course but are usually seen to curve back on their own track, i.e. they move the eye towards, as well as away from, the eye's mean position. This process is fairly slow and most drifts are linear during any particular 0.1 sec period. A directionally weighted measure must be used, then, if short velocity samples are to be compared with longer (intersaccadic) samples. The

[1] The procedure used to establish the mean absolute magnitude of saccadic eye movements necessarily introduces some error into the calculation of saccade size because microsaccades occupy approximately 25 msec (Boyce, 1967) of the 0.1 sec measurement "window". However, it is unlikely that either saccade size or direction are related to the arbitrarily chosen 0.1 sec measurement intervals, or that the eye would have systematically moved in the time remaining in the sample intervals. Thus, the mean of the angular differences between the beginning and end of the 0.1 sec sample periods should provide an unbiased estimate of saccadic extents.

DMCEM vector averaging procedure fulfills this requirement. AS's mean 0.1 sec drift vector (M_N) was 0.6 min arc long corresponding to a directionally averaged drift velocity of 6 min arc/sec. RS's mean vector length (M_N) was 0.8 min arc corresponding to a mean drift velocity of 8.0 min arc/sec. These values are very close to the 6.0 min arc/sec intersaccadic drift velocity estimated from the Ditchburn and Foley-Fisher summary.

The *area of a bivariate contour ellipse* is a two-dimensional variability measure and may be used as an index of fixation stability (See Steinman, 1965 for a description and test of the assumptions underlying this measure of bivariate variability.). The obtained values, 85.5 min arc^2 (AS) and 48.2 min arc^2 (RS) are the areas in which the retinal images of the target object were found 68.3% of the time. These values not only indicate excellent fixation stability but also compare favorably with prior measures of fixation stability for these and other subjects (Nachmias, 1959; Steinman, 1965; Steinman, *et al.*, 1967).

APPENDIX G

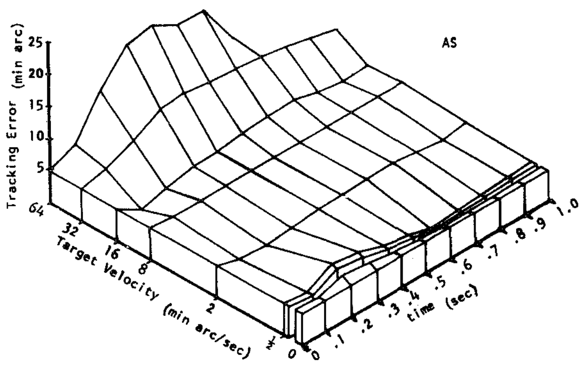
TRACKING ACCURACY

The time required for the eye position control system to start to follow a moving target may be found by studying the change of tracking error magnitude with time from the onset of target motion. One index of the magnitude of tracking error is a measure of the mean angular distance between the position of the target object image and the "optimal" fixation locus. This measure of mean tracking error required an estimate of the target image position before and during target movement. The initial position of the target image was estimated by assuming that the image position in the three seconds before movement was the same as the mean position of the eye measured in that period. The reliability of this estimate of mean target image position was further improved by including measurements of eye position from the second, third, and fourth seconds after the target stopped moving. These latter six measurements were reduced by the distance through which the target had moved (45.0, 22.5, or 0.0 min arc). Once the initial target image position was determined, the target position at any instant during its movement could be computed from the target velocity and direction parameters as follows:

$$X_t = t \cdot v_i \cdot \cos \theta_i + \bar{X} \text{ and } Y_t = t \cdot v_i \cdot \sin \theta_i + \bar{Y}$$

where X_t and Y_t are the estimated horizontal and vertical coordinates, respectively, of the target position at time t; v_i is the target velocity on that trial; θ_i is the target movement direction (in polar coordinates) on that trial and $\bar{X}$ and $\bar{Y}$ are the estimated coordinates of the target prior to target motion. The mean tracking error was then calculated by finding the mean angular distance between the measured eye position and the estimated target position.

Fig. 12 contains three-dimensional plots, for AS and RS respectively, depicting mean tracking error as a function of both target velocity and time from the onset of target motion. For target velocities up to and including 16 min arc/sec, both Ss maintained modest tracking errors approximating those for stationary targets; roughly 5 min arc for AS and 6 min arc for RS. Both Ss tolerated approximately 9 to 10 min arc tracking errors at the 32 min arc/ sec target velocity. However, at the highest target velocity, 64 min arc/sec, both Ss allowed tracking errors to build up to approximately 19 min arc (they did not pursue) in the first 0.3 sec and then required another 0.3 sec to reduce the errors back to the 9 or 10 min arc average tolerated at lower target velocities. (See the following tables for a tabulation of mean absolute tracking errors at each target velocity within each 0.1 sec sampling interval.)



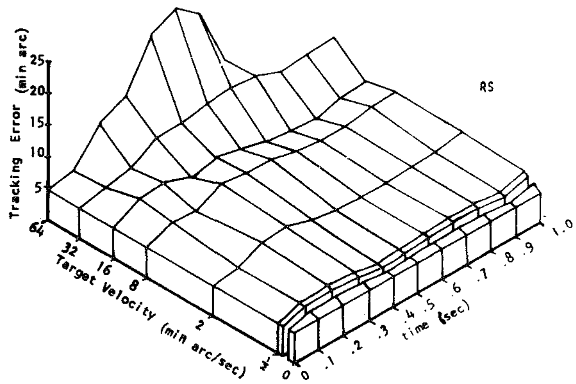


Fig. 12. Mean absolute tracking error as a function of target velocity and time from the onset of target motion. Mean absolute tracking errors are plotted in the left graph for subject AS and in the right graph for subject RS.

AS TRACKING ERROR
(min arc)

Target Velocity (min arc/sec)	Time											
	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.0	N	$\bar{X}$
0.0	3.7	5.0	4.5	5.5	3.7	4.7	5.2	4.6	4.0	7.5	19	4.8
0.5	4.9	6.9	6.2	4.9	4.4	3.6	4.3	4.1	4.3	4.3	17	4.8
2.0	4.2	3.9	4.2	5.4	5.1	5.2	5.1	4.5	4.6	5.0	21	4.7
8.0	4.8	5.2	5.2	5.0	5.2	5.2	5.0	5.1	5.4	5.3	20	5.1
16.0	3.0	3.8	4.9	5.1	5.7	6.0	6.1	4.9	4.6	4.8	19	4.9
32.0	6.1	8.3	10.7	11.1	10.6	10.4	10.0	9.3	8.1	7.8	37	9.2
64.0	7.3	13.3	18.3	19.0	17.0	16.6	9.9				74	14.5

The absolute magnitude of tracking error as a function of target velocity and time from the onset of target motion.

RS TRACKING ERROR
(min arc)

Target Velocity (min arc/sec)	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.0	N	$\bar{X}$
0.0	5.3	5.6	3.6	3.0	3.1	4.1	5.6	6.4	7.7	6.3	18	5.1
0.5	6.8	6.1	5.9	4.7	5.1	5.7	5.9	6.0	5.6	6.3	17	5.8
2.0	5.3	7.3	7.5	6.1	5.7	5.7	5.5	5.9	6.1	6.7	16	5.2
8.0	6.4	6.2	8.0	7.7	7.5	6.6	6.0	6.1	7.1	6.8	18	6.8
16.0	8.1	7.6	6.8	6.7	6.1	5.3	4.5	4.6	5.5	5.5	17	6.1
32.0	5.9	6.9	9.5	10.4	10.7	10.1	8.4	8.9	9.4	9.5	33	9.0
64.0	5.8	11.1	13.0	20.6	22.3	19.4	9.5				73	14.5

The absolute magnitude of tracking error as a function of target velocity and time from the onset of target motion.

APPENDIX H

ERROR ANGLE

AS

target velocity

direction	0.5	2	8	16	32	64
0	48	5	12	22	7	7
45	87	140	11	17	6	5
90	123	76	35	15	17	8
135	75	119	88	31	8	17
180	103	158	52	4	30	14
225	16	66	24	25	5	0
270	2	20	22	0	1	4
315	63	31	41	2	8	7
$\bar{X}$	66.0	70.5	29.4	13.2	9.6	7.8
N	90	105	123	103	187	170
SD	38.9	53.5	23.8	10.8	8.5	3.9

Low velocity eye movement error angles - the mean absolute magnitude of the difference between the direction the eye moved (M_N) and the direction the target moved (θ) for different target velocities and directions. $\bar{X}$ is the overall mean at each target velocity and N and SD refer to this overall mean.

RS

target velocity

direction	0.5	2	8	16	32	64
0	97	100	65	80	41	10
45	9	3	126	77	8	1
90	160	22	175	8	8	4
135	139	28	82	17	18	14
180	105	159	37	42	24	0
225	112	60	31	17	4	8
270	9	32	14	132	1	0
315	37	32	51	63	27	11
$\bar{X}$	86.3	52.0	74.5	53.3	17.1	5.7
N	80	78	82	71	172	163
SD	54.4	48.0	50.5	39.3	12.8	5.1

Low velocity eye movement error angles - the mean absolute magnitude of the difference between the direction the eye moved (M_N) and the direction the target moved (θ) for different target velocities and directions. $\bar{X}$ is the overall mean at each target velocity and N and SD refer to this overall mean.

APPENDIX I

EYE VELOCITY

Target Velocity (min arc/sec)

	0.0	0.5	2.0	8.0	16.0	32.0	64.0	
AS Velocity	6.2	6.9	6.0	4.5	14.0	31.0	60.1	min arc/sec
SD	3.2	5.1	4.2	2.7	3.4	6.1	7.2	min arc/sec
N	245	90	105	123	103	187	170	
% of targ. vel.		1380.0	300.0	56.3	87.5	96.9	93.9	
RS Velocity	7.6	7.8	8.6	10.1	10.3	26.0	60.7	min arc/sec
SD	2.9	2.8	5.7	6.9	4.1	8.8	13.5	min arc/sec
N	264	80	78	82	71	172	163	
% of targ. vel.		1560.0	430.0	126.3	64.4	81.3	94.8	

Smooth movement velocity as a function of target velocity for AS and RS viewing a point target during the period from 0.4 to 1.0 sec after the target started moving.

APPENDIX J

GAIN

target velocity	subject AS	RS
0.5	22.8	23.8
2	9.6	12.6
8	-5.0	2.0
16	-1.2	-3.1
32	-0.3	-1.8
<u>34</u>	<u>-0.8</u>	<u>-2.3</u>
64	-0.5	-0.4
<u>69</u>	<u>-0.9</u>	<u>-2.1</u>
<u>172</u>	<u>-0.6</u>	<u>-1.5</u>
<u>344</u>	<u>-0.3</u>	<u>-1.7</u>
<u>687</u>	<u>-0.8</u>	<u>-4.0</u>

Gain of the low velocity control system at different target velocities. The target velocities (in min arc/sec) and the gain values (in decibels) which are underlined are from Steinman, Skavenski and Sansbury (1969) for these <u>S</u>s. Gain in decibels was calculated from the following formula: Gain = 20 log (eye velocity/target velocity).

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