

Slow Control with Eccentric Targets: Evidence Against a Position-Corrective Model

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Does slow control work by keeping the image at a particular retinal location (position-correction), or by keeping the image relatively stable on whatever position it occupies on the retina (velocity-correction)? The best prior evidence that slow control is not position-corrective was that a stable line of sight can be maintained anywhere on or within a small figure. This result, however, does not preclude position-correction with respect to an imagined reference position selected relative to the figure's contour. To test the importance of an imagined reference position, we compared slow control with targets for which selection of a stable reference position is easy (two points arranged symmetrically about the line of sight) and difficult (one or two points located on one side of the line of sight). We found that the stability, velocity and direction of slow control were the same with both kinds of targets. Slow drifts were in idiosyncratic directions, and not toward the eccentric target. Drift speed increased with eccentricity, but drifts did not exceed 10°/sec even at the largest eccentricity tested (4.1°). The independence of slow control from the spatial configuration of the target shows that slow control does not work by bringing either a visible or an imagined reference position to the optimal fixation locus on the retina. The gradual loss of stability with increasing eccentricity is consistent with prior reports of a reduction in the number of motion detectors tuned to low velocities as eccentricity increases. We conclude that motion signals, not position signals, provide the sole sensory input to slow control.

Eye movements Slow control Eccentricity Gaze stability Motion Oculomotor fixation

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 a stable line of sight can be maintained exclusively with such corrective drifts—now called "slow control"—and that saccades were unnecessary. [See Steinman, Haddad, 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 as 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-correction.

BACKGROUND

Early models of fixation were position-corrective models

Cornsweet (1956) formulated the first detailed model of fixation control. He proposed that the slow, intersaccadic 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,

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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 concluded that there is only one, small "optimal locus" for 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 signs" 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, Haddad and Steinman (1974) did not find any centering tendencies. 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 the 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. Explaining the independence of slow control from target shape and fixation position would require revising or abandoning the position-corrective model of fixation that had been in the oculomotor literature since 1956.

Position- vs 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 exclusively to minimize retinal image motion. The classical observation refuting position-correction came from Rashbass' (1961) 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.

Rashbass 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-errors rather than position-errors.

Subsequent studies reported, in contrast to Rashbass (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 what 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 oculomotor responses by stimulating (albeit weakly) visual motion detectors.

Carl and Gellman's (1987) conjecture that abrupt target displacements can provide velocity signals to slow control was consistent with earlier findings relating motion perception to smooth pursuit. Morgan and Turnbull (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 drifts in the direction of eccentric afterimages (Kommerell & Taumer, 1972), a phenomenon which would seem to support position-correction. But, as was the case with target steps, both position error signals and motion signals are present simultaneously. We know that motion signals are present because afterimages are perceived as moving in the direction of smooth eye movements due to the combination of retinal motion signals with signals coding eye position in the orbit. Thus, some or all of the smooth eye movements observed 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 subjects 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 indistinguishable from the pattern of drifts observed in total darkness (Cushman, Tangney, 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, Budd and Cummings (1988) studied subjects with naturally occurring and simulated macular scotomas. They reported that drift velocity increased with increasing eccentricity of the target, but the line of sight did not drift toward the target, as position-corrective slow control might be expected to do.

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 15°), drift velocity was slower by at least half than the velocity of the drifts in the dark. Whittaker *et al.* observed about the same drift velocity in the dark as Sansbury *et al.*, so 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 scotoma. Whittaker *et al.* suggested that the procedure of rotating the eye to an eccentric position compounds any instabilities created by the eccentric orbital position of the eye with any instabilities due to increasing target eccentricity. We do not know whether this, or some other source of noise, accounted for the high drift velocities Whittaker *et al.* 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.

RATIONALE BEHIND PRESENT EXPERIMENTS

The studies reviewed above did not resolve the question of whether slow control corrects errors in the position of the target with respect to the "optimal locus" for fixation. We argued that neither an abrupt target displacement nor a retinally-stabilized stimulus were 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 intervened so that the visible target did not improve fixation to 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 and drift direction were independent of where, on or within a target form the line of sight was placed 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 slow control works by bringing an imagined reference position to the optimal locus for fixation. We tested this hypothesis by comparing fixation performance with targets that either would, or would not, allow a stable imagined reference position to be maintained. The logic behind the approach was that instabilities in the imagined reference position should show up as instabilities of fixation.

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.

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 (e.g. Levi & Klein, 1990; Burbeck & Yap, 1990). Similar levels of precision have been found for estimates of the location of arbitrary positions defined with respect to the contour of forms (He & Kowler, 1991; DeValois, Lakshminarayanan, Nygaard, Schlus-

*It is not reasonable to explain Murphy *et al.*'s (1974) results by proposing that the position of the optimal locus shifts from trial to trial. For one thing, the strong correspondence between mean eye positions described by Steinman (1965) supports an anatomically fixed and unchanging optimal locus for fixation. Furthermore, if the optimal locus for slow control was allowed to float and be set to a different eccentric retinal position at the start of each trial, then slow control would be acting to correct for drifts away from that position, or stated in another way, acting to keep the image in the same place it was at the beginning of the trial. In other words, a position-corrective model featuring a floating optimal locus would be indistinguishable from a velocity-corrective model that tries to keep images stable regardless of absolute image position. The essence of the position-corrective model we are testing is the same as the position-corrective models described in the oculomotor literature, namely, that eye movements bring the image to a particular anatomical locus that remains the same at all times, regardless of the stimulus. There is much merit in assuming an invariant "optimal locus", usually believed to coincide with the "center of best vision" at the center of the foveal bouquet. This assumption is useful because it anchors the observer's end of his line of sight in a functionally precise and predictable way. A wandering optimal locus would greatly complicate the task set for the oculomotor system (see Steinman, 1965, for further discussion of this point).

& Sladky, 1990; Pizlo & Tarnecki, 1987). Subjects can also make saccades to designated, unmarked locations within eccentric forms with a precision equivalent to that of saccades made to single points (He & Kowler, 1991).

It is much harder to maintain a stable, imagined, reference position defined with respect to a single eccentric point than it is to maintain a stable, imagined reference position defined with respect to the location of two points. A stable imagined reference with respect to two points, e.g. the center of a two point configuration, can be determined at any time during the trial by comparing the distances 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 eccentric point is defined only at the beginning of the trial. This distance must be remembered throughout the trial. There is no visible reference distance available to "refresh" the memory. Thus, the inevitable loss in spatial memory for the reference position over time predicts that the stability of 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 that the visible target, rather than the eye, has moved. If 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 remained stable and there would be no positional error signal generated to trigger corrective eye movements. On the other hand, the imagined midpoint between two symmetric points will remain in the same place, regardless of where the line of sight is positioned and regardless of whether any eye movements are registered accurately. Although there is considerable evidence for accurate registration of relatively large changes in eye position (Hansen & Skavenski, 1977, 1985; Hansen, 1979), the small drift movements occurring during fixation may not be fully registered, resulting in the mislocalization of visual targets (Matin, Pearce, Matin & Kibbler, 1966; Matin, Pola, Matin & Picoult, 1981).

Recent psychophysical results of White, Levi and Aitsebaomo (1992) support the distinctions we have drawn between symmetric and asymmetric targets. Using a procedure similar to the one Matin *et al.* (1966) had developed for a vernier acuity task, White *et al.* (1992) found that the ability to estimate the distance between a single eccentric target and a previously-viewed foveal target becomes poorer the longer the delay between the presentation of the foveal and the eccentric targets. The effect of delay was substantial. For example, with no delay the standard deviation of the distance estimates was 9' for a target at an eccentricity of 2.2° (a value similar to the SD of eye position for symmetric targets at comparable eccentricities; Sansbury *et al.*, 1973). The standard deviation increased two to four

times for delays of 1.6 sec. White *et al.* (1992), like the prior studies of vernier acuity with sequentially flashed targets (Matin *et al.*, 1966), attributed the deterioration of performance with increasing delay to both the decay of spatial memory for the location of the foveal point and to unregistered eye drift.

If slow control works by bringing an imaginary reference position to the optimal locus, we would expect better stability with a target consisting of two points located symmetrically around the line of sight than with either one point, or a pair of points located on one side of the line of sight (asymmetric targets). We might also find directed drifts toward the asymmetric target if the reference position shifts to the visible target itself. On the other hand, if we find no differences between fixation stability with the symmetric and asymmetric target configurations and, in addition, no drifts toward the asymmetric target, then it is unlikely that either visible or imagined reference positions have anything to do with the stability of slow control. We would conclude that slow control senses velocity errors (i.e. retinal image motion) and tries to keep images stable on the retina, regardless of the position of the target or the position of any imagined references with respect to the optimal locus.

METHOD

Subjects

Three subjects served in the experiments. Each served in 10–17 sessions, each lasting about 30 min. Two of the subjects (RS and ZP) were experienced eye movement subjects. The third (JE, one of the authors) had never participated in an eye movement experiment.

Eye movement recording

The Maryland revolving magnetic field-sensor coil instrument (revolving field monitor or RFM) was used to record horizontal and vertical eye positions (see Collewin, Erkelens & Steinman, 1988a, 1988b; Erkelens, Steinman & Collewin, 1989a, 1989b). The fundamental principle behind this 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 revolve 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 Collewin (1977), 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 in a silicone annulus which is inserted in the eye and remains in place because a vacuum is formed between the slightly curved annulus

and the surface of the eye (Collewijn, van der Mark & Jansen, 1975). This type of silicone annulus sensor coil is now available commercially from Skalar-Delft.

The Maryland instrument is unique in that it uses the phase-detection method on both horizontal and vertical meridians. This is accomplished with two orthogonal pairs of cube-surface coil arrangements (Rubens, 1945). Cube-surface coil arrangements are used instead of Helmholtz coils, customarily used with the amplitude-detection method, to assure homogeneity of the magnetic fields, thus virtually eliminating artifacts introduced by eye translations. The orthogonal pair of cube-surface coil arrangements, which is used to measure horizontal eye movements, produces an alternating magnetic field revolving about a vertical axis with a frequency of 976 Hz. The other pair, which is used to measure vertical eye movements, produces an alternating magnetic field revolving about a horizontal axis with the frequency of 3904 Hz. Frequency coding is used to separate horizontal and vertical eye movement signals. Because phase-detection is used on both meridians, the Maryland instrument is insensitive to fluctuations in the strength of the magnetic field and, therefore, capable of absolute calibration. The instrument's noise level is <40 sec arc and its linearity is better than 0.01% over its 360 deg recording range.

In the present experiment, the output of the RFM was rounded to the nearest minute of arc for convenience of data storage. Since only slow control eye movements were of interest, sampling frequency was set at 122 Hz, providing an effective bandwidth of 61 Hz. This bandwidth allowed adequate resolution for all slow control eye movements, (whose frequency is usually <5 Hz; Martins, Kowler & Palmer, 1985), and was high enough to guarantee detection of even the smallest saccades.

Head movements were minimized by using dental impression bite-boards. Viewing was monocular and the non-seeing eye was covered by an eye-patch.

Stimulus display

The stimulus display was located 7.1 m in front of the emmetropic subjects, RS and JE. For subject ZP, a myope who wore his spectacles during the experiment, the display was moved closer by 70 cm in order to make the angular separations of the targets approximately the same for him, as for the other subjects. The stimulus display was placed so that its center was accepted as "straight ahead" by each subject.

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-pt": a single, eccentric point located in one of four positions [right, left, above or below the central point; Fig. 1(a)].
2. "Ang = 36°": two points located to one side of the central point at one of the same four positions as above. The points formed a 36° 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. 1(b)].
3. "Ang = 110°": same as in (2), except that the angle between the two points was 110° [Fig. 1(c, d)].
4. "Sym": two points located to the right and left [Fig. 1(e)] or above and below [Fig. 1(f)] 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 5.5 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

Target position	Subject	1-pt	Ang = 36°	Ang = 110°	Sym
Horizontal	RS	0.2, 0.4, 1.0 2.8, 4.1, 5.5	0.4, 3.7	3.7	0.4, 3.7
	ZP	0.3, 1.7, 3.7	0.3, 3.7	3.7	0.3, 3.7
	JE	0.4, 1.5, 3.2	0.4, 3.2	3.2	0.4, 3.2
Vertical	RS	0.2, 0.4, 1.0	0.4, 3.7	3.7	0.4, 3.7
	ZP	0.3, 1.7, 3.7	0.3, 3.7	3.7	0.3, 3.7
	JE	0.4, 1.5, 3.2	0.4, 3.2	3.2	0.4, 3.2

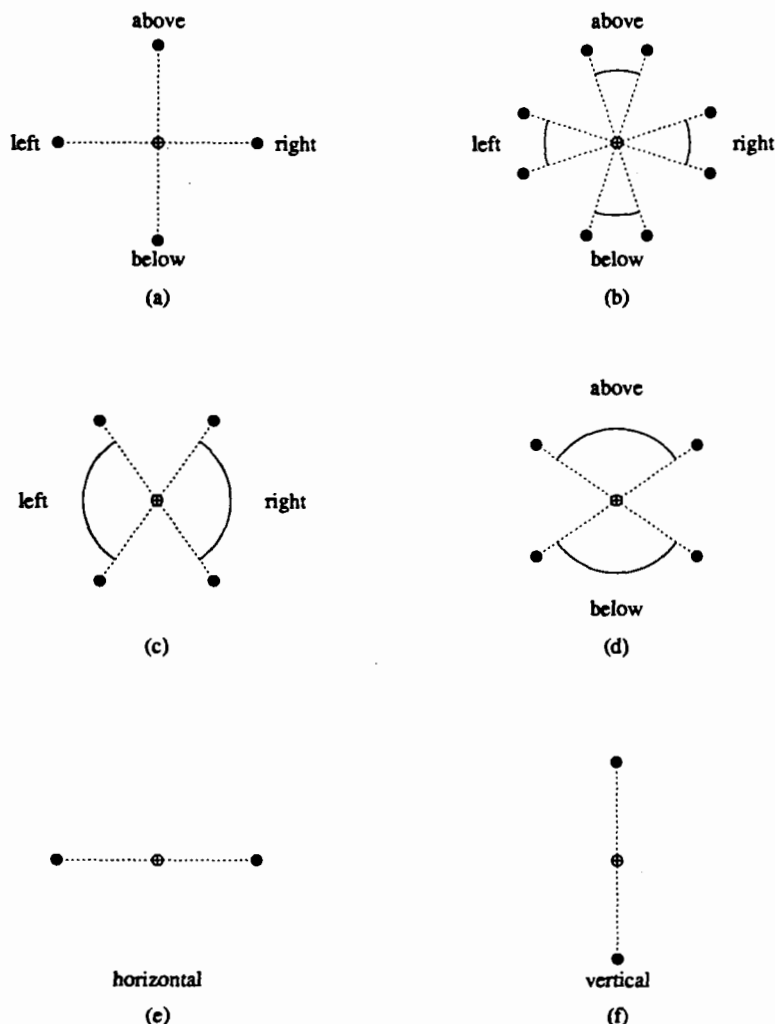


FIGURE 1. The position of targets (●) in different configurations with respect to the central point (⊕). (a) Single eccentric point presented in one of four positions. (b) Two points forming a 36° angle with the central point at the apex, presented in one of four positions. (c) Two points forming a 110° angle with the central point at the apex presented to the left or right of the central point or (d) above and below the central point. (e) Two points arranged symmetrically around the central point in a horizontal or (f) vertical orientation.

remained 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 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 = 36° ", "Ang = 110° " and "Sym" 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

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.

Analysis 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, represented 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 Steinman (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 onsets of the successive 1-sec samples were separated by 100 msec.

In trials containing saccades, samples were taken until 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 2% of RS's trials, 17% of ZP's trials, and 14% of JE's trials. Mean duration of the presaccadic interval used in 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 drifts.

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.

RESULTS

Analog records.

Figure 2 shows examples of typical horizontal (H) and vertical (V) eye movements for ZP (left column) and JE (right column), with a single point target at a relatively small (0.3° —top row) and a relatively large eccentricity (3.7° for ZP and 3.2° for JE—middle row). Eye movements with the symmetric two-point target at the larger eccentricity (3.7° for ZP and 3.2° for JE) are shown on the bottom row. Examination of the records show a tendency for drifts to become more prominent with increasing target eccentricity. Trials often contained high frequency oscillations superimposed on slow drift. Nevertheless, overall stability even at the largest target eccentricity remained good.

Occasionally, faster drifts were observed. Figure 3 shows examples of the poorest stability that we observed in the same three conditions shown in Fig. 2. The drifts took the line of sight about 1° from the target during the 7-sec trial, thus the velocities were in fact relatively low (<10 min arc/sec). There were occasional instances of faster drifts [30 min arc/sec; see the last 2 sec of ZP's record for the 3.7° eccentric point, Fig. 3(c)], but overall instances of drifts faster than 10 min arc/sec that lasted longer than 1 sec were very rare.

Our exhaustive inspection of the analog records also revealed considerable trial-to-trial variability in stability. The variability did not seem to depend on experimental condition, session, or order of presentation. For example, the trials for JE with the 3.2° eccentric point shown in Figs 2(d) and 3(d), are very different, yet they occurred one after another in the same session and with the same target configuration.

The qualitative observations described in this section are supported by the statistical analyses that follow.

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 (<50 min arc²) and generally uniform in size for eccentricities out to 1° . See Fig. 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 [$F(1, 159) = 54$, $P < 0.001$ 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 arc² (SD = 285,

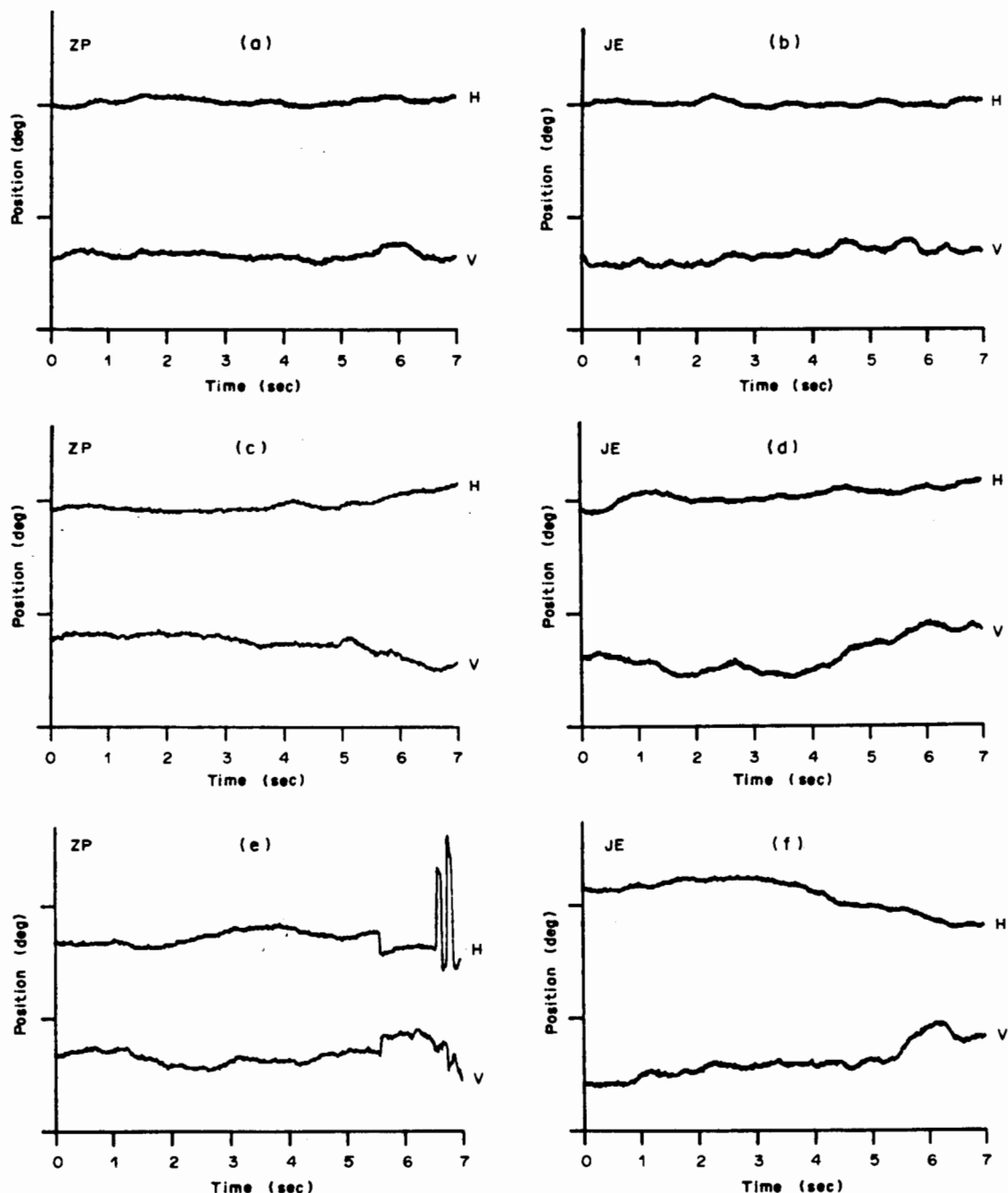


FIGURE 2. Analog records showing typical horizontal (H) and vertical (V) eye movements for ZP (left) and JE (right). At time zero the traces indicate eye position immediately following the extinction of the central LED. Upward changes signify rightward eye movements in the H-trace and upward eye movements in the V-trace. Top row shows eye movements with a single point target located 0.3° (a) above and (b) to the right of the central point. Middle row shows eye movements with a single point located (c) 3.7° to the right and (d) 3.2° below the central point. Bottom row shows eye movements with two points located symmetrically in (e) horizontal (ecc. = 3.7°) and (f) vertical (ecc. = 3.2°) orientations.

$n = 6$), 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 arc^2 , 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 = 535 min arc^2 , 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

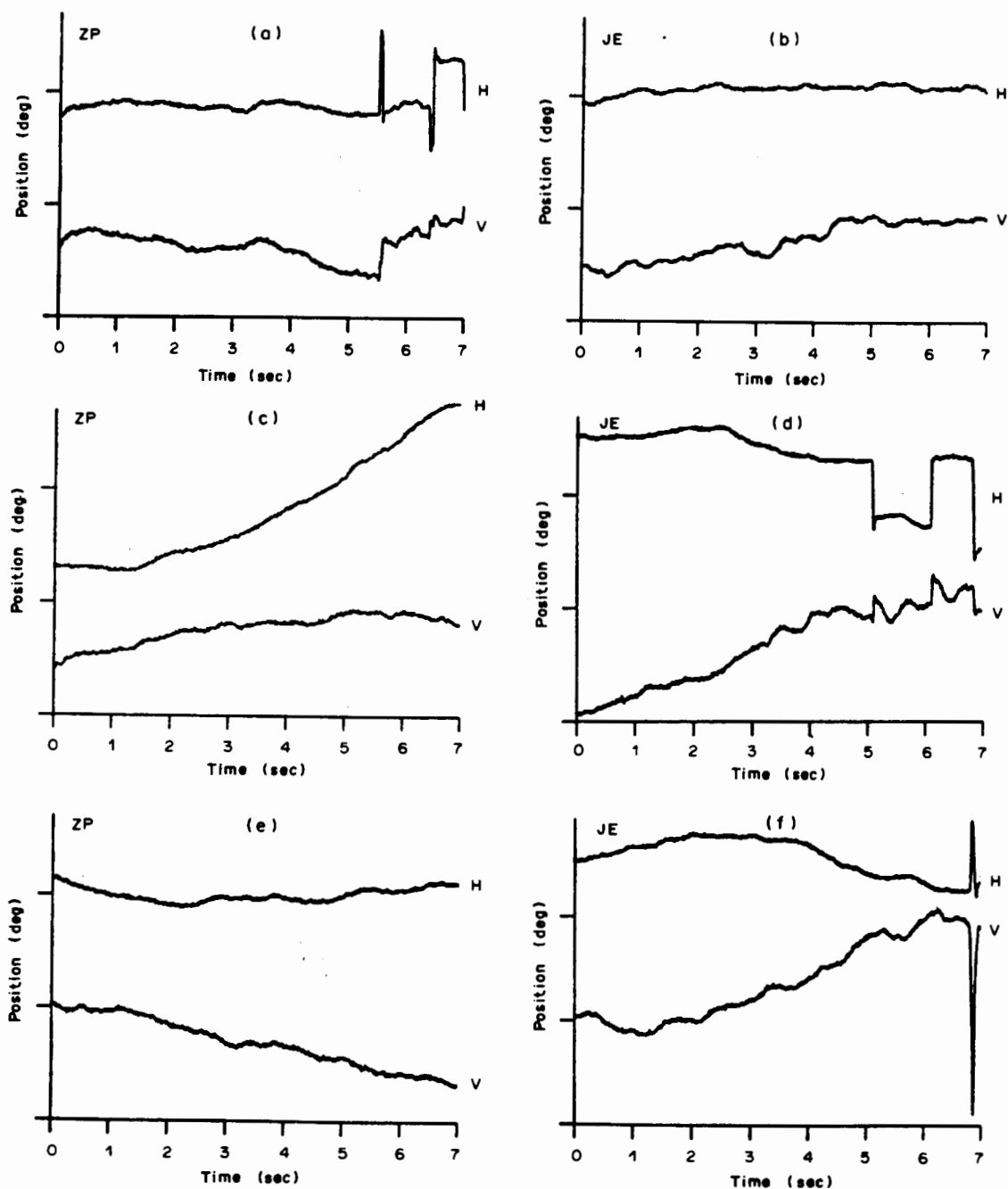


FIGURE 3. Examples of poor fixation stability for ZP (left) and JE (right). At time zero the traces indicate eye position immediately following the extinction of the central LED. Upward changes signify rightward eye movements in the H-trace and upward eye movements in the V-trace. Top row shows eye movements with a single point target located 0.3° (a) above and (b) to the right of the central point. Middle row shows eye movements with a single point located (c) 3.7° to the right and (d) 3.2° below the central point. Bottom row shows eye movements with two points located symmetrically in (e) horizontal (ecc. = 3.7°) and (f) vertical (ecc. = 3.2°) orientations.

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

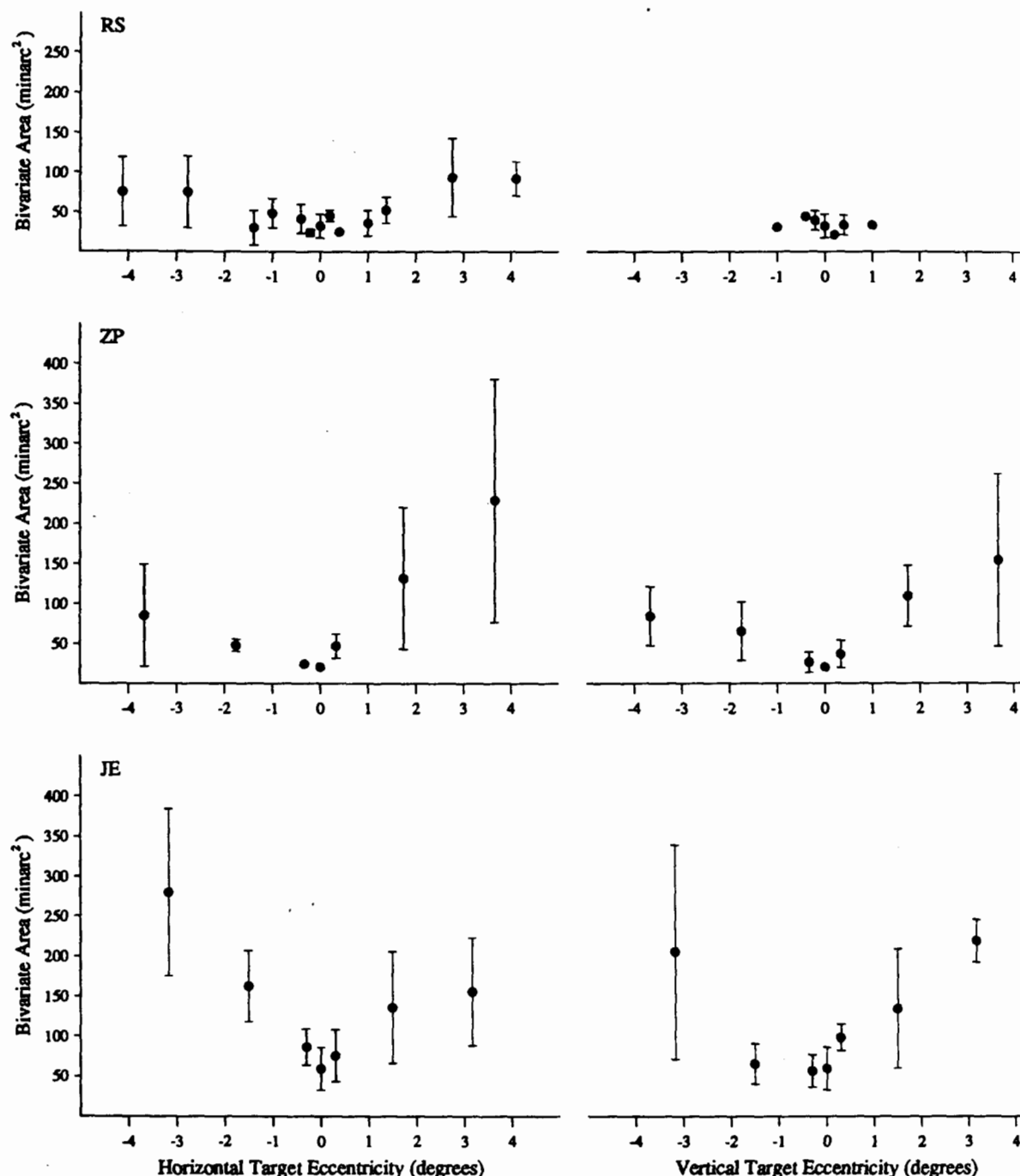


FIGURE 4. Mean bivariate contour ellipse area as a function of horizontal (left) or vertical (right) eccentricity with the single point targets. Error bars indicate ± 1 SD.

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

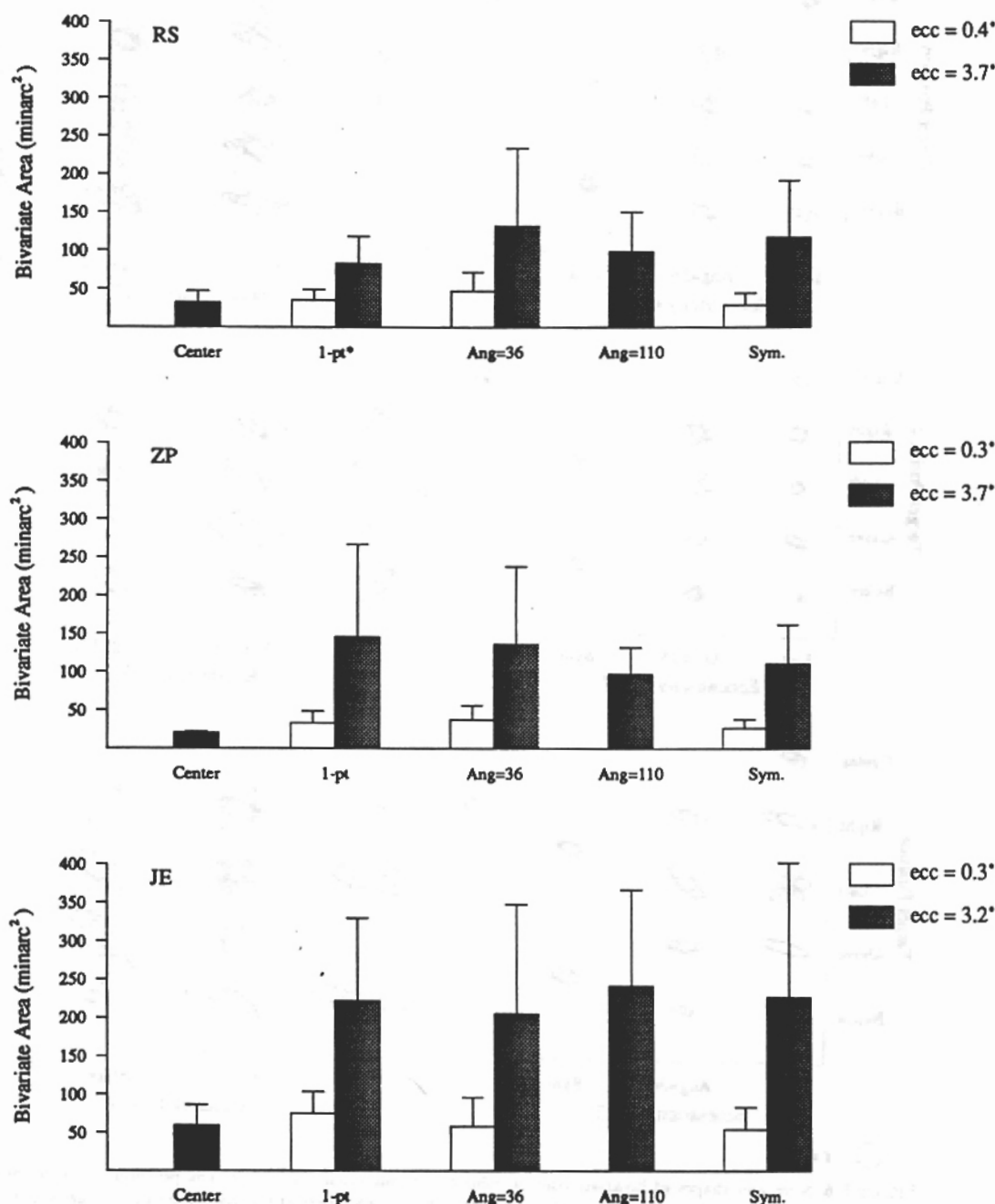


FIGURE 5. Mean bivariate contour ellipse areas for different target configurations at two eccentricities, averaged over target direction (right, left, above and below the line of sight). Each mean is based on 3-39, 5-sec, saccade-free trials. Error bars indicate 1 SD. *For subject RS, the larger eccentricity in the single-point condition was 4.1° and the "above" and "below" target directions were not tested for this configuration.

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 ($<1^\circ$) 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,

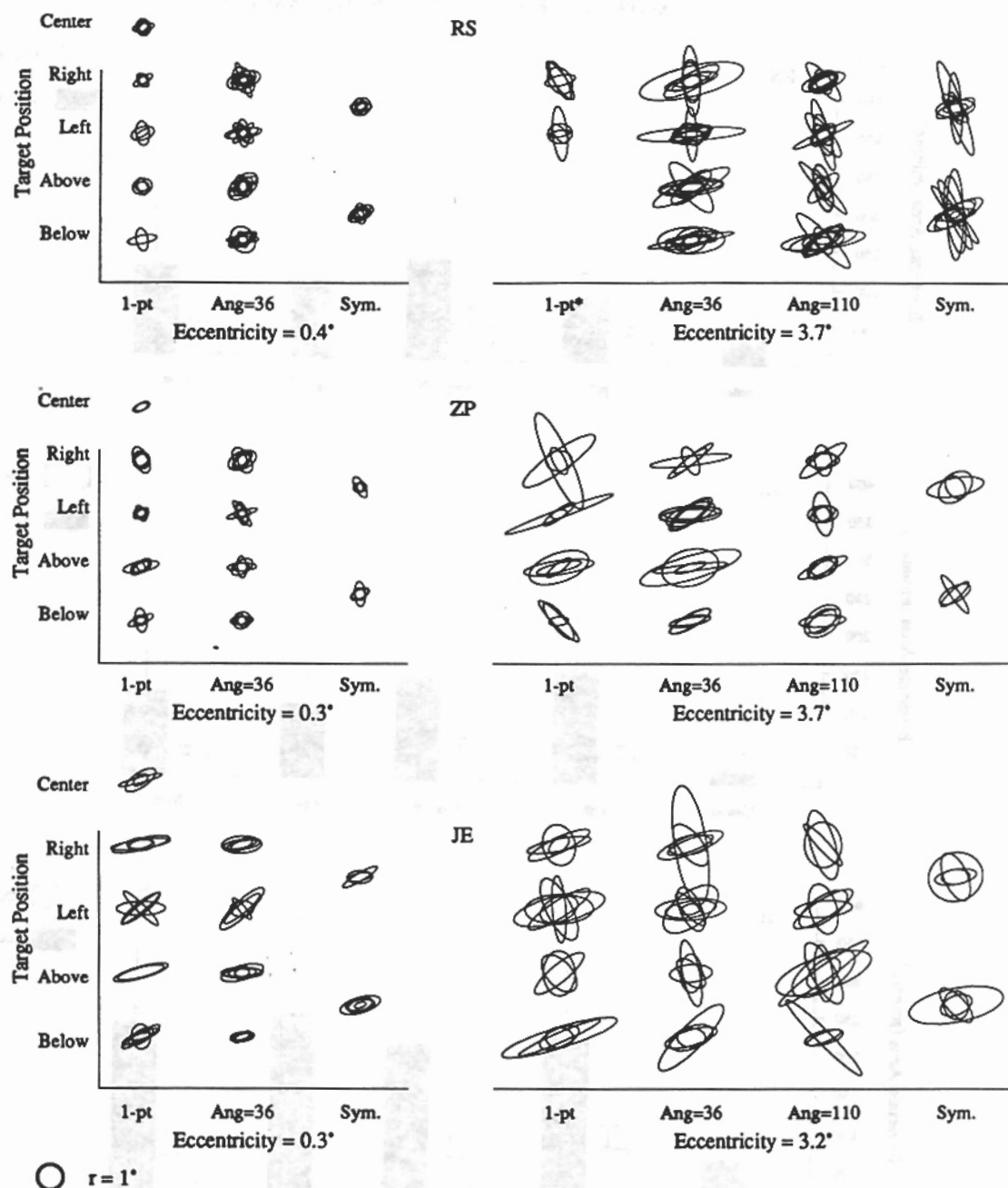


FIGURE 6. Sizes and shapes of bivariate contour ellipses for individual 5-sec trials. The position of the ellipses in the same condition for each subject have been adjusted so that their centers, which are at the mean eye position, are superimposed. Each row shows results for targets located in the same direction with respect to the line of sight. Each column shows results for targets with the same configuration. The three leftmost columns are for targets at a small eccentricity. The four rightmost columns are for targets at a larger eccentricity. *For subject RS, the larger eccentricity in the single-point condition was 4.1° , and the "above" and "below" target directions were not tested for this configuration.

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 slow control with increasing eccentricity (see Fig. 4).

Table 2 shows the mean 5-sec eye displacements for the four different target directions (right, left, above and below). The direction of displacements were 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, and away from

targets located above 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

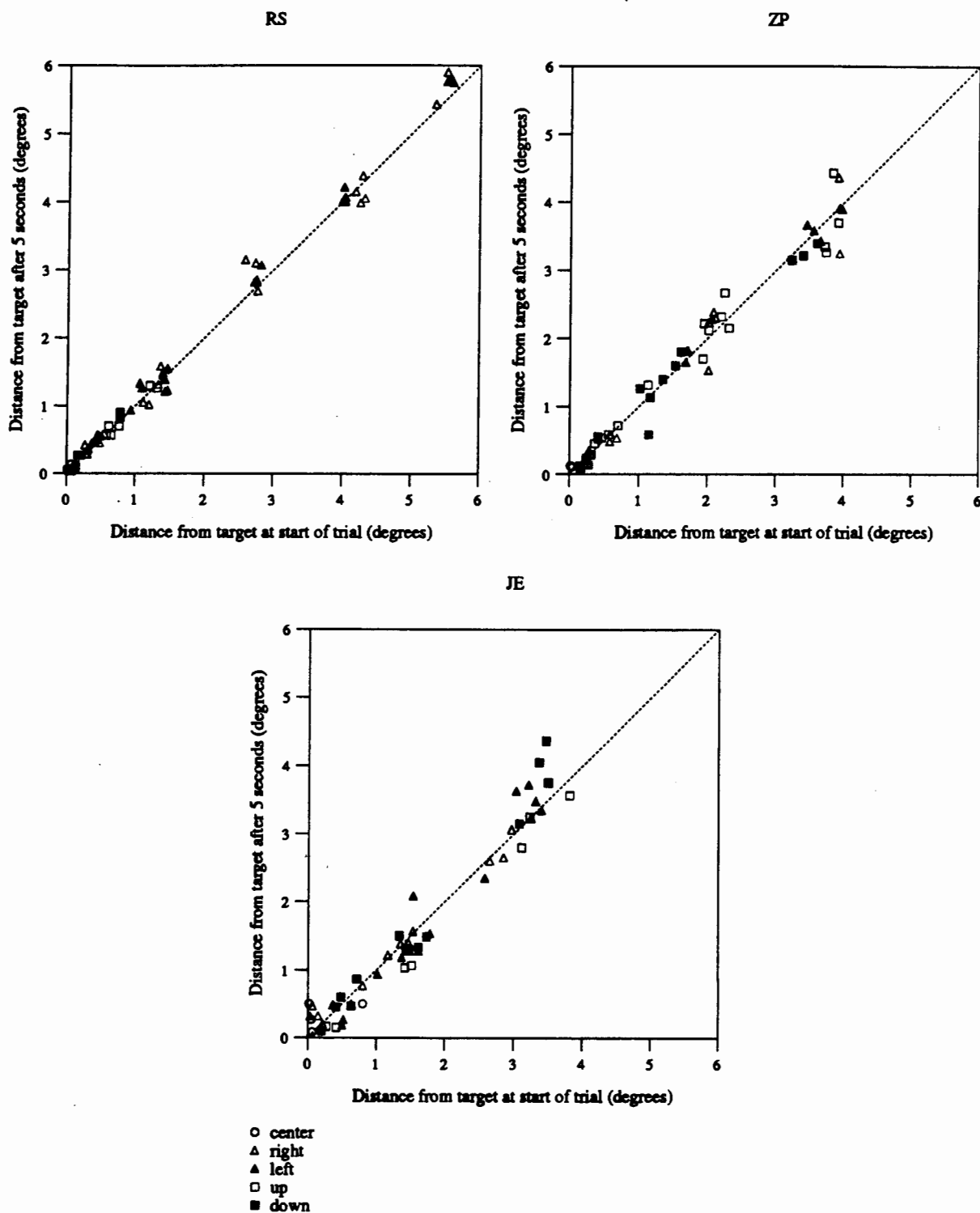
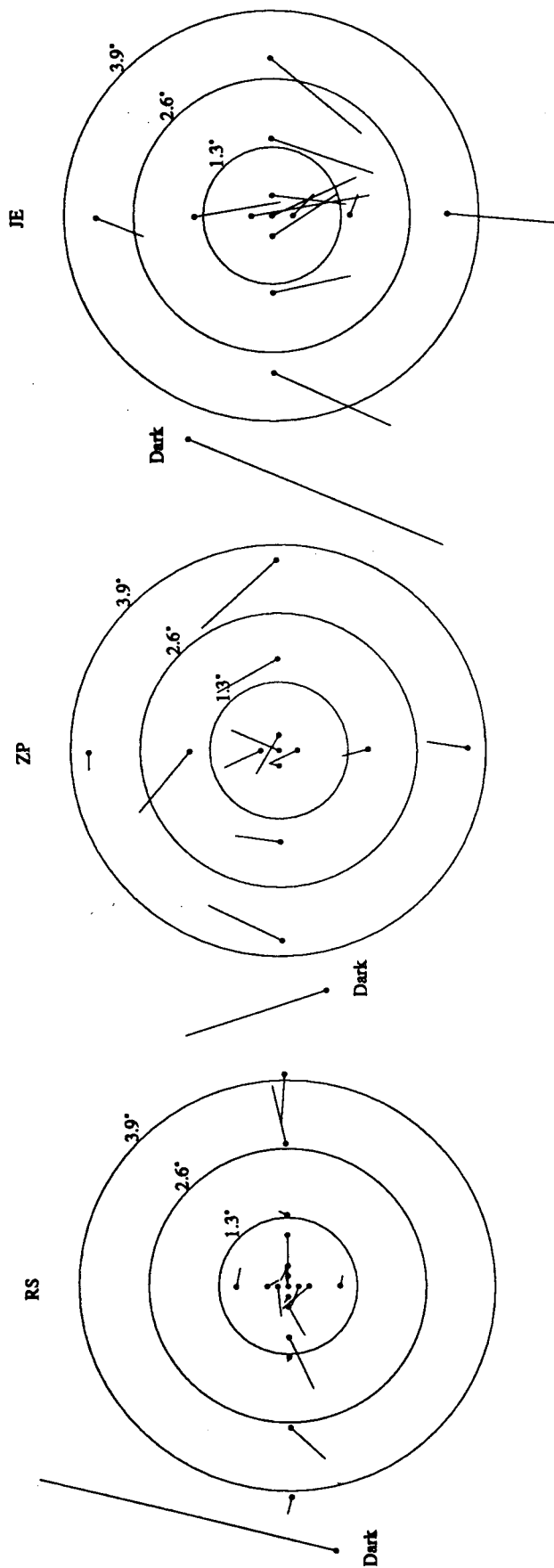


FIGURE 7. The distance between the position of the line of sight and the target at the start of trial and after 5 saccade-free sec, for single point targets at different eccentricities. Each symbol represents one trial. The vertical distance between the symbol and the diagonal line is the net eye displacement for that trial. Symbols below the diagonal represent net eye displacements towards the target. Symbols above the diagonal represent net eye displacements away from the target.

characteristics of position-corrective slow control. To be certain of this we analyzed the velocity of short-term drifts. We chose 1 sec as the duration of the velocity interval because examination of the analog records of the eye movements (see Figs 2 and 3) revealed that the most prominent drifts lasted at least 1 sec.

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



— 1 minarc/sec
 • is target position at start of trial

FIGURE 8. Mean 1-sec retinal image velocity vectors for single point targets. Each vector is a mean of 33-453 ($\bar{x} = 258$) 1-sec, saccade-free, velocity samples. Note that the retinal image velocity vector is a mirror image of the eye velocity vector. The vectors labeled "dark" are the mirror images of mean drifts in the dark.

TABLE 2. Mean eye displacements over 5 saccade-free sec

Target position	Subject RS		Subject ZP		Subject JE	
	Mean (SD)	n	Mean (SD)	n	Mean (SD)	n
Right	-3.17 (0.8)	23	0.69 (5.0)	13	-2.23 (2.3)	13
Left	-4.96 (2.5)	23	-1.10 (2.2)	10	-1.00 (4.9)	15
Above	0.50 (1.6)	6	-1.94 (4.0)	16	14.44 (2.8)	9
Below	-2.00 (1.3)	7	2.80 (2.9)	15	-6.46 (5.6)	13
Center	-0.57 (2.4)	7	-5.00 (0.8)	3	-6.25 (17.2)	4
Overall	-3.06 (1.7)	66	-0.11 (3.5)	57	0.41 (5.0)	54

All entries are in min arc. Positive numbers represent drifts toward and negative numbers represent drifts away from the single point target.

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 in 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, whose drifts were faster than RS's, drifted downward, and JE, who had the fastest drifts, 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 reveal this 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 (solid 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 below 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-corrective slow control whose input is an imagined reference position. To accomplish this we compared slow control with an asymmetric target configuration (one or two points located on one side of the line of sight) to slow control with a symmetric target configuration (two points located on either side of the line of sight). A position-corrective 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

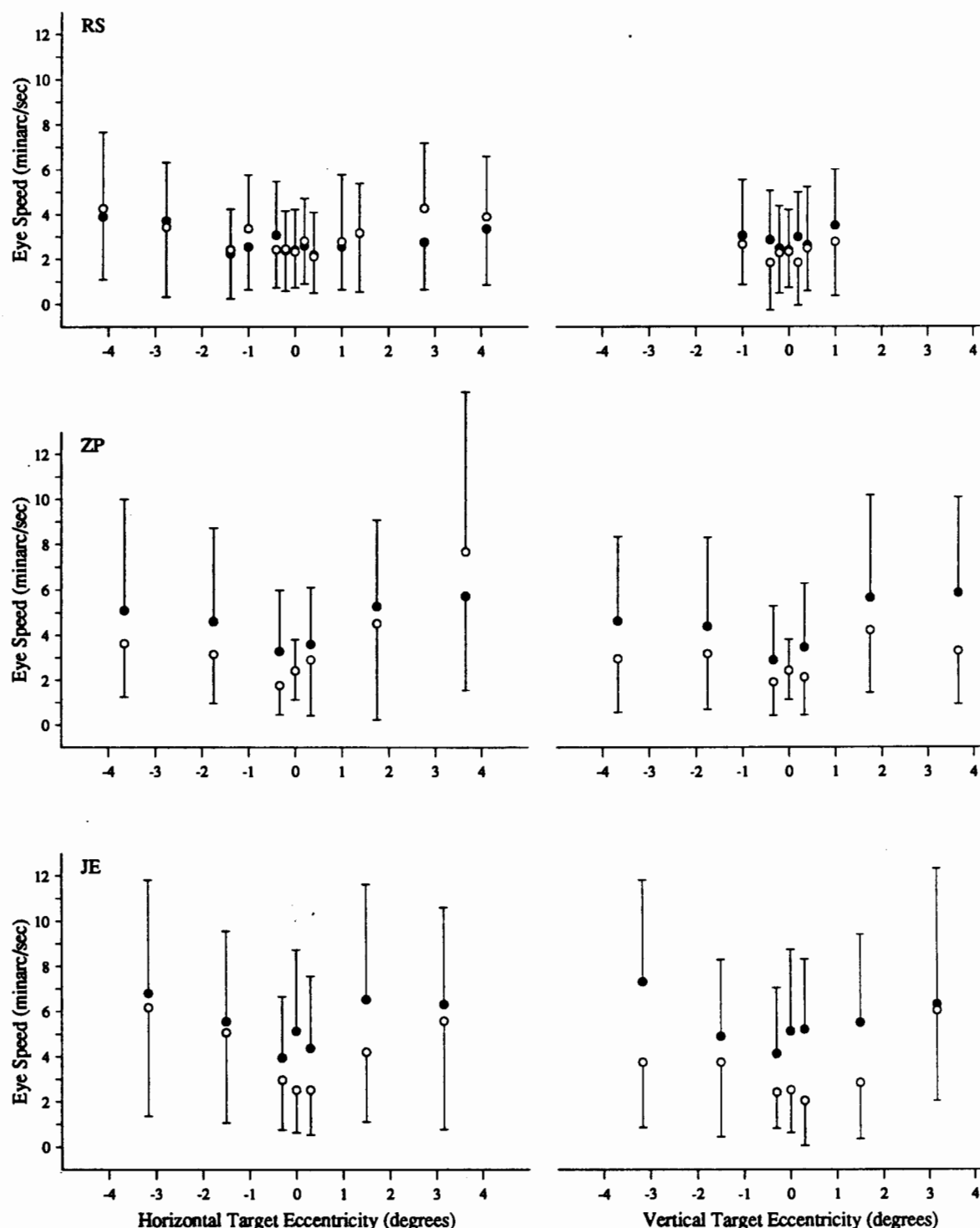


FIGURE 9. Mean horizontal (open symbols) and vertical (shaded symbols) 1-sec eye speeds as a function of the horizontal (left) and vertical (right) eccentricity for single point target configurations. Error bars indicate ± 1 SD.

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.

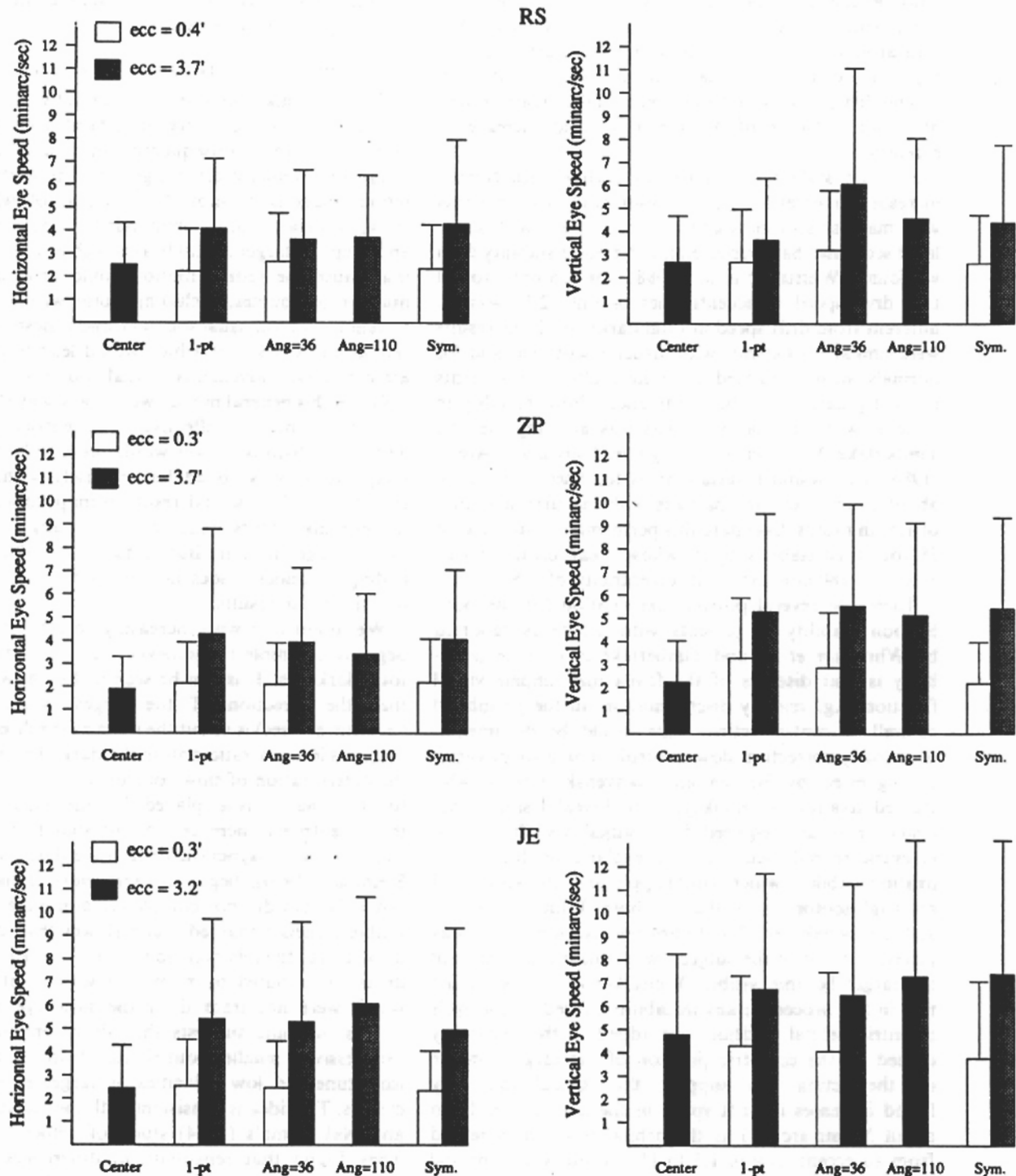


FIGURE 10. Mean horizontal (left) and vertical (right) eye speeds for different target configurations at two eccentricities, averaged over target position. Each bar represents a mean of between 342 and 2333 ($\bar{x} = 1126$) 1-sec, saccade-free eye speed samples. Error bars indicate 1 SD. *For subject RS, the larger eccentricity in the single-point condition was 4.1° and the "above" and "below" target directions were not tested for this configuration.

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 Rattle 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.

Fixation stability continues to decline with further increases in eccentricity, but prior studies of patients with macular scotomas and normal subjects with simulated scotomas have reported much poorer stability than we found. Whittaker *et al.* (1988), for example, found that drift speed at eccentricities of only 2.5° was no different from drift speed in total darkness. Their results were similar for patients with macular scotomas and for normals with simulated scotomas, although patients showed greater individual differences. Poor stability in patients with macular scotomas was also reported by Timberlake, Mainster, Peli, Augliere, Essock and Arend (1986), who found bivariate areas for 5 sec intervals of about 500 min arc² 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 arc² at an eccentricity of 1.5° .

There are several possible explanation 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, as suggested by Heinen and Skavenski (1992), who studied fixation in monkeys with foveal lesions, that faster drifts are required for optimal visibility at an eccentric retinal locus. 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 his eye until the target became visible. Whittaker *et al.* speculated that in this procedure any instability caused by the eye's eccentric orbital position was added to the instability caused by the eccentric position of the target's image on the retina. To support this speculation they found increases 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 all trials.

The 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 eccentric-

ity, 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 motion of the eye, and, consequently, motion of the retinal image (i.e. velocity error signals). The motion of the retinal image is the input to slow control, which issues the appropriate motor commands to "track" the motion and keep the target as stable as possible. The instabilities that cause 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).

Given this general model, we can ask why slow control should 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 imprecise coding of velocity does not provide a complete explanation of our results.

We found that with increasing eccentricity the drifts begin to resemble the idiosyncratic drifts that occur in total darkness. This can be seen in Fig. 8, which shows that the direction of the largest velocity vectors (> 4 min arc/sec) is about the same as the direction of the subject's idiosyncratic drift in the dark. This implies that the deterioration of slow control is due, at least in part, to the smaller role played by the visual target as the eccentricity increases. Non-visual factors, responsible for the idiosyncratic drift in the dark (Skavenski & Steinman, 1970), begin to exert more influence. Non-visual factors did not completely dominate: drifts with visible targets remained much slower than drifts in the dark. It was the relatively low velocity (< 10 min arc/sec) drifts, contributed by nonvisual sources of instability, which were not tracked by the slow eye movements.

This outcome suggests that slow control receives a progressively smaller contribution from visual mechanisms tuned to low velocities as target eccentricity increases. 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% differences) to be achieved. They attributed this result to the increasingly coarser coding of spatial position as eccentricity increases, which, they argued, results in a corresponding shift in the velocity-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 is, in fact, quite good (gain > 0.8; Winterson & Steinman, 1978; Collewijn & Tamminga, 1986), in agreement with this prediction.

The correspondence between our results and the predictions made on the basis of McKee and Nakayama's (1984) 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 locus 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 slow oculomotor mechanism that uses velocity-correction for stationary targets and position-correction for moving targets is unlikely. If smooth pursuit were 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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