

Saccades to Remembered Target Locations: an Analysis of Systematic and Variable Errors

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We studied the effects of varying delay interval on the accuracy and velocity of saccades to the remembered locations of visual targets. Remembered saccades were less accurate than control saccades. Both systematic and variable errors contributed to the loss of accuracy. Systematic errors were similar in size for delay intervals ranging from 400 msec to 5.6 sec, but variable errors increased monotonically as delay intervals were lengthened. Compared to control saccades, remembered saccades were slower and the peak velocities were more variable. However, neither peak velocity nor variability in peak velocity was related to the duration of the delay interval. Our findings indicate that a memory-related process is not the major source of the systematic errors observed on memory trials.

Saccades Memory Remembered targets

INTRODUCTION

Saccades to remembered target locations (remembered saccades) are both less accurate and slower than saccades to persistent visual targets (visually-guided saccades). Compared to visually-guided saccades, monkeys make systematic and variable errors when looking to the remembered location of a target (White & Sparks, 1986; Funahashi, Bruce & Goldman-Rakic, 1989; Gnadt, Bracewell & Andersen, 1991). A pronounced component of the pattern of systematic errors is an upward bias; saccades usually end above the location at which the target was presented. Thus, saccades to targets in the upper visual field are hypermetric, saccades to targets in the lower hemifield are hypometric, and saccades to targets on the horizontal meridian are directed obliquely upward. The horizontal component of saccades to remembered target locations is usually hypometric. Saccades to remembered target locations are also characterized by greater variable error; the end points of remembered saccades are much more scattered than the end points of visually-guided saccades.

The general goal of this experiment was to provide additional baseline behavioral data for both neurophysiological studies that use remembered saccades to investigate mnemonic processes (e.g. Joseph & Barone, 1980; Funahashi, Bruce & Goldman-Rakic, 1989, 1990, 1991; Pierrot-Deseilligny, Rivaud, Gaymard & Agid, 1991) and for studies that exploit the differences in saccadic velocity to investigate the coding of movement metrics (e.g. Rohrer, White & Sparks, 1987). A major aim was

to examine the time-course of error accumulation for saccades to remembered target locations. Separate measures of systematic and variable error were obtained to determine if both types of error could be produced by the same neural process. A second aim was to study the effects of varying delay interval on saccadic velocity. As is true for the quick phases of vestibular and optokinetic nystagmus (Dichgans, Nauck & Wolpert, 1973; Whitaker & Cummings, 1990), saccades to auditory targets (Zambarbieri, Schmid, Prablanc & Magenes, 1981; Jay & Sparks, 1990), and saccades made when subjects are instructed to miss a target by a certain distance (Hallett, 1978; Smit, van Gisbergen & Cools, 1987), the peak velocities of remembered saccades are lower than those of comparable visually-guided saccades (Becker & Fuchs, 1969; Sharpe, Troost, Dell'Osso & Daroff, 1975; Hikosaka & Wurtz, 1985; White & Sparks, 1986; Smit *et al.*, 1987; Gnadt *et al.*, 1991). It is not known if saccades to remembered targets display more variability in peak velocity and if so, if the amount of variability is related to the duration of the delay interval.

METHODS

Surgical and recording procedures

Two sterile surgical procedures were performed on each of the three rhesus monkeys (*Macaca mulatta*) serving as subjects. Surgical procedures were performed while the animals were under general anesthesia. First, a stainless steel post was attached to the skull using stainless steel screws and dental acrylic. The post was used to immobilize the head during training and data collection sessions. In the second procedure, a coil of fine wire was implanted on one eye (Judge, Richmond & Chu, 1980) to permit recordings of eye position. All

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experimental and animal care procedures were in accordance with the NIH Guide for the Care and Use of Laboratory Animals.

Eye position signals were obtained with a sensitivity of at least 0.25 deg, using the implanted search coil. Exposure of the animal to two alternating magnetic fields in spatial and phase quadrature generated signals in the coil that could be phase detected to produce two voltages—one proportional to horizontal eye position and one proportional to vertical eye position (Fuchs & Robinson, 1966). Eye position signals were calibrated by having the monkey sequentially fixate light-emitting diodes (LEDs), separated by 4 deg, extending to 12 deg above, below, to the right and to the left of center. Eye position signals were calibrated first in normal room illumination. When subjects were placed in total darkness for testing performance on memory trials, they developed an offset in fixation position (Snodderly, 1987). Addition of horizontal and vertical d.c. bias voltages re-centered the eye position signals within the voltage windows used to establish reinforcement contingencies and eliminated the fixation offset as a source of systematic error in the measurements obtained.

Behavioral training

Data collection sessions were initiated after 2–4 weeks of behavioral training. During data collection and training sessions, the monkey was seated in a primate chair (inside a sound-attenuated chamber) and the head was restrained. Data were obtained while the animal was in total darkness unless indicated otherwise. Monkeys were maintained on a water restriction schedule for 5–6 days each week and trained to fixate and generate saccades to small (0.1 deg) visual targets. An array of LEDs served as targets. The array consisted of 11 rows of 13 LEDs, equally spaced at 4 deg intervals, that extended ± 24 deg horizontally and ± 20 deg vertically from a central fixation position. A PDP 11/23 or 11/73 laboratory computer controlled the onset and offset of LED targets and delivered liquid reinforcement for appropriate tracking of targets. Details of the computer system and training procedures have been previously described (Sparks & Holland, 1975; Sparks, Holland & Guthrie, 1976).

Large data sets were obtained from two subjects (M333 and M340) performing a remembered saccade task.

Remembered saccade task. During remembered saccade trials, the monkey was permitted 500 msec to acquire the initial center target (0). After a variable fixation interval, a second target (A) was flashed for 250 msec but the trial was terminated, without reinforcement, if the animal failed to maintain fixation of target 0. The monkey was required to continue fixating target 0 (the only target in the totally dark room) for a variable delay interval. At the end of that interval, the offset of target 0 was the cue for the monkey to look to the remembered location of the previously-flashed target A. The monkey was rewarded for looking to the approximate position of target A; greater errors were tolerated

on these trials since the monkeys were unable to perform the remembered saccade task as accurately as a control task in which a delay was not imposed between target offset and the signal to initiate a saccade (see Results). The delay interval was initially very short and gradually lengthened until, after weeks of training, the animals were able to perform the task with delay intervals up to 5.6 sec.

Control trials. Measures of baseline performance were obtained from the remembered saccade task with a delay interval of 0 msec. These trials were identical to remembered trials except the subjects were not required to delay saccade initiation when the target was extinguished; the fixation stimulus and the eccentric target were extinguished simultaneously.

To test hypotheses that arose during analysis of the data of the first two monkeys, data were obtained from the third monkey (M4781) performing two additional tasks.

Visually-guided saccade task. On visually-guided saccade trials, an initial fixation target (0) was presented centrally. If the initial target was acquired within 500 msec and fixation was maintained for a variable period (1–3 sec), target 0 was extinguished and target A appeared at another location. If target A was acquired within 500 msec and fixation maintained for 1 sec, reinforcement was delivered on a continuous ratio schedule.

Brief A saccade task. After a variable fixation interval of the center target (0), target 0 was extinguished and a peripheral target (A) was flashed for 50 msec. The animal was reinforced for looking to the location of target A (now absent) and maintaining that position for 500 msec. Saccades elicited in this trial type were compared with saccades to remembered targets.

Experimental design and data analysis

A target set of 20 LEDs was used to study remembered saccades. The horizontal positions of the targets were -16 , -12 , -8 , 0 , 8 , 12 and 16 deg (negative numbers represent positions to the left of the vertical meridian and positive numbers, to the right of the vertical meridian). The vertical positions were -12 (below the horizontal meridian), 0 (along the horizontal meridian) and 12 deg (above the horizontal meridian). Target 0,0 always served as the initial fixation position. Before each trial, a target position was randomly selected from a table of the 20 positions. Remembered saccade trials with at least two delay intervals (from 400 to 5600 msec) were intermixed with control trials each day. An attempt was made to collect data from at least 30 trials at each target location and delay interval. Data for each monkey were collected over a period of several weeks.

Digital codes representing the following events or experimental parameters were stored on digital magnetic tape or disk: target position, onset, offset and duration; horizontal and vertical eye position (sampled at 500 Hz); time of target acquisition; and time of reinforcement.

The sequence of target presentation and eye movement could be reconstructed off-line for analysis.

Estimates of systematic and variable error were based upon measures of the amplitude and end point of the horizontal and vertical components of the first (primary) saccade. Saccade onset and offset were defined using velocity criteria (onset = 40 deg/sec; offset = 30 deg/sec). After linearization of the eye position signals and correction for the location of the target on the tangent screen, vectorial eye velocity was computed from the horizontal and vertical eye position data using the central-difference differential algorithm (Bahill & McDonald, 1983). Trials in which the reaction time was < 100 msec or > 500 msec and trials in which the movements were obviously incorrect (i.e. directed to the opposite hemifield from the target location) were eliminated.

An index of the magnitude of systematic error, one that does not discriminate between horizontal and vertical bias, was obtained by computing the angular distance between the target location and mean saccade end point (represented graphically as the length of line segments connecting the targets and mean saccadic end points in Figs 3 and 4). An estimate was obtained for each target location at each delay interval.

An index of variable error, the scatter in the end points of saccades, was obtained by first computing the average horizontal and the average vertical eye position at the end of the initial saccade to a single target at a particular delay interval. Then, for each saccade in this target/delay-interval data set, the straight line distance of each individual end point from the computed average end point was obtained using the following formula:

$$d_i = \sqrt{(\bar{X} - X_i)^2 + (\bar{Y} - Y_i)^2}$$

where

d_i = deviation of a saccadic end point from the average end point;

\bar{X} = average horizontal end position;

X_i = horizontal end point for a particular saccade i ;

\bar{Y} = average vertical end position; and

Y_i = vertical end position for saccade i .

The mean of the d values for all saccades to a particular target at a given delay interval provides a measure of the variability of saccade end point about the average end position.

RESULTS

In general, saccades to remembered targets were less accurate, displayed greater variability in end position and, when matched for amplitude, were of lower peak velocity than saccades on control trials.

Systematic and variable error

The systematic and variable errors observed on memory trials are shown in Figs 1 and 2 for monkeys 333 and 340, respectively. For both control [Figs 1(A) and 2(A)] and remembered [Figs 1(B-D) and 2(B-D)] trials, the end points of many saccades are plotted for each of six

target locations (for clarity, only a subset of target locations are shown). For both monkeys, saccades on control trials (delay = 0) are relatively accurate and display little variability in end point. Figures 1(A) and 2(A) show saccade end points to be tightly clustered and distributed to within 1-3 deg of each target location (the actual locations of the targets are indicated by the open circles). In contrast, the end points of saccades to remembered locations [Figs 1(B-D) and 2(B-D)] show systematic deviations from the actual target locations and a high degree of variability. A better illustration of the systematic error is presented in Figs 3 and 4 in which mean saccadic end point is plotted in relation to target location for the same data shown in Figs 1 and 2. Additional target locations, omitted for clarity from Figs 1 and 2, are included in Figs 3 and 4. Note the upward deviation of end points of remembered saccades.

The effects of delay interval on systematic and variable error are plotted in Fig. 5. The points plotted for each delay interval represent mean values obtained by pooling data for all target positions. Note that both systematic and variable error are much greater on memory than on control trials (delay = 0 msec). Systematic error reaches a maximum at the shortest delay intervals of 400 msec for monkey 333 and 800 msec for monkey 340. In contrast, variable error rises monotonically as a function of increasing delay intervals of up to, at least, 2400 msec.

Two three-way repeated measures ANOVAs (delay interval \times target location \times monkey) were performed using the seven delay intervals (0, 800, 1600, 2400, 3200, 4000, and 5600 msec) tested on both monkeys and the 20 target locations. Variable error was the dependent measure for one analysis; the dependent measure for the second analysis was systematic error. The main effect of delay was significant for both variable [$F_{6,6} = 19.57$, $P < 0.01$] and systematic [$F_{6,6} = 21.2$, $P < 0.001$] error. The main effect of target location was significant for variable error [$F_{19,19} = 2.42$, $P < 0.05$] but only approached significance for systematic error [$F_{19,19} = 2.15$, $P > 0.05$]. Delay by target interactions were not significant for either variable error [$F_{114,114} = 1.14$, $P > 0.10$] or systematic error [$F_{114,114} = 0.95$, $P > 0.10$].

Tukey's multiple comparisons test which holds the overall significance level at 0.05 indicated that both variable and systematic error are significantly greater on memory trials than on control trials. However, while the amplitude of systematic error does not vary with the duration of the delay interval on memory trials ($P > 0.05$), significant increases in variable error do occur when the delay interval is lengthened. For example, average variable error observed with delays of 800 msec is significantly smaller than those observed for all longer delays. The average variable error occurring with delays of 5600 msec is significantly larger than the variable errors occurring on memory trials with shorter delays.

Horizontal and vertical error components

Visual inspection of the plots shown in Figs 3 and 4 (A-D) suggests a relationship between error magnitude

and target position. Most apparent is the relationship between vertical error and vertical target position. For both monkeys, the upward bias increased with downward target eccentricity and decreased with upward eccentricity. Also apparent is the tendency for horizontal error (hypometria) to be greater for targets of greater horizontal eccentricity.

The general analyses of systematic and variable error described in the previous section may not be sensitive to effects specific to only one (horizontal or vertical) of the components. In order to better characterize the systematic error of saccades to remembered targets, two separate ANOVAs (vertical target position \times horizontal target position \times delay interval \times monkey) were performed using either the horizontal or the vertical component of the error as the dependent measure. Horizontal error was defined

as the difference between horizontal target location and mean horizontal eye position after the first saccade; vertical error as the difference between vertical target location and mean vertical eye position after the first saccade. The main effect of vertical target position (three levels: vertical position = -12, 0, 12 deg) on the magnitude of vertical error ($F_{2,2} = 1729.8$, $P < 0.001$) and the main effect of horizontal target position (seven levels: horizontal position = -16, -12, -8, 0, 8, 12, 16 deg) on the magnitude of horizontal error ($F_{6,6} = 147.1$, $P < 0.001$) were significant. As suggested by the plots in Figs 3(A-D), 4(A-D), and 5, delay interval had a significant effect upon vertical error magnitude ($F_{6,6} = 5.32$, $P < 0.05$), but not upon horizontal error ($F_{6,6} = 1.41$, $P > 0.05$). Tukey's multiple comparisons test indicated that vertical error on control trials was significantly smaller than

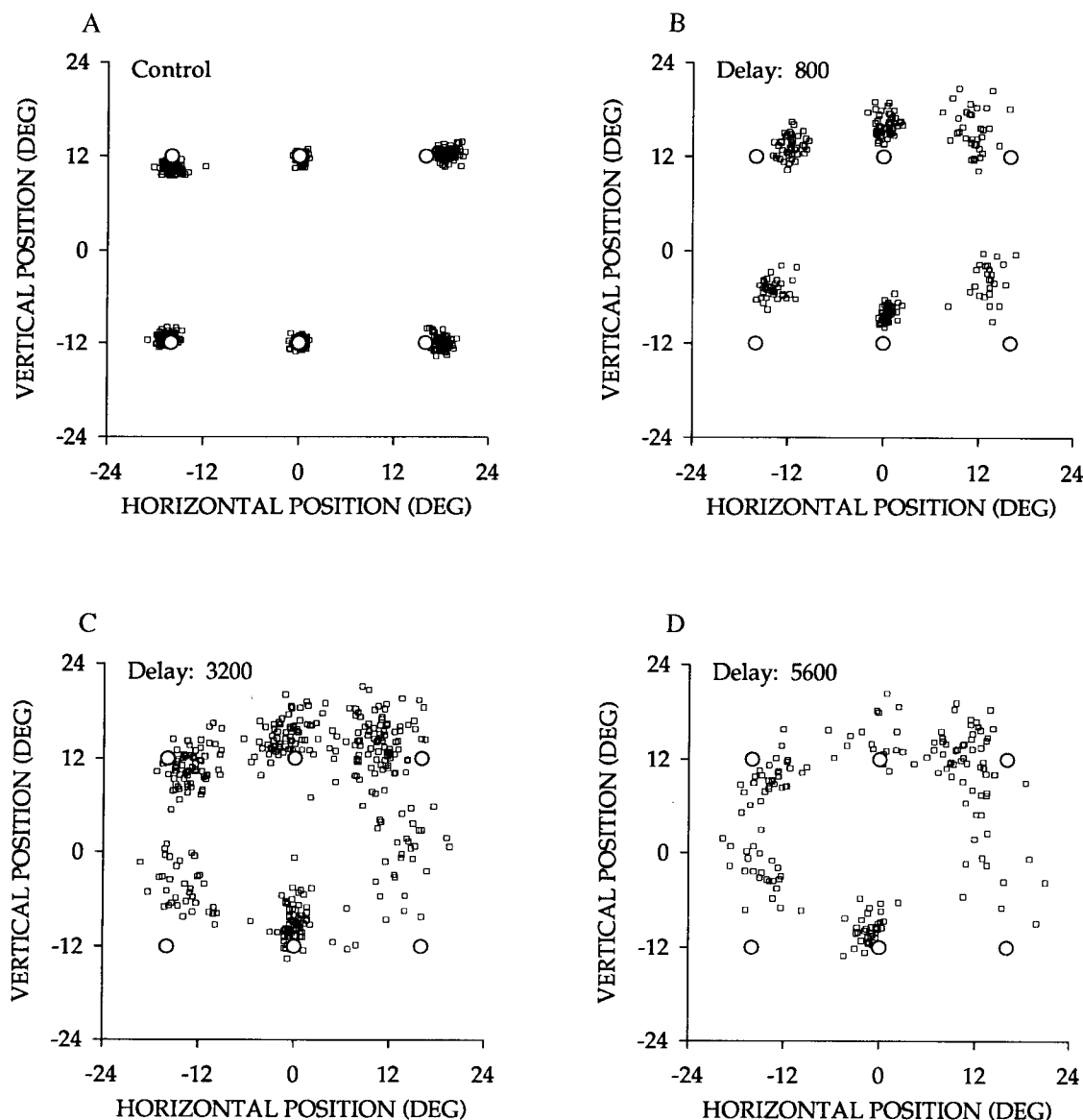


FIGURE 1. End points of saccades (open squares) to targets (open circles) with horizontal and vertical coordinates of -16, 12; 0, 12; 16, 12; -16, -12; 0, -12; 16, -12 (monkey 333). Saccades on control trials (A) and saccades to remembered targets with delay intervals of 800 (B), 3200 (C) and 5600 msec (D). Note that end points of remembered saccades are less accurate and more scattered than those of control saccades.

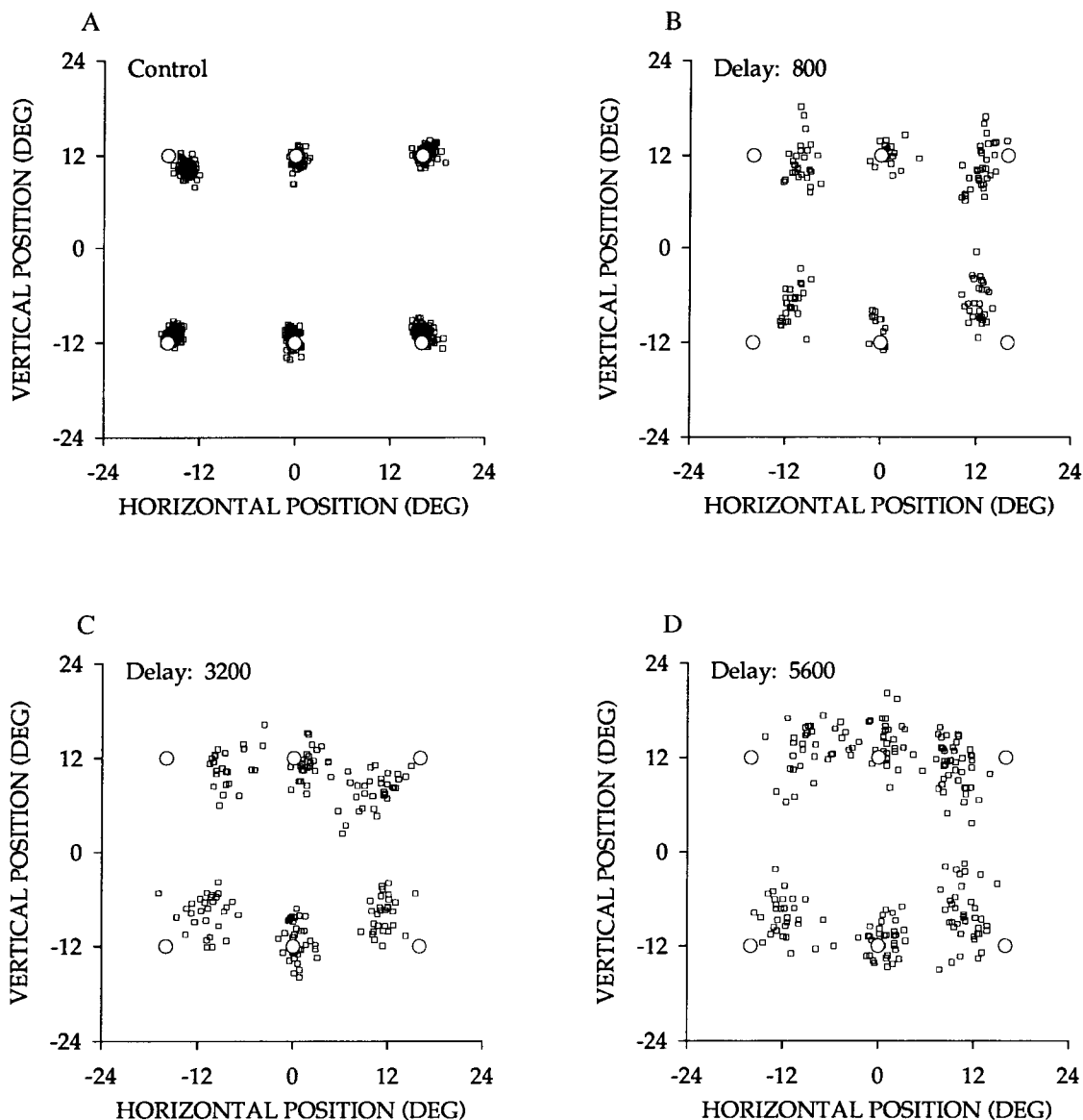


FIGURE 2. End points of saccades to targets with horizontal and vertical coordinates of $-16, 12$; $0, 12$; $16, 12$; $-16, -12$; $0, -12$; $16, -12$ (monkey 340). See Fig. 1 legend for other details.

vertical error on delay trials but there were no significant differences in error for the different delay intervals.

Inspection of Figs 3 and 4 also suggests that vertical error increases with horizontal target eccentricity for targets below the horizontal meridian, but decreases as a function of horizontal eccentricity for targets above the horizontal meridian. Main effects for horizontal target position on vertical error magnitude, and vertical target position on horizontal error magnitude were not significant. However, there was a significant interaction between the effects of horizontal and vertical target position on the magnitude of vertical error ($F_{11,11} = 5.27$, $P < 0.005$). Embedded within this interaction is an effect of horizontal target position on vertical error that is evident in Figs 3 and 4.

Peak velocity

Saccades to remembered targets had lower peak velocities than amplitude-matched saccades on control

trials. This difference can be seen by comparing Fig. 6(A) with Fig. 6(B) in which peak velocity is plotted as a function of saccade amplitude for saccades on control [Fig. 6(A)] and remembered trials [Fig. 6(B)]. At each amplitude, saccades to remembered targets have lower peak velocities. Least squares lines fit to the data are shown. For clarity, only the least squares regression lines are shown for remembered saccades at each delay interval and for control saccades in Fig. 6(C, D) for monkey 333 and 340, respectively. A one-way ANOVA (excluding control trials) indicated that the slope of the least squares lines for remembered saccades does not vary significantly with delay interval ($F_{5,5} = 4.25$, $P > 0.05$). Although the peak velocity of remembered saccades is lower than that of control saccades, further reductions in the peak velocity of remembered saccades with increasing delay interval are not statistically significant.

Variability in peak saccadic velocity for remembered saccades is greater than the variability in peak velocity

of control saccades. The standard error of estimate ($s_{y \cdot x}$), a measure of variability of peak velocity about the line of best fit of the velocity/amplitude plots, is smaller for control saccades ($s_{y \cdot x} = 65.6$ and 65.5 for M333 and M340, respectively) than for remembered saccades (average $s_{y \cdot x} = 81.3$ and 70.8 for M333 and M340, respectively). Bartlett's test for the homogeneity of variance indicated that these variances were not homogeneous ($\chi^2 = 562$, $P < 0.001$) and *post hoc* comparisons (Tukey's) indicated that the zero delay was significantly different from all the other delay intervals. On memory trials with delay intervals between 800 and 5600 msec,

the variability of points about the line of best fit does not increase as delay intervals are lengthened (Tukey's multiple comparisons, $P > 0.05$). This is unlike the variability of saccade end points, which does increase as a function of delay interval [see Fig. 5(B)].

Other observations

Previous observations suggest a relationship between the systematic error of remembered saccades and the availability of nontarget visual cues. Specifically, Gnadt *et al.* (1991) reported that the upward bias occurring on remembered trials became smaller when the level of

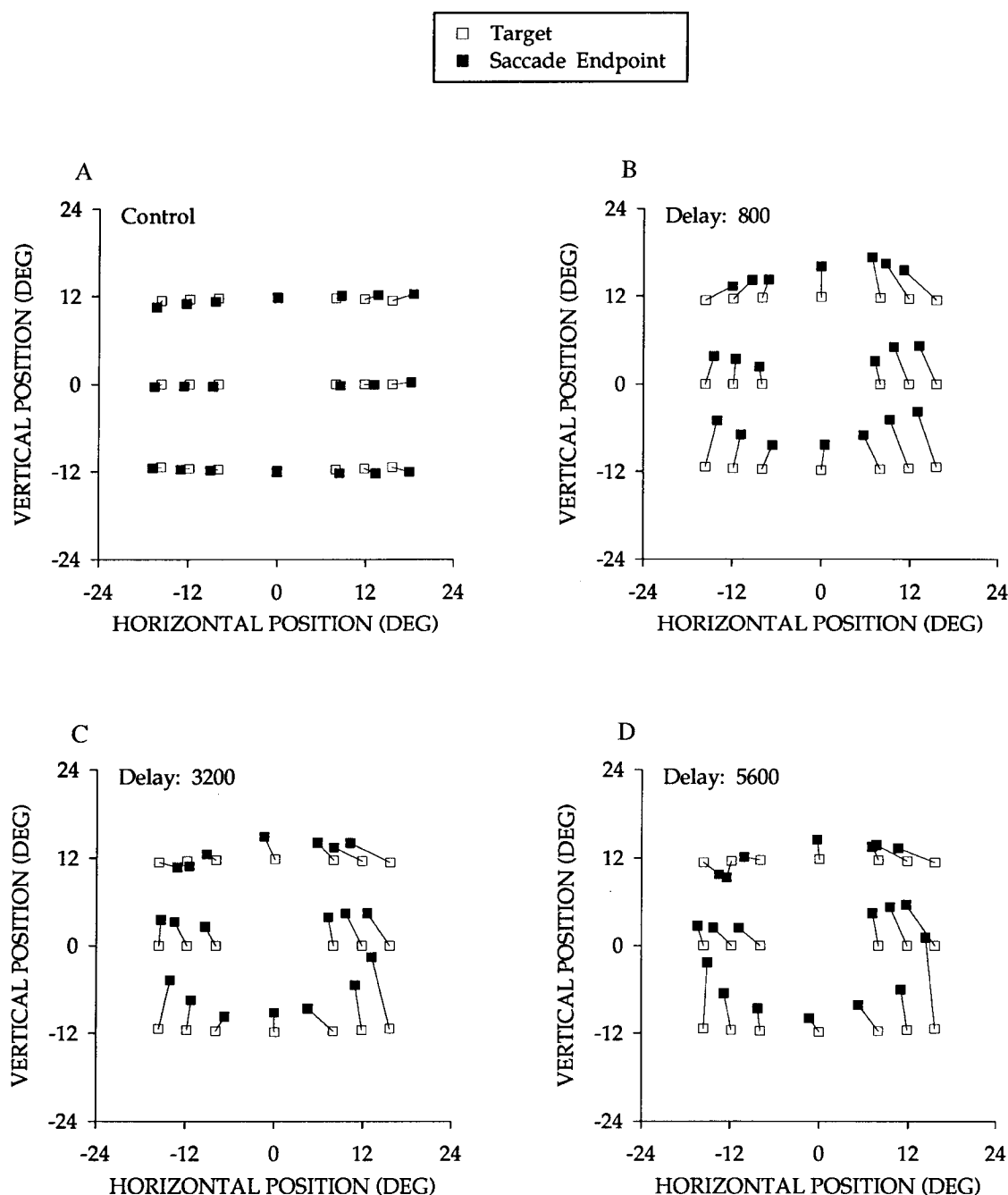


FIGURE 3. Pattern of systematic errors of saccadic end points (monkey 333). The mean end points of saccades are represented by solid squares and target location, by open squares. Control saccades (A) and saccades to remembered targets with delay intervals of 800 (B), 3200 (C) and 5600 msec (D). Mean end points of remembered saccades are further from the targets and generally displaced upward relative to mean end points of control saccades.

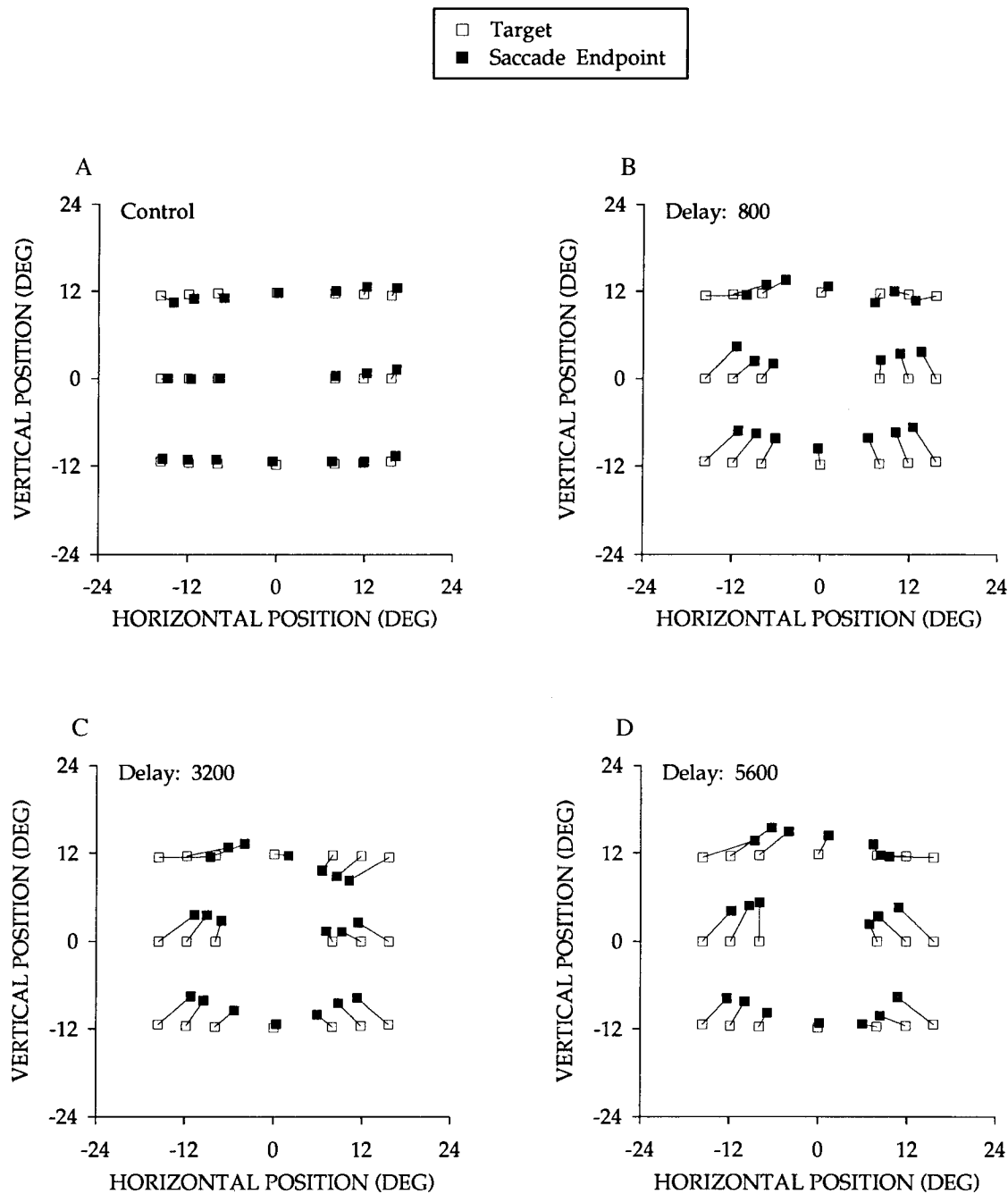


FIGURE 4. Pattern of systematic errors of saccadic end points (monkey 340). See Fig. 3 for other details.

background illumination was increased. The fact that the systematic error on memory trials is sensitive to background cues indicates that it is not solely due to a memory-related process. As an extension of their finding, the dependence of systematic error on light level was examined in the absence of an imposed delay interval for one monkey (4781). Figure 7(A) shows the average end points of saccades (solid squares) for a control condition in which the animal made saccades to persistent visual targets presented in a dimly lit room. For comparison, Fig. 7(B) shows the average end points of saccades made to persistent visual targets in a completely dark room. Compared to saccades made in dim light, saccades made in the dark room have greater error, largely due to an

upward displacement between average end point and target position. Figure 7(C) shows the end points of saccades made to visual targets that were briefly flashed in a totally dark room. In this condition, the only delay interval is the interval associated with the saccadic reaction time. Compared to saccades to a persistent visual target presented in total darkness [Fig. 7(B)], the end point errors are increased further, with a noticeable upward displacement. Finally, average end points of saccades to remembered targets (with a delay interval of 500 msec) are shown in Fig. 7(D). The pattern of errors typical of remembered saccades is present. These results indicate that the systematic errors reflected in the upward bias of saccade end points are not solely related to

memory-dependent processes. A dark environment or the lack of a structured visual background contributes to the observed pattern of errors. This factor may interact with memory processes to produce larger errors when animals are required to look to the remembered location of targets in the dark.

Skavenski, Robinson, Steinman and Timberlake (1975) reported that monkeys show a predominantly upward drift in eye position when in complete darkness. Monkeys used as subjects in this experiment also demonstrated slow and steady drifts in eye position when placed in total darkness without a fixation target. If there is a failure to compensate for these drifts during the computation of saccade amplitude and direction, the pattern of errors observed on memory trials should be related to the rate and direction of the drift. We did not observe an obvious relationship between the pattern of errors and the drift occurring during the memory trials. Figure 8 plots measurements of drift velocity for the monkey whose saccade end points are illustrated in Fig. 7. Estimates of horizontal and vertical drift velocity were obtained for three 200-msec epochs: during the delay interval while the monkey attempted to maintain fixation [Fig. 8(A, B)], between trials during the interval between the first and second spontaneous saccades [Fig. 8(C, D)], and during "blank trials" in which neither the fixation nor target LED was illuminated [Fig. 8(E, F)]. Vertical and horizontal drift velocities were very low during the delay interval [Fig. 8(A, B)] indicating that the monkey successfully compensated for drift when provided with a target to fixate. However, in the absence of a visual target,

upward and leftward drifts of approximately equal velocity (1–2 deg/sec) were apparent [Fig. 8(C–F)]. The similarity of the plots in Fig. 8(C–F) indicates that drift rate does not depend on the duration of time spent in complete darkness without a fixation stimulus. The measurements for Fig. 8(C, D) were made within 200–300 msec of the end of the previous trial, while those for Fig. 8(E, F) were made after 2–3 sec in total darkness. Comparing the estimates of drift velocity to the pattern of errors observed on memory trials (Fig. 7) fails to indicate the existence of a straightforward relationship. While upward drift is consistent with the upward bias, a reflection of the leftward drift is not apparent in the pattern of errors shown in Fig. 7. How to relate the rate of drift to the magnitude of error is less clear. At a rate of 1–2 deg/sec, the drift cannot fully account for the magnitude of errors observed on most remembered saccades.

DISCUSSION

Our results confirm and extend previous findings regarding the characteristics of saccades to remembered targets. In general, the data obtained from different subjects and in different laboratories are in excellent agreement.

Accuracy

Compared to control saccades, saccades to the remembered location of visual targets are less accurate; the end points of remembered saccades are systematically displaced above the location of the target. Gnadt

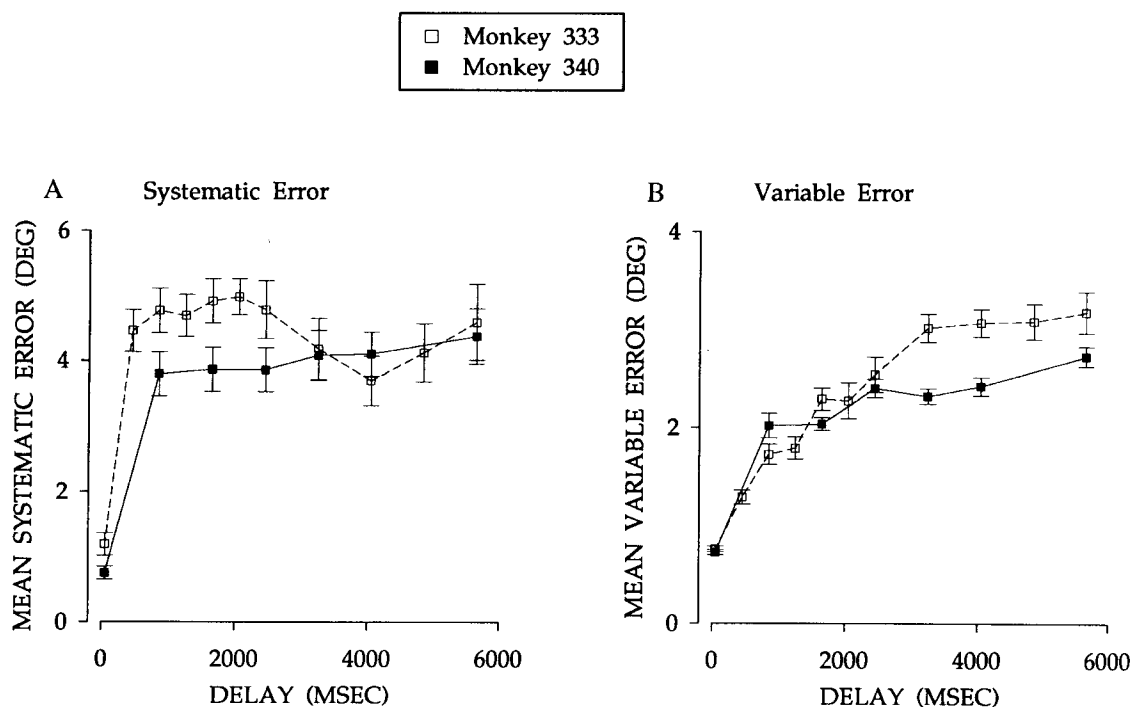


FIGURE 5. Systematic error (A) and variable error (B) as a function of delay interval (monkey 333, open squares; monkey 340, solid squares). Plotted points are the errors averaged across all target locations. Error of control saccades is shown at a delay interval of 0 msec.

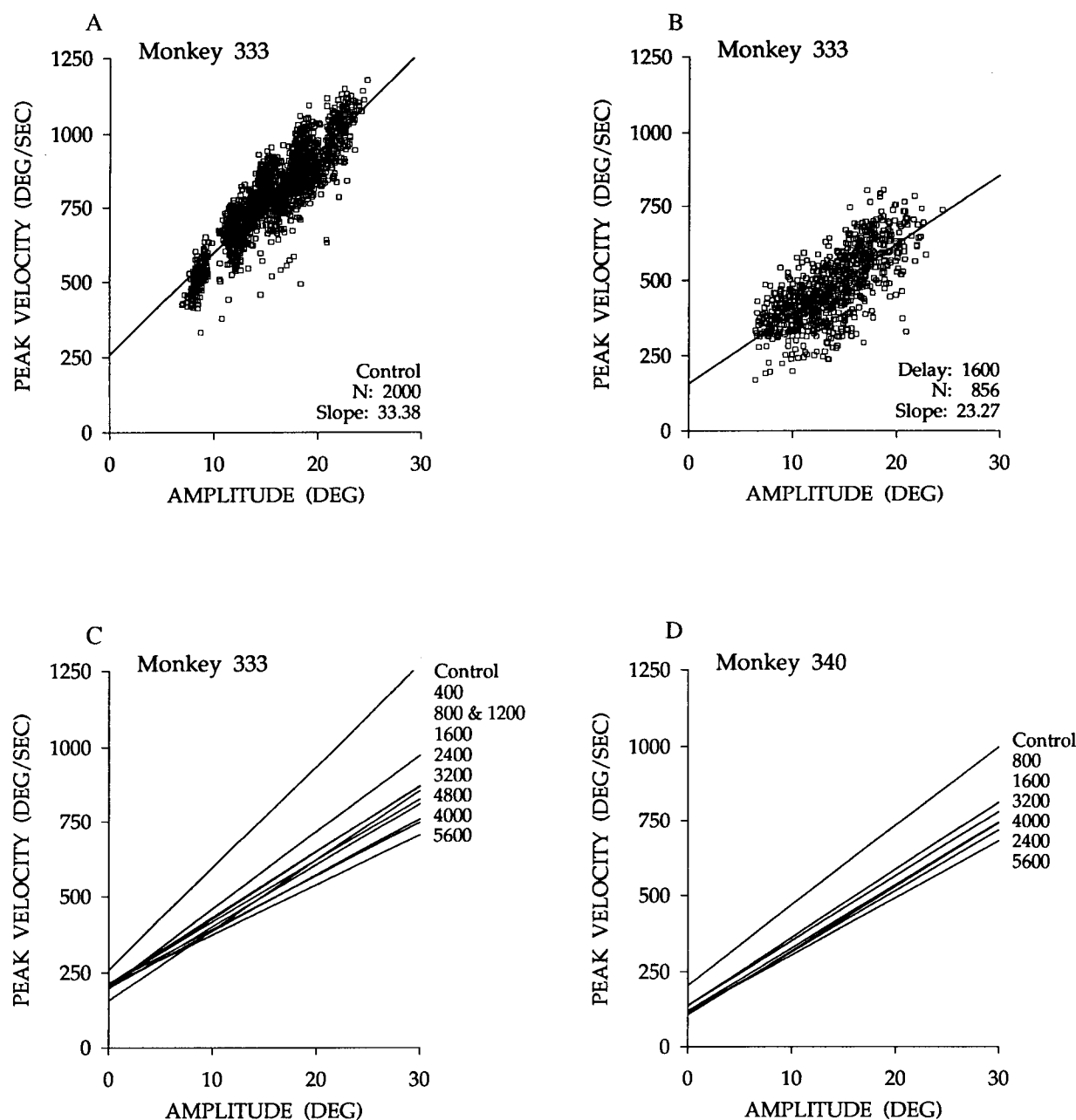


FIGURE 6. Peak saccadic velocity as a function of saccadic amplitude. (A) Scatter plot for control saccades made by monkey 333 to all targets. The line is the least squares line fit to the data. (B) Scatter plot for saccades to all remembered targets made by monkey 333, at a delay interval of 1600 msec. The least squares line of best fit is shown. (C) Lines of best fit for control saccades (shown at a delay interval of 0) and remembered saccades, with delay intervals indicated by the numbers. Monkey 333. (D) Lines of best fit for control saccades (shown at a delay interval of 0) and remembered saccades, with delay intervals indicated by the numbers. Monkey 340.

et al. (1991) report that the magnitude of the displacement depends upon the duration of the delay interval. For one monkey, they estimated the vertical error for all saccades made to the remembered location of a target presented 15 deg to the right. Vertical error increased as a function of the interval between target offset and saccade onset, accumulating rapidly within the first 800 msec and rising more slowly at delays of up to 2 sec, the longest interval tested.

We also found that systematic error on remembered trials is significantly greater than the error observed on control trials. Consistent with the finding of Gnadt *et al.*

(1991) that the upward bias accumulates and stabilizes rapidly, we did not observe a significant relationship between error magnitude and the delay intervals we tested [800 (400)–5600 msec] for either the overall error or the vertical component of the error. The error of remembered saccades was similar across all delay intervals.

Compared to control saccades, saccades to the remembered location of visual targets are characterized by greater variability in end position (Gnadt *et al.*, 1991). We confirmed this finding. Variable error on memory trials was significantly greater than that observed on

control trials. However, unlike systematic error, variable error increased as the delay interval was lengthened.

Gnadt *et al.* (1991) report that the increase in variable error of remembered saccades follows the same time-course as the accumulation of systematic error and, therefore, argue that it may be part of the same process, a process that proceeds and stabilizes rapidly. Our data, based upon a larger range of delay intervals, indicate

that the systematic and variable components follow different time-courses. The magnitude of systematic error reaches a maximum after delays of only 400 msec. Variable errors increased monotonically as delay intervals were lengthened to 5.6 sec. This agrees with studies of other types of motor memory tasks which report that the accumulation of variable error is relatively slow when compared to systematic errors (e.g. Kinchla & Allan, 1969; Steenhuis & Goodale, 1988).

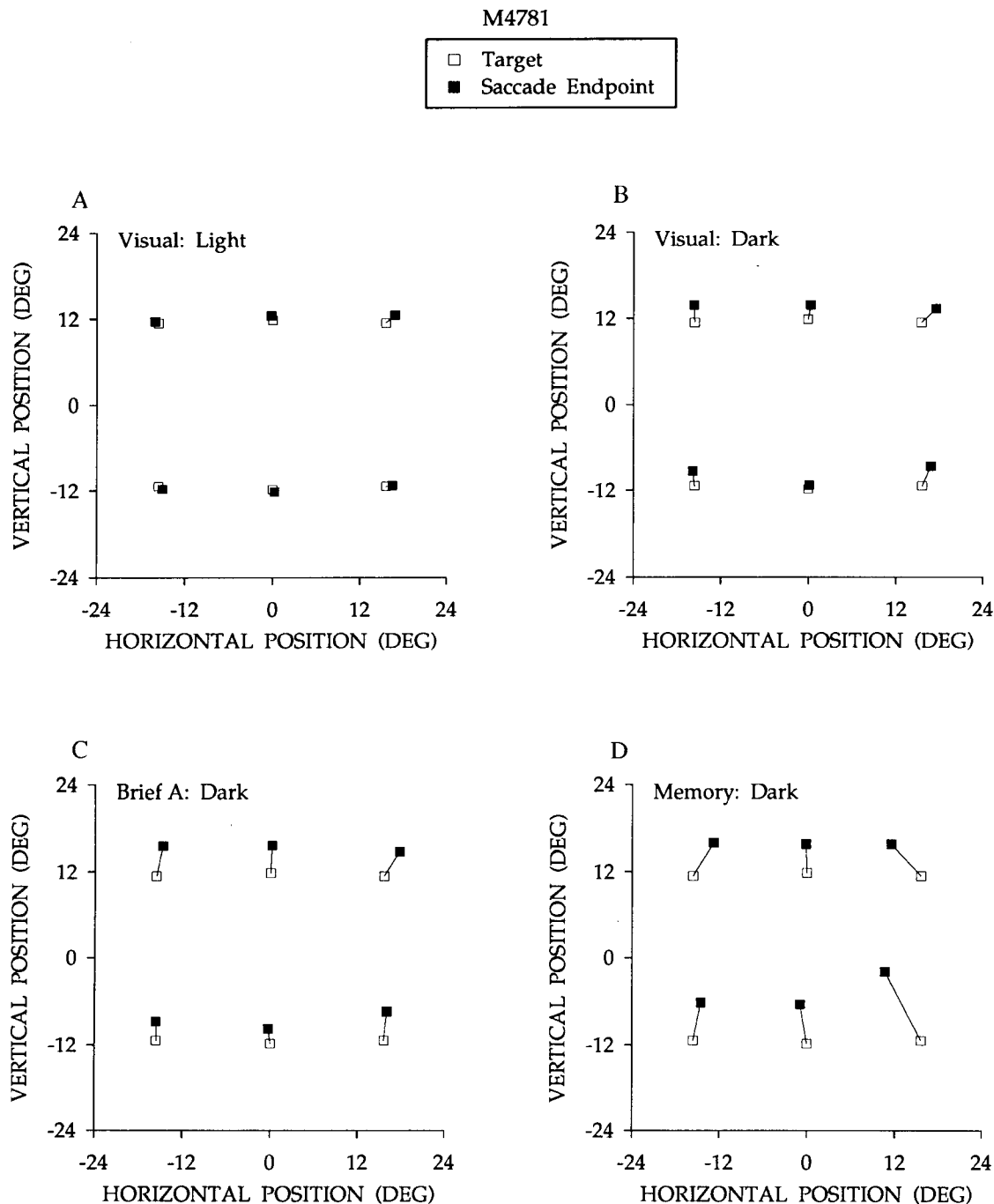


FIGURE 7. Pattern of end point errors of saccades (monkey 4781). The mean end points of saccades (in horizontal and vertical coordinates) are represented by the solid squares and target locations, by the open squares. (A) Mean end points of saccades to visual targets under dim illumination. (B) Mean end points of saccades to visual targets in a totally dark environment. (C) Mean end points of saccades to briefly-flashed (for 50 msec) visual targets in a totally dark environment. (D) Mean end points of saccades to the remembered location of visual targets (delay interval of 500 msec) in a totally dark environment.

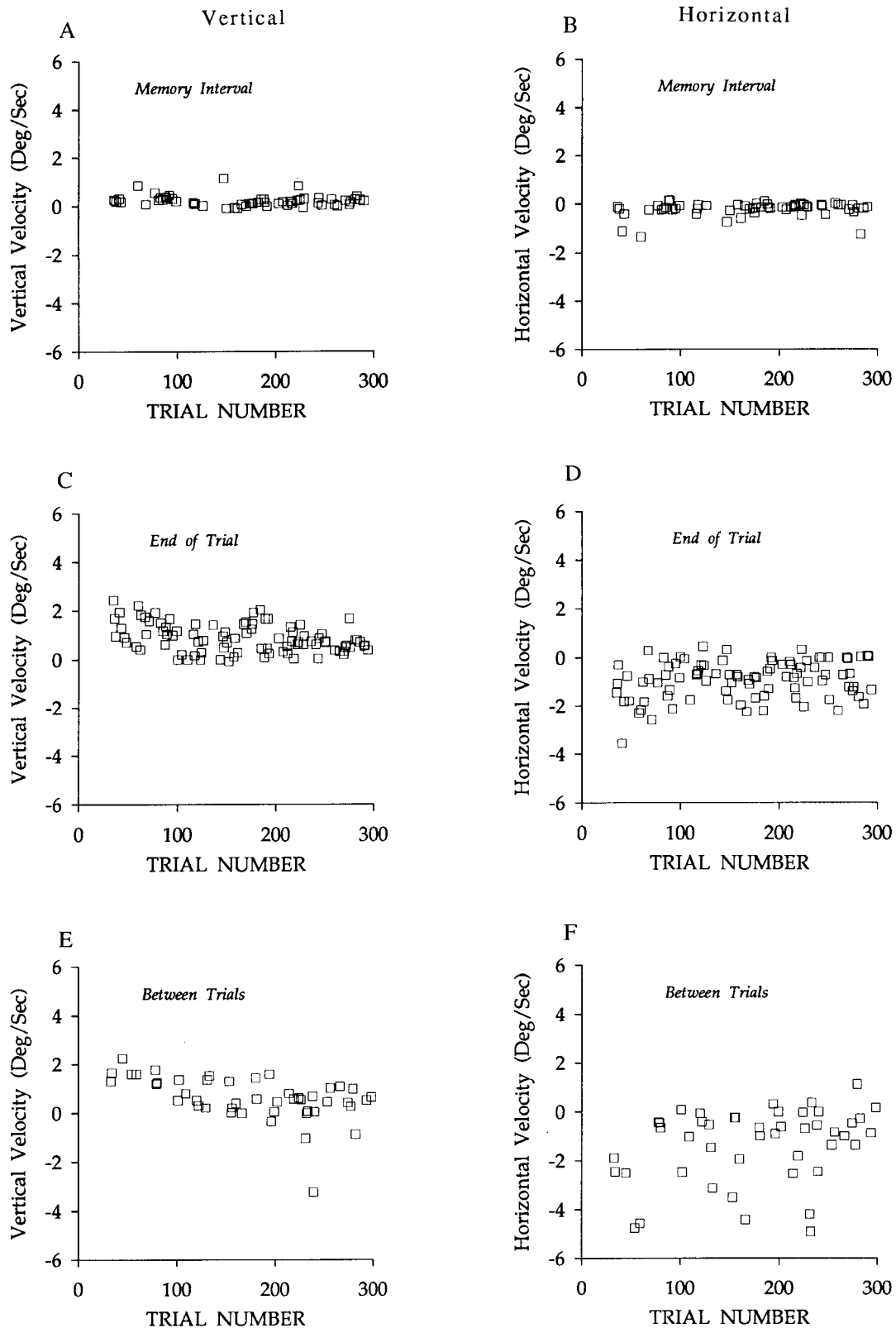


FIGURE 8. Drift velocity during the delay interval (A, B), at the end of the trial (C, D), and between trials (E, F) for monkey 4781. Vertical (A) and horizontal (B) drift velocity (deg/sec) during the delay interval across the trials of one data collection session. When a fixation target is present, drift is suppressed. When the fixation target is extinguished, the eye tends to drift up (C) and to the left (D) at a velocity up to 2°/sec. A similar drift velocity is observed in vertical (E) and horizontal (F) position between trials, when the animal is in a totally dark environment.

Sources of variable error

We can only speculate about the neural basis of variable error and its relationship to delay interval. Neurophysiological signals that persist throughout the delay interval have been observed in the superior colliculus (SC) (Mays & Sparks, 1980), parietal cortex (Gnadt & Andersen, 1988), and frontal cortex (Joseph & Barone, 1987; Boch & Goldberg, 1989; Bruce & Goldberg, 1985; Seagraves & Goldberg, 1987; Funahashi *et al.*, 1989, 1990, 1991; Goldberg & Bruce, 1990). At these sites, the signals are already in motor coordinates and specify the metrics of the movement rather than the location of the target. In the SC, two types of cells are known to exhibit sustained firing during long delay intervals: quasi-visual (QV) cells (Mays & Sparks, 1980) and saccade-related burst cells with a prelude of low-frequency activity (Glimcher & Sparks, 1992). The collicular activity occurs within a topographically organized motor map in which information about the direction and amplitude of an impending saccade is coded anatomically; it is the location of the active population within the motor map that determines the metrics of a saccade. Reversible deactivation of subsets of the active population demonstrates that each member of the active population (Lee *et al.*, 1988) contributes to the ensuing saccade in such a way that the metrics of a movement are based upon the average of the movement tendencies produced by the entire active population. Thus, asynchronous variations in the firing rate of individual members of the active population are a possible source of variable error. Fluctuations in rate of firing during delay intervals are commonly observed in both the prelude burst neurons and QV cells. These variations in discharge rate have not been examined closely and it is not known if fluctuations in firing rate follow a time-course similar to the accumulation of variable error. Nonetheless, unless these fluctuations are synchronized throughout the active population, variations in the average output of the population could occur on a moment-by-moment basis and be one source of the variable error observed on memory trials.

Sources of systematic error

The amplitude of systematic errors occurring on memory trials is significantly reduced by the addition of a textured background (random dots) or by dim illumination that exposes the visual contours of the experimental room (Gnadt *et al.*, 1991). We found a pattern of systematic errors, similar to that observed on memory trials, when saccade tasks without an imposed delay interval were performed in the dark. Collectively, these findings indicate that the systematic errors reflected in the upward bias are not solely related to memory-dependent processes. The dark environment or the lack of a structured visual background, usually associated with memory trials, may contribute to the observed pattern of errors. Also, it should be noted that both head position and the initial position of the eye in the orbit influence the amplitude of systematic errors observed after remembered saccades (Gnadt *et al.*, 1991).

Another potential source of the systematic errors observed is an offset in fixation position. In monkeys, the position of fixation of a visual target in darkness is displaced above the position of fixation in the light. This effect is not large enough to account for all of the systematic error. Snodderly (1987) reports a displacement of about 1 deg whereas the average end points of remembered saccades were often 4–5 deg from the target location. Fixation offset was eliminated as a source of systematic error in our data by our calibration procedures (see Methods).

Other sources of systematic error should also be considered. In total darkness, monkeys demonstrate an upward drift in eye position. In some animals, the drift includes a horizontal component (Skavenski *et al.*, 1975). We measured the drift in eye position observed when the animal was in darkness without a fixation target, and during the first intersaccadic interval after the fixation target was extinguished. The pattern of drift observed in the dark cannot fully account for the pattern of systematic error observed on memory trials for several reasons. First, the drift seems to occur continuously, but the accumulation of systematic error on remembered trials is complete within 400 msec. Second, if horizontal errors were produced by the failure to compensate for horizontal drift, the animal should always look to the left (or right, depending on the direction of drift) of targets on either side of the vertical meridian. This is not what is observed. Horizontal movements to leftward and rightward targets are hypometric. One animal exhibited horizontal drifts that were as large in amplitude and velocity as the vertical drift. However, the pattern of errors observed in this animal was very similar to the pattern of errors observed in monkeys displaying only vertical drift. If some fraction of the error of saccades to remembered targets is due to drift in eye position, it is unclear why the vertical, but not the horizontal, drift bias should be reflected in the pattern of errors. Finally, the velocity of the drift does not account for the magnitude of the error. An error imposed by the failure to account for a drift of 2 deg/sec for 800 msec should produce an error of <2 deg. The observed errors were usually larger.

Memory dependent processes

Gnadt *et al.* (1991) concluded that the systematic and variable errors of remembered saccades were specific to the remembered task and assumed that they were a function of a memory dependent stage in the process of translating retinotopic signals into motor commands. They speculated that the upward bias of saccadic end points occurs because the “memory” of intended eye movements does not remain in register with the original retinotopic representation, or that the “memory” of the retinotopic map of space becomes shifted with respect to the real gaze direction of the eyes. Bracewell, Barash and Andersen (1990) described a neural analogue of the vertical bias by recording from neurons in the lateral intraparietal cortex of rhesus monkeys, an area where memory-related saccadic motor error signals have been

observed (Gnadt & Andersen, 1988). If the systematic errors observed on memory trials are based primarily on memory dependent processes, decrements in performance should become larger with increasing delay intervals. Neither the pattern nor the amplitude of systematic error was significantly altered by increases in delay interval beyond 400 msec. Moreover, the observation of an upward bias when monkeys performed tasks in total darkness that do not require a memory of target position, indicates that memory dependent processes are not the only source of the systematic error observed on memory trials. In contrast, the variability in end points of remembered saccades does increase with longer delay intervals and may be based upon a memory dependent process.

Velocity

Becker and Fuchs (1969) reported that saccades to remembered targets were slower and longer in duration than visually-guided saccades. A reduction in velocity was apparent after delays of only 100–350 msec. Peak velocity decreased as delay intervals were lengthened up to about 1 sec. Further increases in delay interval had no additional effect on saccadic velocity. These findings have been confirmed by all subsequent studies of remembered saccades (Sharpe *et al.*, 1975; Hikosaka & Wurtz, 1985; White & Sparks, 1986; Smit *et al.*, 1987; Gnadt *et al.*, 1991). In this experiment, we found that the slope of least squares lines fit to velocity/amplitude plots does not vary significantly with delay intervals ranging from 800 to 5600 msec (Fig. 6). Moreover, unlike the scatter of saccadic end points which increases as a function of delay interval, variability in peak velocity is unrelated to delay interval.

Although slower than visually-guided saccades, the movements made to remembered targets are almost certainly saccades. The peak velocities of the movements are substantially higher than the velocity of other types of eye movements such as smooth pursuit and vergence. Furthermore, neural signals believed to be commands for saccadic eye movements are observed before remembered movements. Neurons in the frontal eye fields (Bruce & Goldberg, 1985), posterior parietal cortex (Bracewell *et al.*, 1990), as well as saccade-related burst neurons in the SC (White & Sparks, 1986; Rohrer *et al.*, 1987; Stanford & Sparks, 1993) discharge before remembered saccades and a decrease in the firing rate of neurons in the substantia nigra pars reticulata is observed before both remembered and visually-guided saccades (Hikosaka & Wurtz, 1983).

Neurons in the substantia nigra pars reticulata are thought to tonically inhibit cells in the SC. The firing rate of nigral neurons decreases prior to remembered or visually-guided saccades, releasing collicular neurons from inhibition (Hikosaka & Wurtz, 1983). When, by injection of bicuculline, the SC is released from inhibition by the substantia nigra pars reticulata, the velocities of saccades to remembered targets become comparable to the velocities of visually-guided saccades (Hikosaka & Wurtz, 1985). Thus, the reduced velocity of remembered saccades could be due to an incomplete release of collicular neurons from nigral inhibition. Consistent with this hypoth-

esis, pharmacological reductions in the number of active neurons in SC produce dramatic reductions in saccadic velocity (Hikosaka & Wurtz, 1985; Lee *et al.*, 1988). The hypothesis is also supported by several reports of correlations between the discharge frequency of saccade-related burst neurons in the SC and the peak velocity of visually-guided and remembered saccades (Berthoz, Grantyn & Droulez, 1986; Rohrer *et al.*, 1987; Munoz & Guitton, 1987). For reasons presented in the following paper, correlations between neural activity in the SC and saccadic velocity on memory trials must be interpreted cautiously.

CONCLUSIONS

These findings have important implications for neurophysiological studies using remembered saccades to study mnemonic processes or to investigate the neural encoding of saccadic velocity. Memory studies correlating measures of neural activity with changes in performance that occur with different delay intervals should focus on measures of variable error, not measures of systematic error. Increasing the delay interval from 400–5600 msec has little effect on systematic error but does produce increases in variable error. For studies of how saccadic velocity is encoded, there is no advantage to training animals to perform memory tasks with long delay intervals. The same reduction in saccadic velocity is observed with delay intervals of 800 and 5600 msec.

The failure to observe increases in systematic error with longer delay intervals suggests that the major source of systematic error may not be a memory-related process. The sensitivity of systematic error to the level and texture of the background illumination in tasks that have no memory demand supports this conclusion. With respect to the neural sources of systematic error, Gnadt *et al.* (1991) hypothesized that the error results from a visual-to-motor transformation process in higher control centers that has, inherently, less precise spatial resolution. However, there is no compelling evidence for this hypothesis and the signals producing systematic error could originate at a much lower level. For example, collicular commands for saccadic movements do not take into account the initial position of the eye in the orbit; compensatory signals are thought to be introduced downstream from the SC (see Sparks & Mays, 1990). The sensitivity of systematic error to initial eye and head position (Gnadt *et al.*, 1991) raises the possibility that signals producing systematic error could also originate at a site downstream from the SC. These conflicting hypotheses regarding the source of signals producing systematic error stimulated the experiment described in the following paper (Stanford & Sparks, 1993).

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