INTRODUCTION

The role of slow eye movements in maintaining stable gaze has been appreciated since Nachmias's experiments in 1959 and 1961. He demonstrated that slow eye movements during fixation were not exclusively noisy drifts, as had been proposed by Cornsweet (1956), but found instead that drifts could serve a corrective function, which he likened to smooth pursuit of a zero-velocity target. Several years later, Steinman, Cunitz, Timberlake and Herman (1967) showed that small movements of light in the line of sight can be maintained exclusively with such corrective drifts—now called "slow control"—and that saccades were unnecessary [see Steinman, Hadad, Skavenski and Wyman (1973) and Kowler (1990, 1991) for reviews.]

In these many years since Nachmias's original observations, there is still uncertainty about a fundamental property of slow control. Namely, is slow control position-corrective or velocity-corrective? By position-corrective we mean that slow control senses the position of target with respect to the foveal center (the assumed "optimal locus" for fixation) and then issues commands for corrective slow movements to reduce the error. By velocity-corrective we mean that slow control senses the motion of the target on the retina, regardless of the particular target position, and issues commands for corrective slow movements to nullify the retinal motion and keep the target stationary as possible. Although many investigators have assumed that slow control is velocity-, rather than position-corrective, the issue has never been resolved. Our goal was to provide the answer.

We will describe the rationale behind our approach after a brief review of the position-corrective models discussed in the past and the evidence for and against position-corrective.

BACKGROUND

Early models of fixation were position-corrective models. Cornsweet (1956) formulated the first detailed model of fixation control. He proposed that the slow, saccadic drift movements took the image of the target away from the retinal "optimal locus" for fixation. This displacement constituted a position-error signal that triggered a corrective saccade whenever position error approached 6°. Later, Nachmias (1959, 1961) demonstrated that along certain meridians drifts corrected,
rather than created, fixation errors. Nachmias proposed that drift correction was carried out by means of the "pursuit mechanism", but he did not speculate about whether drifts corrected errors in position (as saccades did in Cornsweet's model) or whether drifts acted to keep images stable.

Steinman (1965) extended the position-corrective model but did not distinguish the roles of saccades and drifts. He found a remarkable degree of similarity between trial-mean eye positions during fixation (standard error of trial-mean eye position was 2.3°) and casual observation that saccades were infrequent. However, during fixation on the retina, and that the same locus is used on each experimental trial regardless of the physical attributes of the stimulus. Steinman (1965) also found that both mean fixation position and fixation stability were independent of target size, at least up to diameters of 87° (the largest target he studied). To explain the independence from target size, he proposed that the "error" signal driving corrective movements was the "resultant of the direction and distance "local sign" of all the signal elements stimulated by the edges of the target" (p. 1165). In other words, the error signal was based on the distance between the center-of-gravity of the target and the "optimal locus". Steinman's (1965) model predicted that the fixation control mechanism would move the eye to the center-of-gravity of a target and keep it relatively stable at that position.

This prediction, however, was not confirmed in later work. Murphy, Hadad and Steinman (1974) did not find any systematic deviations. When subjects were asked to fixate various unmarked positions on or within the contour of small (<80") forms, both the stability and the average direction of eye movements were not affected by either the shape of the target or the fixation position. Murphy et al. obtained the same result regardless of whether subjects made saccades during fixation or maintained the line of sight exclusively by means of slow control. Explanations of the independence of slow control from target shape and fixation position would require a position-correction model of fixation that had been in the oculomotor literature since 1956.

Position versus velocity-corrective models of smooth pursuit

At about the same time that position-corrective models of fixation were being developed, evidence was obtained that smooth pursuit eye movements were insensitive to position errors and functioned collectively to minimize retinal image motion. The classical observation of smooth pursuit movements was performed by Ragabba (1981) in a study in which a target abruptly jumped away from the line of sight, and at the same time began to move smoothly from the eccentric position toward the line of sight. Ragabba found that the eye did not move toward the target, but instead moved in the direction of the smooth target motion, demonstrating that smooth eye movements were correcting velocity- in error rather than position-errors.

Subsequent studies reported, in contrast to Ragabba (1961), that there were some smooth eye movement responses to an abrupt target displacement. Wyman and Steinman (1973). For example, observed slow drifts in response to a small proportion of very small abrupt target displacements (< 7°). Carl and Gellman (1987) found slow responses to target displacements as large as 2°, but, in contrast to one would expect from a position-corrective system, eye velocity diminished with further increases in target step size. Carl and Gellman proposed that abrupt target displacements produce slow postmotor responses by stimulating (albillo weak) visual motion detectors.

Carl and Gellman's (1987) conjecture that abrupt target displacements can produce slow control was consistent with earlier findings relating motion perception to smooth pursuit. Morgan and Tornell (1978) found that a target moving in a discrete series of steps could elicit smooth pursuit, but only when the target is perceived as moving continuously (see also Westheimer, 1954).

From these considerations, it can be concluded that abrupt target displacements can stimulate the motion system, and hence, are not the appropriate stimuli for determining whether position error signals are in and of themselves, able to drive slow control. Position error signals may only become important when targets are stationary—the usual stimulus for slow control. When the target is moving, the contribution of position signals might be masked by the contribution of velocity signals.

Stabilized targets

Some investigators have reported shifts in the direction of eccentric afterimages (Kornmer & Taumer, 1972). Such shifts would seem to support position-correction. But, as was the case with target steps, both position error signals and motion signals are present and the two signals might not be separate. We know that motion signals are present because afterimages are perceived as moving in the direction of smooth eye movements due to the movement of light on the retina. Thus, some or all of the smooth eye movements measured could be due to the motion signal or to a bias in the registration of the orbital position of the eye. Moreover, there is some doubt about the generality of pursuit of eccentric afterimages. While some authors may drift toward an eccentric afterimage, others are able to produce a variety of voluntary patterns of smooth eye movements and others show a pattern of smooth eye movements indicating a difference in the pattern of drifts observed in total darkness (Cushman, Tingney, Steinman & Ferguson, 1984).

Slow eye movements with single eccentric targets

As noted above, drifts toward an eccentric afterimage would constitute evidence for position correction, but there is disagreement about what the eye actually does. For reasons to be described below, studies of performance with eccentric unstabilized targets also have not
provided convincing evidence to support or refute position-correction.

Whittaker, W. and Whittaker, C. (1988) studied subjects with naturally occurring and simulated macular system. They reported a new model of eye with increasing eccentricity of the target, but the line of sight did not drift toward the target, as position-correction would predict. The absence of centripetal drifts did not resolve the issue of position vs. velocity correction because the targets turned out not to stimulate slow control at all. Drifts were as fast as those observed in total darkness. This was a puzzling result because earlier Sansbury, Skavenski, Haddad and Steinman (1973) had found much slower drifts when they asked subjects to maintain fixation at the center of a configuration of four disks. Even at the largest disk separation they tested (30°), equivalent to a disk eccentricity of 1.25, drift velocity was slower by at least half the velocity of the drifts in the dark. Whittaker et al. observed about the same drift velocity in the dark as Sansbury et al., and the question is: Why were Whittaker et al.'s drifts with visible targets so fast?

In an attempt to explain their high velocity drifts observed with eccentric targets, Whittaker et al. pointed out that Sansbury et al. had the subjects look straight ahead, while Whittaker et al. had put the target straight ahead, and had the subject rotate the eye until the target fell outside of the real or simulated window. Whittaker et al. suggested that the procedure of rotating the eye to an eccentric position compounds any instabilities created by the eccentric position of the eye with any instabilities due to increasing target eccentricity. We do not know this, or some other source of noise, that Whittaker et al. had not found. But given that the single eccentric target they used proved not to constitute an effective stimulus for slow control, their data do not resolve the question of position vs velocity correction.

RATIONAL BEHIND PRESENT EXPERIMENTS

The studies reviewed above did not resolve the question of whether slow control corrects errors in the position or velocity of the target. We studied the target displacement and the retinally-stabilized stimulus ideal for resolving this issue because these stimuli provide both motion and position error signals at the same time. A single eccentric target would seem to be a more suitable stimulus, but prior results were inconclusive with respect to position correction because in these studies other sources of variability were included so that the visible target did not improve fixation at levels better than levels observed in total darkness. Probably the best evidence so far refuting position correction is Murphy et al.'s (1974) finding that fixation stability was independent of where, or within a target form the line of sight was stimulated initially. A position-corrective model of slow control would predict systematic drifts of the eye to the center of gravity of the stimulus. Steinman (1965). To explain Murphy et al.'s results in terms of position-correction, it would be necessary to allow any arbitrarily selected, imagined position in the target (not necessarily the center-of-gravity) to act as the reference point, which is brought to the "optimal locus" by slow control. The positional error signal would then be defined as the distance between this imagined location and the optimal locus for fixation.

Our experiments were designed to test the hypothesis that one of the targets with the "optimal locus" for the imagined position defined with respect to the symmetry target should remain more stable than the defined with respect to an asymmetric target. We used symmetric and asymmetric target configurations. The symmetric target consisted of two points located on either side of the line of sight. The asymmetric target consisted of a single point, or a pair of closely spaced points, located on one side of the line of sight. For reasons to be described below, an imagined reference position defined with respect to the symmetric target should remain more stable than one defined with respect to an asymmetric target.

We consider first the two symmetric points. Subjects are very good at psychophysically estimating the midpoint of a configuration of two targets, with standard deviations of the judgments equal to about 2-5% of the separation (Levi & Klein, 1990). Barb et al. (1990) and Okawa, Ngaard, and Schlussel (1991) have shown that a small error in the location of the target is introduced by the operator, and this error is magnified by the observer. A waiving tectonic target would greatly complicate the task set for the oculomotor system (see Steinman, 1965, for further discussion of this point).
It is much harder to maintain a stable, imagined, reference position defined with respect to the location of two points, e.g. the center of a two point configuration, can be determined at any time during the trial by comparing the distance between the imagined midpoint of the configuration and the location of each point. On the other hand, the distance between an imagined reference position and a single asymmetric point is defined only after the head has been moved. Thus, the relative distance between the eye positions for point targets has remained in the same position regardless of whether the eye movements are registered accurately. Inaccurate registration of drifts of the eye may lead to the impression that the subject is continuing to look at the reference position and that the subject has the erroneous impression that he is continu- ing to look at the reference position when in fact the eye has drifted; then, in effect, the reference position has not been kept. This distance must be remembered throughout the trial. There is no visible reference distance available to refresh the memory. Thus, the inestimable loss in spatial memory for the reference position over time prevents the stability of the slow control would be better with two symmetric points than with a single asymmetric point.

The ability to maintain a stable imagined reference position with respect to a single asymmetric point also requires that the internal registration of any changes in eye position be accurate. Inaccurate registration of drifts of the eye may lead to the impression that the subject is continuing to look at the reference position and the subject has the erroneous impression that he is continuing to look at the reference position when in fact the eye has drifted; then, in effect, the reference position has not been kept. This distance must be remembered throughout the trial. There is no visible reference distance available to refresh the memory. Thus, the inestimable loss in spatial memory for the reference position over time prevents the stability of slow control would be better with two symmetric points than with a single asymmetric point.

The Maryland revolving magnetic field-sensor coil instrument (rotating field monitor or RFM) was used in the present study, and Collewijn, Erkels and Steinman, 1988a, 1988b; Erkels, Steinman & Collewijn, 1989, 1992. The fundamental principle behind the recording method is that when a coil of wire is placed in an alternating magnetic field, an alternating voltage is induced in the coil. The amplitude of the induced voltage is proportional to the sine of the angle between the plane of the coil and the magnetic field vector. In the amplitude-detection method, introduced by Robinson (1963), a coil is attached to the eye and the voltage amplitude is used to compute eye rotation. Alternately, if the magnetic field vector is made to rotate around the eye coil, the phase of the alternating voltage induced in the coil is linearly related to the coil's angular orientation. The phase-detection method for recording eye movements was described by Collewijn (1975), who used it first in his work with the rabbit, by attaching the sensor coil directly to the rabbit's eye. Presently, this technique is used with human subjects by embedding the coils of wire into a silicone cushion which is inserted in the eye and remains in place because a vacuum is formed between the slightly curved antemesis.

Subjects
Three subjects served in the experiments. Each served in 10-16 sessions, each lasting about 30 min. Two of the subjects (RS and ZP) were experienced eye movement subjects. The third (YE, the authors) had not participated in the eye movement experiment.
The targets consisted of red LEDs that subtended 2.6° of visual angle at the distance of 7.1 m. The intensity of the LEDs was set at about 1.5 log units above the light-adapted, absolute foveal threshold. The LEDs were the only objects visible during trials in an otherwise completely dark environment. To keep the subject light-adapted, room lights were turned on between trials.

One LED, which served as the initial fixation point, was mounted permanently at the center of the display. Each trial began with the subject looking at this central point which disappeared at trial onset leaving on only the eccentric target. The target consisted of one or two red LEDs. Three parameters of the target were varied, namely, (1) configuration, (2) direction with respect to the central point, and (3) eccentricity.

**Target configurations**

Six target configurations were used:

1. "1-pi": a single, eccentric point located in one of four positions (right, left, above or below the central point; Fig. 1a).
2. "Ang = 30°": two points located to one side of the central point at one of the same four positions as above. The points formed a 30° angle, with the central point at the apex. The eccentricity of the target was defined as the distance between the central point and each eccentric point (Fig. 1b).
3. "Ang = 110°": same as in (2), except that the angle between the two points was 110° (Fig. 1c,d).
4. "Sym": two points located to the right and left (Fig. 1e) or above and below (Fig. 1f) the central point.
5. "Center": a single central point.
6. "Dark": total darkness.

**Target eccentricity**

The conditions described above were tested with several different eccentricities ranging from 0.2 to 3.5 deg. Table 1 summarizes the conditions and eccentricities tested with each subject.

**Procedure**

The central point and the target were visible in the otherwise totally dark room just before the start of each experimental trial. The subject was asked to look at the central point and initiate the trial when ready by pressing a button. Then, the central point disappeared and

### Table 1: Target eccentricities (deg) tested under different stimulus conditions

<table>
<thead>
<tr>
<th>Target position</th>
<th>Subject</th>
<th>1-pi</th>
<th>Ang = 30°</th>
<th>Ang = 110°</th>
<th>Sym</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horizontal</td>
<td>RS</td>
<td>0.2</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>ZP</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>JE</td>
<td>0.4</td>
<td>0.4</td>
<td>0.4</td>
<td>0.4</td>
</tr>
<tr>
<td>Vertical</td>
<td>RS</td>
<td>0.2</td>
<td>0.3</td>
<td>0.3</td>
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<tr>
<td></td>
<td>ZP</td>
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<tr>
<td></td>
<td>JE</td>
<td>0.4</td>
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</tr>
</tbody>
</table>
retrained off until the end of the trial, leaving only the eccentric target configuration visible. Trials lasted 7 sec.

There were two exceptions to this general procedure. In the “center” condition, the central point, and no other target, remained visible throughout the trial. In the “dark” condition, no targets remained visible after the central point was extinguished.

The subject’s task was to maintain stable gaze without making saccades until the end of each 7 sec trial.

Experimental sessions

Sessions, run on or different days, consisted of 20–60 trials. The first four sessions for each subject consisted of “1-pt” and “dark” trials. The remaining sessions consisted of “Ang = 30°”, “Ang = 110°” and “Rym” trials. All sessions started with a “center” trial. The trials within each session were blocked by target eccentricity. The order of conditions within a block was varied between sessions. The same condition was often run on

2–3 consecutive trials in order to speed up the process of arranging the targets between trials and minimize annulus wearing time, which is limited to 40 min.

Each subject continued running new sessions until a total of at least 3 trials that were saccade-free during the first 5 sec were obtained in each experimental condition. This was accomplished in 8 sessions for RS, 14 sessions for ZP, and 10 sessions for JE.

Analysis

The variables of interest were the stability and the direction of slow control eye movements. Stability was evaluated in several different ways. Short term stability was assessed by the horizontal and vertical eye velocities and eye speeds computed for 1-sec intervals. Long term stability was evaluated by the bivariate contour ellipse area (BCEA), the area of the best-fit ellipse within which the line of sight fell during a 5-sec interval. The orientation of the ellipse was used to study long term drift direction. Long term drift direction was also assessed by

![Diagram](image-url)
comparing eye position at the start of the trial to eye position after 5 saccade-free sec. The details of computing eye velocities and best-fit ellipses follow.

The basis of stability of slow control. Bivariate contour ellipse area (BCEA) was used to evaluate the stability of slow control. The ellipse, centered around the mean eye position, represents the area where the line of sight was likely to fall 68% of the time, assuming a bivariate Gaussian distribution of the eye position. See Sininman (1965) for a detailed description of this measure and tests of its underlying assumptions. Bivariate areas for 5-sec intervals, as well as the major and minor axes, and the orientation of these ellipses, were computed for all trials that were saccade-free during the initial 5 sec. The area of the ellipses represented inverse stability. The shapes of the ellipses (orientation and ratio of major to minor axis) were examined for effects of stimulus configuration on the nature of the dispersion of eye positions. The length of the interval used for computing BCEAs was set to 5 sec based on mean time to first saccade computed for the three subjects after the first four sessions. Using the entire trial (7 sec) would make too many trials unusable because of saccades. The initial 5 sec were saccade-free on 87% of the trials for RS, 28% of the trials for ZP, and 54% of the trials for JE.

Slow control velocities. Horizontal and vertical eye velocities were measured within 1-sec intervals. For each interval, eye velocity was the slope of a line fitted in the least-squares fashion, to discrete eye position data. The onset of the successive 1-sec samples were separated by 100 msec. Saccades, samples were taken only when the occurrence of the first saccade. The rest of the trial after the saccade was not analyzed. Trials that contained saccades during the first second were not included in the analysis because the saccade altered the original target eccentricity. This occurred on 5% of RS’s trials, 17% of ZP’s trials, and 14% of JE’s trials. The velocity was computed by digitally fitting to linear velocity analysis (mean time to first saccade) was 6.4 (SD = 1.2) sec for RS, 4.2 (SD = 2.0) sec for ZP, and 5.4 (SD = 1.9) sec for JE.

The duration of the interval used to compute velocity samples was set at 1 sec because we were interested in sustained trends (e.g., centripetal drifts), rather than the higher frequency oscillations of slow control. Exhaustive inspection of analog records suggested that 1 sec was the appropriate interval to capture the drift.

Saccades. Saccades were detected from the eye position records by a computer program which used an acceleration criterion. The criterion was established empirically for each subject by examining a large number of eye movement records on a computer display where saccades that passed the criterion were flagged. Once the correct criterion was established, the program was reliable in detecting even the smallest saccades.

The stability of slow control depends on target eccentricity. Two-dimensional stability was excellent when the targets fell within the central 2° of the retina. Bivariate contour ellipse areas for 5-sec, saccade-free intervals were small (<0.5 min arc) and generally uniform in size for eccentricities out to 1°. See Figure 4 for mean bivariate areas for single point targets displaced either horizontally (left column) or vertically (right column) from the line of sight.

Figure 4 also shows that slow control was less stable for targets outside the fovea, and that stability diminished as eccentricity increased. The effect of eccentricity on the bivariate area was statistically significant for all subjects (F(1, 119) = 54, P < 0.001 for RS; F(1, 95) = 50, P < 0.001 for ZP; F(1, 91) = 38, P < 0.001 for JE). Stability did not differ significantly among the four target directions (left, right, above, or below: F(3, 159) = 0.6, P > 0.5 for RS; F(3, 95) = 1.5, P > 0.2 for ZP; F(3, 91) = 0.8, P > 0.5 for JE).

Stability with any of the single point targets was much better than stability in total darkness. Mean bivariate area in the dark for RS was 645 min arc (SD = 285,554).
n = 6), almost five times larger than his mean area in the single point target condition that led to the poorest stability. Similarly, ZP's mean bivariate area in the dark (mean = 436 min arc², SD = 594, n = 3) was more than three times larger than his largest area with a visible target. JE's was more than two times larger in the dark (mean = 335 min arc², SD = 234, n = 3) than with a visible target. This improved stability with a visible target is consistent with the findings of Sansbury et al. (1973), but different from those of Whittaker et al. (1988), who found equivalent stability in the dark and with visible targets at eccentricities ranging from 2.5 to 10°.

Stability was not influenced by the number of target points, nor by their arrangement around the line of sight.

It was suggested in the Introduction that slow control might be more stable with two points arranged symmetrically around the line of sight than with a single point because a symmetric configuration should make it easier for the subject to find and maintain a stable imagined
reference position. We did not find any such effect of target symmetry on stability. Figure 5 shows mean bivariate areas for the different target configurations (one-point and two-point symmetric and asymmetric targets), averaged over target direction. There were no statistically reliable differences among the bivariate areas for the different configurations at either the smaller or the larger eccentricity that we tested \( F(3, 159) = 2.2, P > 0.09 \) for RS; \( F(3, 95) = 2.0, P > 0.1 \) for ZP; \( F(3, 91) = 0.4, P > 0.7 \) for JE). In other words, stability of slow control with a single eccentric point was as good as the stability when maintaining the line of sight between two symmetric points. Neither adding a second point, nor arranging the two points symmetrically around the line of sight, made any difference in the subject’s ability to maintain stable gaze.

The shapes of the two-dimensional distributions of eye positions during 5-sec intervals was not affected by target configuration.

Bivariate contour ellipse areas alone do not convey any information about where the line of sight tended to
fall with respect to the target. Such information can be obtained by examining the shapes of these contour ellipses. It is possible for the shape, but not the area, of the contour ellipse to be affected by target configuration. For example, one would expect that with a symmetric target, any drifts, however small, will be centered around the midpoint of the target, whereas with a single eccentric point the line of sight might drift toward the point. To find out if this were the case, we examined the shapes and orientations of the bivariate contour ellipses for individual trials with different target configurations.

The ellipses are shown in Fig. 6. Each ellipse represents an individual trial. There was no relationship between ellipse shape and the target configuration. We found considerable trial-to-trial variability in both the shape and the orientation of the ellipses. Even ellipses for consecutive trials in the same condition often varied greatly in shape and orientation. This observation is consistent with our observation of trial-to-trial variability in the analog records.

The bivariate area provides a measure of the stability of slow control but does not provide any information
about the direction of eye movements because the temporal order of eye positions during the trial is not reflected in this measure. We next analyzed the direction of eye displacement during the course of a trial to find out whether the line of sight tended to drift toward or away from the target.

The direction of net eye displacement during the course of the trial was independent of the location of the eccentric target.

We compared the distance between the line of sight and the target at the start of the trial and after 5 saccade-free sec. Figure 7 is a plot of the distance between the eye and the target after 5 sec as a function of the distance between the eye and the target at trial onset. Only trials with single point targets are shown. The results for the two-point configurations were very similar. Each symbol in the graph represents one trial. The vertical distance between the symbols and the diagonal line is the amount of eye displacement.

Eye displacements were small (<1°) and about equally likely to be towards or away from the target. RS drifted toward the target (symbols falling below the diagonal) on 36% of the trials, ZP on 51% of the trials.
and JE on 56% of the trials. Displacements tended to increase with increasing target eccentricity, a result that is consistent with the loss of stability of low control with increasing eccentricity (see Fig. 4). Table 2 shows the mean 5-s eye displacements for the four different target directions (right, left, above and below). The direction of displacement was idiosyncratic and did not depend on target position. For example, ZP tended to drift downward (towards targets that were located below the line of sight), while JE tended to drift upward. The direction of short-term drifts varied idiosyncratically, but was not influenced by the position of the eccentric target.

Our results thus far show equivalent stability for single point and two-point symmetric and asymmetric configurations and no evidence of systematic drift toward the target, i.e. none of the predicted
The vectors in Fig. 8 show mean 1-sec retinal image velocities for trials with one-point targets. Drifts in the dark are also shown. Since we tested targets at different eccentricities with the eye at the same orbital position at the start of trial, a plot of eye velocities would produce an illegible graph containing overlapping vectors for...
different eccentricities. So we plotted the velocity of the target's image on the retina, instead of eye velocity, in order to produce a clearer graphical representation of our results.

Each vector in Fig. 8 represents mean velocity of the retinal image for trials in which the initial target position on the retina is shown by the solid circle at the tail of the vector. The direction of the actual eye movement was opposite to the direction of the plotted retinal image movement, i.e., if the image moved down and to the right, the eye had moved up and to the left. Figure 8 shows that subjects tended to drift in the same direction regardless of target position. The direction of the drift was about the same as the direction of the drift is the dark for ZP and JE, but not for RS. RS drifted down and to the left in the dark, while his drifts were either rightwards (image motion leftwards) or leftwards (image motion rightwards) with visible targets. ZP's drifts were faster than RS's, drifted downward and, while JE, who had the fastest drift, drifted upward in the presence of a target. These directions were the same as their dark drifts. Figure 8 also shows that eye velocity increased with increasing eccentricity, a result consistent with our analyses of bivariate area (Figs 4-6) and long-term (5 sec) drifts (Fig. 7). The results were very similar for the symmetric and asymmetric two-point configurations.

The effect of the target configuration, direction, and eccentricity on eye speed is considered next. The speed of slow control eye movements increased with target eccentricity, regardless of target direction of configuration.

We analyzed eye speed (unsigned velocity) to assess how fast the eye moved. Mean eye velocity may not be relevant because high drift velocities in opposite directions will cancel each other out and produce a low mean velocity. Figure 9 shows horizontal (open circles) and vertical (closed circles) eye speeds measured during 1-sec, saccade-free intervals for single point targets. Mean eye speed increased with target eccentricity, but did not vary systematically with target direction. This can be seen by comparing eye speeds in trials where the target was displaced horizontally (left column) and vertically (right column), and noting that in both columns speed increased with eccentricity at about the same rate (<0.5 min arc/sec per 1° of eccentricity). Also, drift speeds were about the same for targets located to the left or right of the central point (represented by negative numbers on the abscissa) and to the right or above (positive numbers). This insensitivity to direction held for both horizontal and vertical eye speeds, although vertical eye speeds were generally faster.

Target configuration had no effect on eye speed. Figure 10 compares eye speeds in different configurations, averaged over target direction. Neither horizontal (left column) nor vertical (right column) eye speeds were influenced noticeably or systematically by target configuration in either of the two eccentricities shown.

**DISCUSSION**

**Slow control is not sensitive to position errors**

Slow control eye movements do not correct errors between the position of the target and the position of the line of sight. Previous results had argued against position-correction by showing that the stability of slow control did not depend on the shape of the target, nor on where, within the target, the subjects were asked to look (Murphy et al., 1974). These results, however, could still be accounted for by a positional model if the subjects were able to select and maintain an imagined reference position, defined with respect to the target's contour. Slow control would then be acting to minimize the distance between the retinal optimal locus for fixation and this imagined reference position. The goal of this study was to test the possibility of position-correction slow control whose input is an imagined reference position. To accomplish this we configured slow control with an asymmetric target configuration (one or two points located on one side of the line of sight) to contrast with a symmetric target configuration (two points located on either side of the line of sight). A position-correction model predicts better performance with the symmetric target because it is easier to maintain a stable imagined reference position with this target.

We found the stability of slow control to be excellent for all our target configurations, anywhere within the fovea. Stability was as good with single point targets as it was when subjects were asked to maintain the line of sight between two points arranged symmetrically about the line of sight, even though a stable imagined reference
position is much easier to maintain in the latter case. Neither the number of points in the target (one or two), nor their arrangement about the line of sight (symmetric or asymmetric), produced reliable differences in either the stability or the velocity of slow control.

We found that drifts did become faster with increasing target eccentricity, but the direction of the drift was idiosyncratic. The line of sight did not drift toward the single eccentric point target, nor did it drift toward a position between the two symmetric targets, as a positional model would predict. Drift direction was independent of where the target was located with respect to the line of sight.

Our results, together with the findings of Murphy et al. (1974) provide a strong argument against a position-corrective model of slow control, regardless of whether position is evaluated with respect to the visible target, or with respect to an imagined reference position.
The following sections will address the question of why stability diminishes with increasing eccentricity. We will first compare our results to related studies of fixation of eccentric targets and then show how the pattern of results supports a velocity-corrective model.

Comparison with prior studies

We found the stability of slow control, as well as the speed and velocity of drifts, to be nearly uniform for targets within the fovea. Similar results were obtained by Steinman (1965) and by Rattle (1969), both of whom used symmetric targets and included saccades in their analyses. Rattle (1969) also studied targets at eccentricities out to 4°. He found that the decrease in fixation stability, which he defined as the r.m.s. deviation from the mean eye position, was less than a factor of two for symmetric targets as their separation increased from 19 to 240°.
Since Rattie used the r.m.s. deviation from the mean eye position to assess stability, whereas we used the area around the mean position, our bivariate areas are expected to be the square of his. Consistent with this prediction, we found an increase in the bivariate area of about a factor of 3.8 for a ten-fold increase in eccentricity.

The eccentric stability continues to decline with further increases in eccentricity, but prior studies of patients with macular scotomas and normal subjects with simulated scotomas for normals with simulated scotomas, although patients showed greater individual differences. Poor stability in patients with macular scotoma was also reported by Timberlake, Mainster, Peli, Augliere, Essoc and Arent (1986), who found bivariate areas for 5 sec intervals of about 500 min arc for patients with macular scotomas of 1.5° in radius. Compare this performance with that of JE (our least stable subject) whose mean bivariate area was only 180 min arc at an eccentricity of 1.5°.

There are several possible explanations for the poor fixation stability in patients with scotomas reported by Whittaker et al. and Timberlake et al. One possibility is that diseases of the fovea may impair visual function, e.g. velocity discrimination, in the peripheral as well as central retina. This would be detrimental to velocity-corrective slow control. It is also possible that patients studied fixation in monkeys with foveal lesions, that faster drifts are required for optimal visibility at eccentric visual environmental load. A third explanation for poorer fixation stability, which would apply to both natural and artificial scotomas, is that in both Whittaker et al. and Timberlake et al.'s studies the fixation target was placed in front of the subject, who rotated the eye until the target became visible. Whittaker et al. speculated that in this procedure any instability caused by the eye's movement was caused by the eccentric position of the target's image on the retina. To support this speculation they studied drifts in drift speed in the dark (from 10 to about 30 min arc/sec) as the orbital position increased from an eccentricity of 1.5 to 15°. In our study, orbital position remained approximately straight ahead during 1.5° in radius. Compare this performance with that of JE (our least stable subject) whose mean bivariate area was only 180 min arc at an eccentricity of 1.5°.

Comparison of our results with prior work shows that the decrease in the stability of slow control with increasing target eccentricity is more modest than would be inferred from studies with both artificial and natural macular scotomas. We find that both the bivariate contour ellipse area and the mean eye speed increased by only a factor of three as target eccentricity increased to 4°. Also, mean eye speed was slow—well under 10 min arc/sec—even at eccentricities as large as 4°. As will be argued below, the fact that mean eye speed increased, but only modestly, with increasing eccentricity supports the conclusion that slow control is indeed a velocity-corrective system.

Slow control is sensitive to velocity errors

When we talk about velocity-corrective slow control, we mean that some source of instability causes movement of the eye, and, consequently, motion of the retinal image. The motion of the retinal image is the input to slow control, which issues the appropriate motor commands. The motion and keep the target as stable as possible. The instability that causes the retinal motion could originate from a number of sources, including noise within the motor system itself (nonvisual sources), and misestimates of the retinal image velocity, which would lead to inappropriate corrective movements (visual sources).

This general model, we can ask why slow control would become less effective as eccentricity increases. The most obvious answer would seem to be that retinal image velocity is coded less precisely with increasing eccentricity. This would result in inappropriate corrective eye movements, which would, in turn, generate even more image motion. But it turns out that inaccurate coding of velocity does not provide a complete explanation of our results.

We found that with increasing eccentricity the drifts began to resemble the idiosyncratic drifts that occur in total darkness. This idea is consistent with the results of McKee and Nakayama's (1984) study of velocity perception. They found that sensitivity to differences in velocity declined with increasing eccentricity, but only for low-velocity targets. More specifically, the greater the eccentricity, the faster a target had to move in order for precise velocity discrimination (sensitivity to 5% difference) to be achieved. They attributed this result to the increasingly poorer coding of spatial position as eccentricity increases, which, they argued, results in a corresponding shift in the frequency tuning of motion detectors to higher and higher velocities. A reduction in the number of motion detectors tuned to low velocities would be expected to diminish the effectiveness of slow control with stationary targets, but still allow effective smooth pursuit of moving targets.
This is because the retinal image velocity during pursuit of moving targets is considerably higher than image velocity during slow control (Kowler & McKee, 1987). Smooth pursuit of eccentric targets, in fact, quite good (gain > 0.8: Wintersen & Steinman, 1978; Collewijn & Tammings, 1986), in agreement with this prediction. The correspondence between our results and the predictions made on the basis of McKee and Nakayama’s (1986) study of velocity perception provides further support that velocity, not position, signals drive slow control.

Implications for pursuit of moving targets

We showed that slow control is insensitive to the error between the position of the target and the optimal fixation point on the retina. These results apply to stationary targets. Do position errors become relevant, either in place of or in addition to, velocity errors when targets are in motion? It is not possible to answer this question based on our results because we did not study moving targets. However, a saccadic oculomotor mechanism that uses velocity-correction for stationary targets and position-correction for moving targets is unlikely. If smooth pursuit was position-corrective, and slow control were velocity-corrective, then slow eye movements would be using velocity signals when the target is stationary, and position signals when the target is moving. This would be a rather odd arrangement. It is much more plausible for the sensory inputs to slow eye movements to consist exclusively of velocity signals, regardless of whether the targets are stationary or moving.

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