

# Saccades to Remembered Targets: The Effects of Smooth Pursuit and Illusory Stimulus Motion

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## SUMMARY AND CONCLUSIONS

1. Measurements were made in four normal human subjects of the accuracy of saccades to remembered locations of targets that were flashed on a  $20 \times 30$  deg random dot display that was either stationary or moving horizontally and sinusoidally at  $\pm 9$  deg at 0.3 Hz. During the interval between the target flash and the memory-guided saccade, the "memory period" (1.4 s), subjects either fixated a stationary spot or pursued a spot moving vertically sinusoidally at  $\pm 9$  deg at 0.3 Hz.

2. When saccades were made toward the location of targets previously flashed on a stationary background as subjects fixated the stationary spot, median saccadic error was 0.93 deg horizontally and 1.1 deg vertically. These errors were greater than for saccades to visible targets, which had median values of 0.59 deg horizontally and 0.60 deg vertically.

3. When targets were flashed as subjects smoothly pursued a spot that moved vertically across the stationary background, median saccadic error was 1.1 deg horizontally and 1.2 deg vertically, thus being of similar accuracy to when targets were flashed during fixation. In addition, the vertical component of the memory-guided saccade was much more closely correlated with the "spatial error" than with the "retinal error"; this indicated that, when programming the saccade, the brain had taken into account eye movements that occurred during the memory period.

4. When saccades were made to targets flashed during attempted fixation of a stationary spot on a horizontally moving background, a condition that produces a weak Duncker-type illusion of horizontal movement of the primary target, median saccadic error increased horizontally to 3.2 deg but was 1.1 deg vertically.

5. When targets were flashed as subjects smoothly pursued a spot that moved vertically on the horizontally moving background, a condition that induces a strong illusion of diagonal target motion, median saccadic error was 4.0 deg horizontally and 1.5 deg vertically; thus the horizontal error was greater than under any other experimental condition.

6. In most trials, the initial saccade to the remembered target was followed by additional saccades while the subject was still in darkness. These secondary saccades, which were executed in the absence of visual feedback, brought the eye closer to the target location. During paradigms involving horizontal background movement, these corrections were more prominent horizontally than vertically.

7. Further measurements were made in two subjects to determine whether inaccuracy of memory-guided saccades, in the horizontal plane, was due to mislocalization at the time that the target flashed, misrepresentation of the trajectory of the pursuit eye movement during the memory period, or both.

8. The magnitude of the saccadic error, both with and without corrections made in darkness, was mislocalized by  $\sim 30\%$  of the displacement of the background at the time that the target flashed. The magnitude of the saccadic error also was influenced by net

movement of the background during the memory period, corresponding to  $\sim 25\%$  of net background movement for the initial saccade and  $\sim 13\%$  for the final eye position achieved in darkness.

9. We formulated simple linear models to test specific hypotheses about which combinations of signals best describe the observed saccadic amplitudes. We tested the possibilities that the brain made an accurate memory of target location and a reliable representation of the eye movement during the memory period, or that one or both of these was corrupted by the illusory visual stimulus. Our data were best accounted for by a model in which both the working memory of target location and the internal representation of the horizontal eye movements were corrupted by the illusory visual stimulus. We conclude that extraretinal signals played only a minor role, in comparison with visual estimates of the direction of gaze, in planning eye movements to remembered target locations during our illusory paradigms.

## INTRODUCTION

We previously have studied the effects of illusory motion of a visual stimulus on eye and head tracking (Zivotofsky et al. 1994, 1995a). This illusory stimulus was induced by moving both a small target laser spot and the background display (Duncker 1929). Vertical movement of the target was synchronized to horizontal movement of the background, producing a strong illusion of diagonal motion. Like prior studies, we found that such illusory motion had small effects on pursuit eye movements (Collewyn and Tamminga 1984, 1986; Kowler et al. 1984; Worfolk and Barnes 1992; Yee et al. 1983), but we found striking errors of predictive saccades during tracking of a regularly stepping target (Zivotofsky et al. 1994). Although the target motion was purely vertical, the trajectory of predictive saccades was diagonal, in the direction of the illusion. These diagonal saccades were followed by corrective, horizontal saccades to bring the eye back on target. This finding prompted us to investigate whether memory-guided saccades were also affected by illusory stimuli.

If subjects are required to remember the location at which a small visual stimulus is briefly flashed and later make a saccadic eye movement to it, they can do this with an accuracy of  $\sim 1$  deg (Becker and Fuchs 1969; Stanford and Sparks 1994). This ability is maintained even if eye position is perturbed by electrical stimulation after the target disappears (Sparks and Mays 1983) or if the subject performs smooth pursuit after the target flash (Ohtsuka 1994; Schlag et al. 1990).

Differences exist between the programming of predictive

saccades in response to a regularly stepping target and memory-guided saccades to a previously flashed target. Predictive saccades are generated without a retinal error signal and appear to be directed by a memory of the spatial location of the target. On the other hand, when saccades are made to the remembered location of a flashed target, retinal error signals are present during the target flash but then are consigned to working memory. Nonetheless, both predictive saccades to a stepping target and saccades to the remembered location of a flashed target are generated based on stored information regarding the location of a previously seen target. We therefore hypothesized that the Duncker illusion would cause inaccuracies of saccades to remembered targets. In a first series of experiments, we were able to confirm this. We subsequently investigated the factors that were responsible for the saccadic errors. Preliminary results have been previously published (Zivotofsky et al. 1995b). The work reported here constitutes a portion of the research performed by A. Z. Zivotofsky as part of the requirements for his doctoral dissertation.

## METHODS

### Subjects

We studied four normal subjects (2 male, 2 female, age range 30–48 yr, mean age 36.5). Three of the subjects were emmetropes and did not require glasses; the one subject who did, was able to wear his glasses (−3 diopters) because, as described below, the experiment was self-calibrating and the head was stationary. No subject was taking medication. All four subjects participated in the first set of experiments, and two were subjects for the second set. All subjects gave informed consent in accordance with the Declaration of Helsinki.

### Stimulus and recording techniques

Subjects viewed a red He-Ne laser spot (the primary target) that was superimposed on a background consisting of black random dots on a white background (the background). The primary target subtended 0.2 deg and its luminance was 6.1 ft-lamberts. The background subtended  $20 \times 30$  deg; the luminance of its dark areas was 2.7 ft-lamberts and of its light areas was 22.9 ft-lamberts, and its mean luminance was 18.4 ft-lamberts as measured with a Spectra Pritchard Model 1980A Photometer. Both the primary target and background were rear projected onto a semitranslucent tangent screen at a viewing distance of 1.2 m; the room was otherwise darkened. The background moved only horizontally and the primary target only vertically, both under the control of General Scanning CX660 mirror galvanometers. They were controlled individually so that four modes were possible: both stationary, only the background moved (horizontally), only the primary target moved (vertically), or both moved. When both were moved, motion of the primary target was synchronized to that of the background, producing a strong illusion of diagonal motion of the primary target (Zivotofsky et al. 1995a). The horizontal component of the illusory motion was opposite to the direction of the background movement. In these experiments, the illusory movement was always from the upper left to the lower right (Fig. 1, A and B). The driving stimulus in all experiments was a sine wave. An additional red He-Ne laser spot (the secondary target), subtending 0.1 deg with a luminance of 130 ft-lamberts, also was rear projected onto the screen and was under the control of General Scanning model DX2003 X-Y mirror galvanometers. It thus could be projected to any coordinate on the tangent screen. Each of the three rear-projected images (the

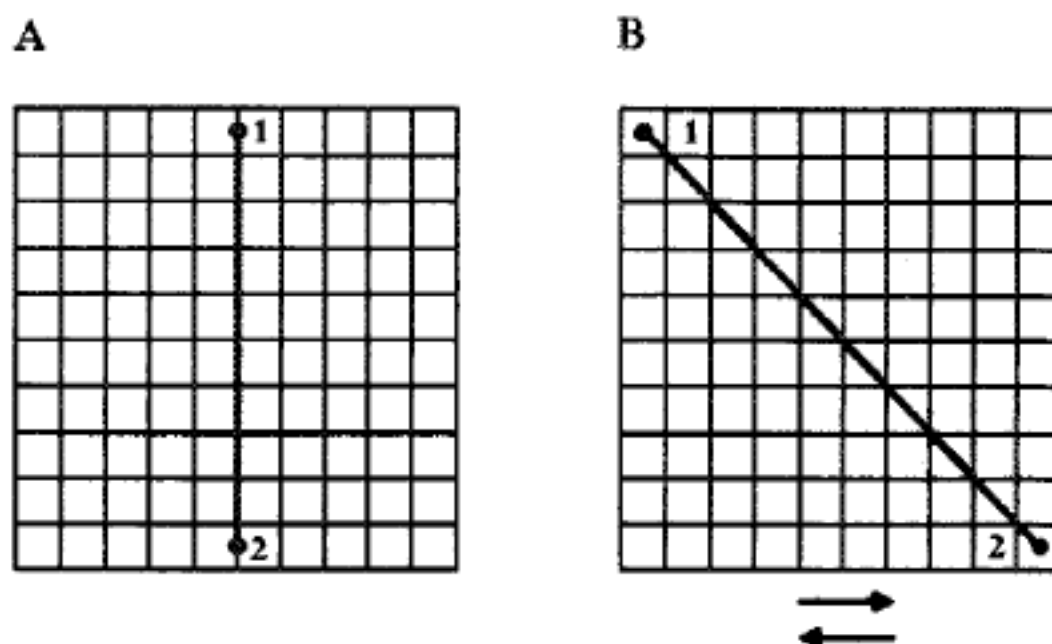


FIG. 1. A graphical representation of perception of primary target motion produced by a stationary background (A) or a horizontally moving background (B). The actual target motion is purely vertical in both A and B, but it appears to be diagonal in B (hatched line) because of synchronized background motion. Points 1 and 2 correspond to 2 primary target positions, separated in time by half a cycle.

background, primary target, and secondary target) could be turned off by a computer-controlled shutter (Vincent Associates, UniBlitz model 100-2B).

Horizontal and vertical eye rotations were measured using the magnetic search coil technique, with 6-ft field coils (CNC Engineering, Seattle, WA). The coil was precalibrated on a protractor device. The system was 98.5% linear over an operating range of  $\pm 20$  deg in both planes, cross-talk between horizontal and vertical channels was  $< 2.5\%$ , and the SD of system noise of  $< 0.02$  deg. Subjects wore a scleral search coil (Skalar, Delft, The Netherlands) on their dominant eye. All trials were head-fixed, as previously described (Zivotofsky et al. 1995a).

### Experimental paradigms

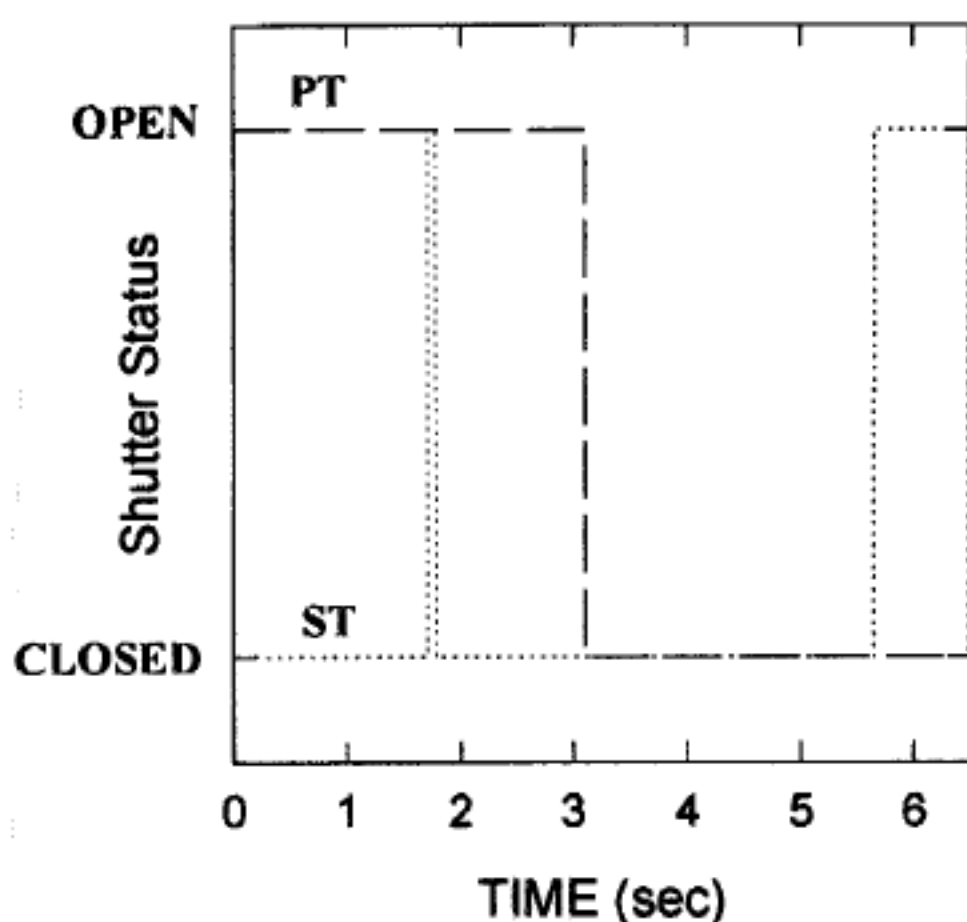
We conducted two studies.

**STUDY 1.** This study included five test paradigms for which a minimum of 50 trials were collected from each subject and two control paradigms for which a minimum of 30 responses were collected. All trials started with the subject viewing the primary target, whether it was stationary or moving. After 1.7 s the secondary target was flashed for 75 ms on the tangent screen. The subjects were instructed to continue to view the primary target and not to make a saccade to the flashed secondary target location. Only when the primary target and background were extinguished, after an additional 1.4 s (the memory period), were they to make a saccade to where the secondary target had flashed. After an additional 2.5 s, allowing time for the subject to settle on the remembered location, the secondary target would reappear. The subject then would refixate the secondary target, thereby correcting for any errors in the memory-guided saccade and providing an objective measure of the target's true location. The shutter timing diagram for this protocol is shown in Fig. 2A. Each trial lasted 6.5 s, and there were eight trials in each run of 52 s. Instructions were given for each test paradigm, and some practice was allowed before the eye coil was inserted and data collection begun. Secondary targets were presented at 17 locations in a pseudorandom sequence; these positions were at 5 or 10 deg to the right, left, up, down, along one of the 45 deg diagonal lines, or at the center, selected so that they did not flash near the edge of the projected background.

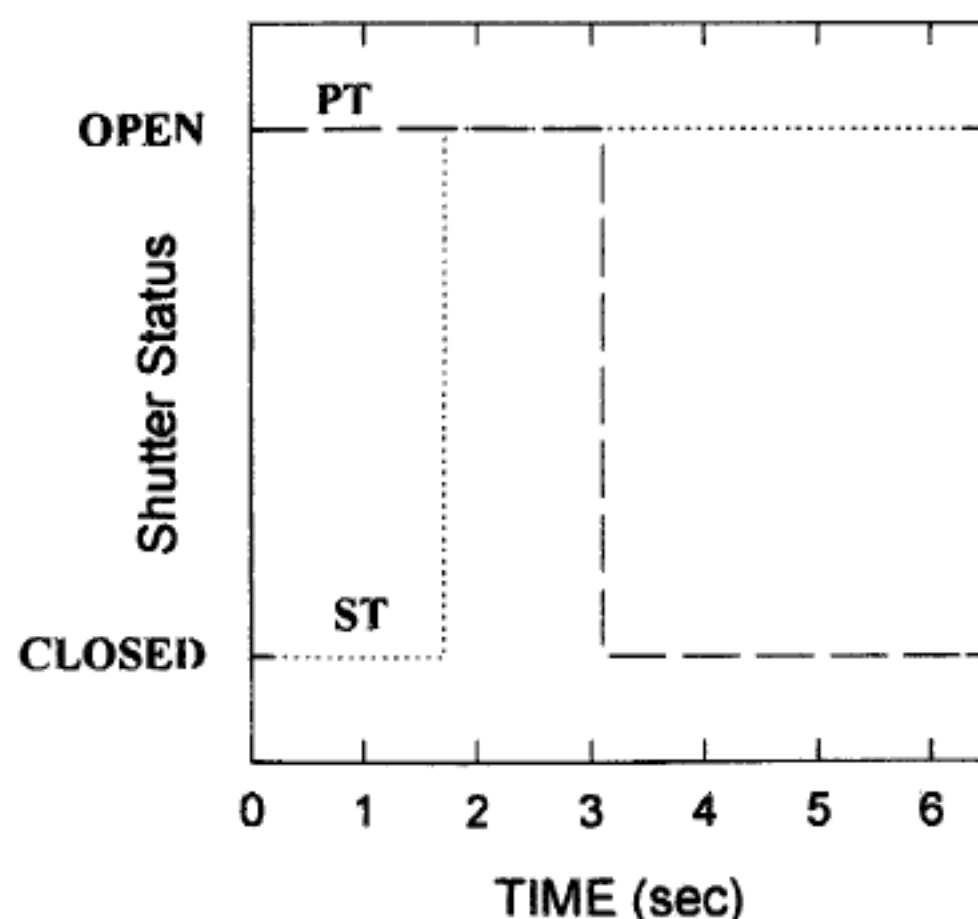
The five test paradigms were as follows: 1) fixation/stationary background (FSB), the subject fixated a stationary primary target located in the center of a stationary background; 2) pursuit/stationary background (PSB), the primary target moved sinusoidally at



## A) TEST PARADIGMS - 1



## B) CONTROL PARADIGMS



## C) TEST PARADIGMS - 2

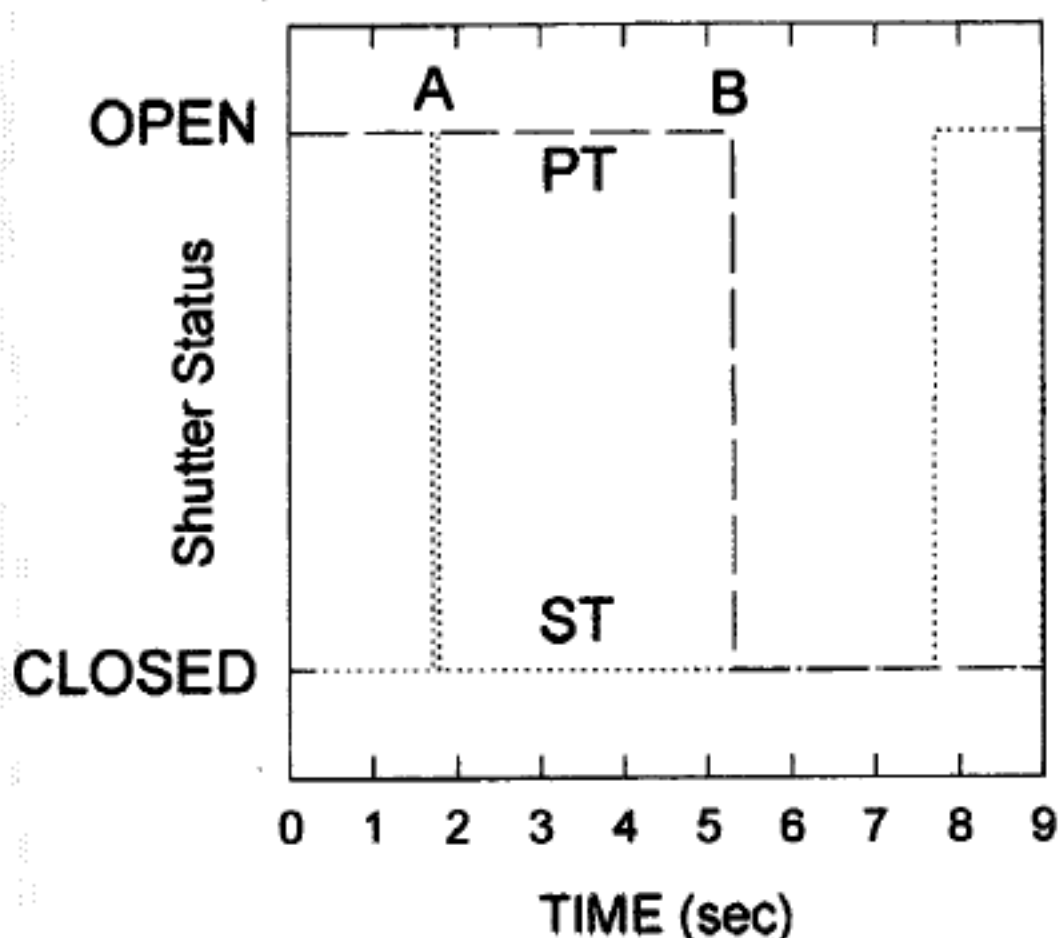


FIG. 2. Shutter timing diagrams. A: timing diagram for all of test paradigms in 1st set of experiments. Note secondary target flashed on briefly at 1.7 s. B: timing diagram for 2 control paradigms. Note that once secondary target is presented at 1.7 s, it remains visible. C: shutter timing diagram for 2nd set of experiments. Flash of secondary target occurred at time A; background and primary target were extinguished at time B. In those trials in which flash occurred while primary target was at top or bottom, time to A was 0.85 s and trial lasted 8.1 s. In those trials in which primary target was at center and target traversed half a cycle rather than a quarter cycle before secondary target flashed, time to A was 1.7 s and trial lasted 9.0 s (shown here). Time in darkness, from extinction of pursuit target and background until target reappeared, was always 2.4 s. Time interval between A and B (memory period) was randomly assigned to 200 or 833 ms or 1.67, 2.5, 3.33, 3.53 (shown here), or 4.17 s.

— Primary target and background (PT)  
 ..... Secondary target (ST)

0.3 Hz,  $\pm 9$  deg vertically, and the subject was instructed to pursue it as it moved over the stationary background; 3) fixation/moving background (FMB), the primary target was stationary while the background moved sinusoidally at 0.3 Hz,  $\pm 9$  deg horizontally. The subject was instructed to fixate the stationary primary target while the background moved. The moving background produced a weak illusion (Duncker 1929) of horizontal movement of the primary target. 4) Pursuit/moving background (PMB); subjects pursued the primary target as it moved vertically across the hori-

zontally moving background. We verified that all subjects perceived a strong illusion of diagonal movement of the target. 5) Pursuit/moving-stationary background (PMSB), this began with subjects pursuing the primary target as it moved vertically across the horizontally moving background. However, when the secondary target flashed, the background and primary target ceased moving and remained illuminated and stationary for the next 1.4 s until they were extinguished. There was, therefore, an illusion of diagonal motion of the primary target only until the secondary

target flashed. The goal of the PMSB paradigm was to remove the effect of illusory motion of the primary target after the secondary target was flashed. We compared saccadic accuracy during PMSB with that during PMB to gain insight into the contribution of illusory target motion after the flash of the secondary target to saccadic mislocalization.

The two control paradigms were 1) fixation/stationary background control, the FSB paradigm was rerun but so as to test saccades to visual, rather than remembered, targets. This was achieved by leaving the secondary target visible after it was presented. The subject was instructed to continue looking at the primary target until it was extinguished, and at that time make a saccade to the visual secondary target. 2) Pursuit/moving background control, the PMB paradigm was rerun, but the secondary target remained visible after it was presented so as to test saccades to visual, rather than remembered, targets. The shutter timing for both controls is shown in Fig. 2B.

**STUDY 2.** All trials in this study were similar to the PMB paradigm in study 1. We selected this paradigm for further study because it produced the strongest, most robust illusion and the largest horizontal errors and because we had studied previously its effects on several aspects of eye and head tracking (Zivotofsky et al. 1995a). These trials were designed to isolate the effect of two factors: the location of the visual stimuli (background and pursuit target) at the time of the target flash and the net movement of the visual stimuli during the memory period (the time from when the secondary target flashed to when the pursuit target was extinguished). These effects could not be separated in the first study in which the length of the memory period and the stimulus frequency were both fixed. To isolate the effect at the time of the secondary target flash, the location of the background at the time of the secondary target flash was controlled such that it was only at one of three predetermined locations: 9 deg right (primary target at 9 deg up), 9 deg left (primary target at 9 deg down), or center. To isolate the effect of background movement during the memory period, the interval between the target flash and extinction of the background was fixed at one of seven predetermined values, thus varying the length of the memory period. The time intervals used were 200 and 833 ms and 1.67, 2.5, 3.33, 3.53, and 4.17 s, which corresponded to 0.06, 0.25, 0.5, 0.75, 1.0, 1.06, and 1.25 cycles of sinusoidal motion of the visual stimuli. The secondary target was flashed at seven possible locations: 8 deg up, down, right, left, diagonally up and right, diagonally down and left, and center. The seven possible target positions and the seven memory period durations were presented in a randomized sequence. Each trial lasted either 8.1 s (if the secondary target flashed while the background was at the right or left) or 9.0 s (if the background was at 0 during the flash); seven trials were performed in each run. An example of the shutter timing diagram for this protocol is shown in Fig. 2C.

#### Data collection and analysis

Horizontal and vertical gaze signals were low-pass filtered using Krohn-Hite Butterworth filters with a cutoff at 90 Hz, before digitization with 16-bit precision at 200 Hz. Using interactive programs, each trial was analyzed and the following points (see Fig. 3) were identified and measured:  $E_a$ , eye position during the secondary target flash (averaged over the 75 ms flash);  $E_i$ , initial eye position at the start of the first saccade in darkness;  $E_{s1}$ , eye position at the end of the first saccade in darkness;  $E_{s2}$ , final eye position in darkness (which usually followed one or more "corrective" saccades made in darkness); and  $E_f$ , final eye position after the secondary target had reappeared. Based on the assumption that, at the time of this final eye position, the subject was fixating the target,  $E_f$  was used as an internal calibration of the target position and

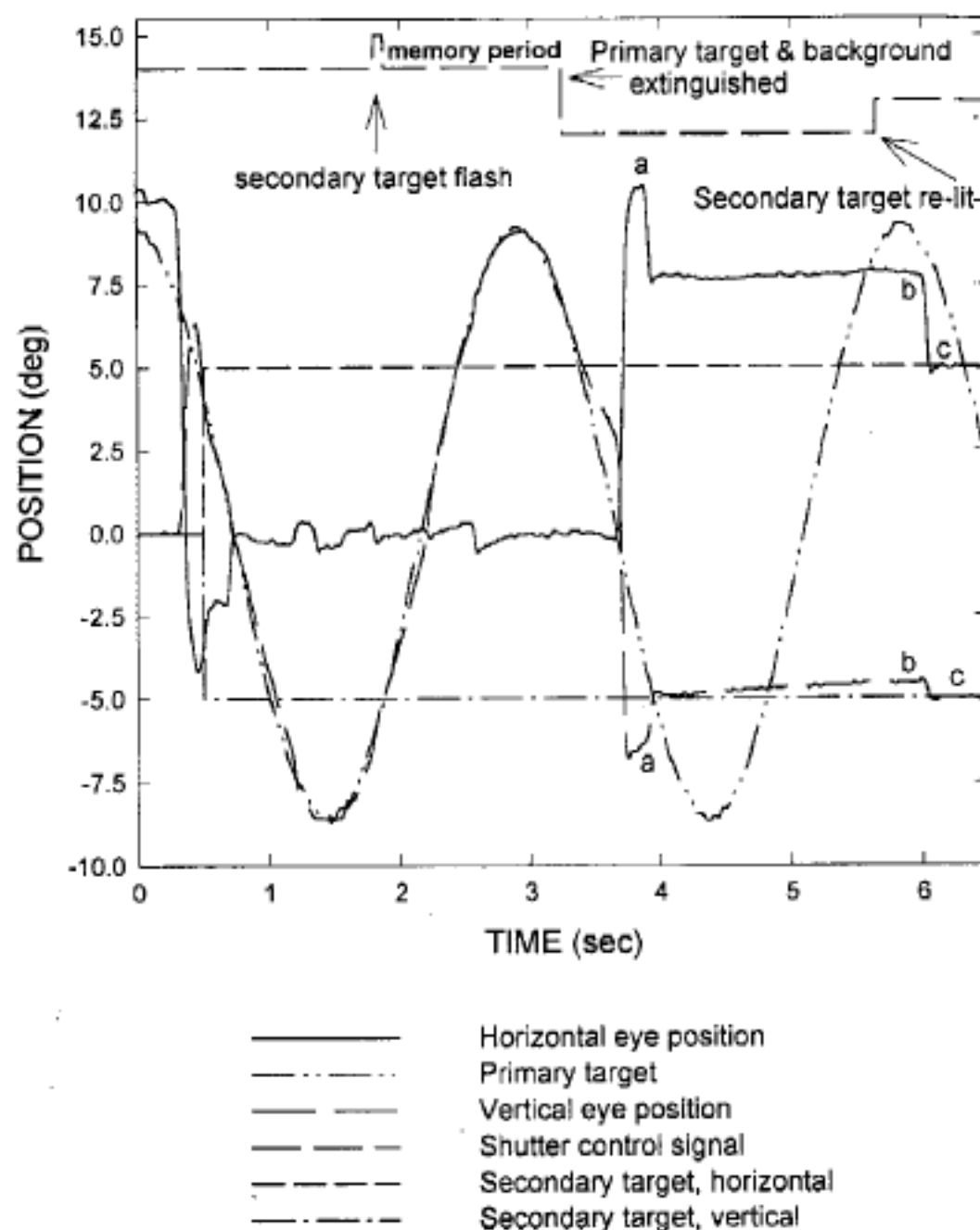


FIG. 3. Sample of eye movement recording of pursuit/moving background (PMB) paradigm. For eye movements and target position, up is a rightward or upward deflection and down is leftward or downward. Shutter control signal is offset near top for clarity and is a combination of the signals shown in Fig. 2. Positions of eye, primary stimulus, and background were all stored at time of secondary target flash. In addition, other points that were stored include, both horizontally and vertically, 1st saccade, "a," final eye position due to all corrective movements made in the dark, "b," and final corrective saccade made to the reilluminated target, "c." Note how initial memory-guided saccade and final eye position in darkness are inaccurate horizontally but not vertically.

permitted reliable calibration for the subject who wore glasses during testing.

In addition to the above eye positions, the location of the primary target and background at the time the secondary target flashed and at the time the background shutter closed also were measured. All trials in which subjects did not follow instructions, such as by making a saccade to the target before the primary target was extinguished, were discarded. This occurred in <5% of trials.

From the above measurements, we calculated: 1) initial error, the error of the initial saccade made in darkness. It is the difference between the initial saccade size ( $E_{s1} - E_i$ ) and the required saccade size ( $E_f - E_i$ ). Thus a hypometric saccade yields a negative initial error and a hypermetric initial saccade gives a positive value. 2) We also calculated final error, the error of the final eye position in darkness. It is the difference between the total eye movements made in the dark ( $E_{s2} - E_i$ ) and the required saccade ( $E_f - E_i$ ).

The following two terms are used in the sense originally defined by McKenzie and Lisberger (1986). *Retinal error* corresponds to the amplitude of the saccade that would be required had the saccade been executed when the target flashed; this equals the difference between actual target location and eye position at the time of flash ( $E_f - E_{s1}$ ). *Spatial error* corresponds to the required saccadic amplitude at the time that the initial saccade in darkness is exe-



cuted. It is the difference between actual target location and eye position at the start of the initial saccade ( $E_f - E_i$ ).

Although these terms are used as previously defined, caution is required because "error" is used in the above definitions in two ways: it describes both possible inputs for the saccades (retinal error and spatial error) as well as the accuracy of the saccades actually made (initial error and final error). All errors were calculated in cartesian (horizontal and vertical) coordinates.

To compare the performance of all four subjects on all seven paradigms in the first study, two points need to be addressed. First, saccade gain (actual saccade size divided by required saccade size) would not suffice, at least not in the horizontal plane, because of the unusually large errors that were generated in the PMB paradigm even when the required saccade size was small. For example if a saccade of 0.2 deg was required because the secondary target flashed near 0, and the subject made an erroneous 5-deg saccade, the gain would be 25. Such results would obfuscate other gains. We therefore measured absolute errors. (See also White et al. 1994, who used absolute vectorial distance). This was justified because all paradigms contained approximately equal numbers of each of the required saccade sizes.

Second, in any particular paradigm of saccades to remembered targets, no subject was always hypo- or hypermetric (see RESULTS). Thus some of the errors were positive and some negative. To gauge overall accuracy, and because the data were not always normal in distribution, absolute error values were used and the median absolute error was calculated for each paradigm and for each subject (1 for the initial error and 1 for the final error). Comparison between the absolute error values for the initial saccade in each paradigm for each subject were made using a Mann-Whitney rank sum test. Because multiple pairwise tests were performed, we performed a Bonferroni correction (Glantz 1992) by a factor of 8 and used a cutoff for  $P$  values of 0.00625 instead of 0.05 to determine significance.

Because most of the saccadic errors that occurred with this illusory stimulus were in the horizontal plane, the analysis in the second study was directed toward horizontal errors and horizontal movement of the background visual stimulus. Initial and final horizontal saccadic errors were studied as functions of the mean position of background during the 75-ms flash of the secondary target and the duration of the memory period (expressed as the amount that the background moved from the time of secondary target flash to the extinction of the background and primary target), using the techniques of linear regression.

## RESULTS

### *Study 1: saccadic errors for each paradigm*

We describe the results by paradigm because the initial and final errors tended to covary across the various paradigms; Fig. 4 summarizes the results.

**FIXATION/STATIONARY BACKGROUND.** Saccadic error was smaller than in any other test paradigm, but was larger than during the control experiments. The mean error horizontally and vertically for all subjects in the FSB experiments was 1.6 deg, similar to that previously reported (Gnadt et al. 1991). We encountered no systematic error with an upward bias (Gnadt et al. 1991; White et al. 1994).

**PURSUIT/STATIONARY BACKGROUND.** Horizontal error was greater than during FSB, but the difference was only significant statistically in *subject 4* ( $P < 0.00625$ ). No subject showed a significant increase of vertical errors compared with the FSB paradigm.

**FIXATION/MOVING BACKGROUND.** Horizontal saccadic error was significantly increased for all subjects compared with FSB ( $P < 0.00625$ ); however, the vertical error was not increased ( $P > 0.3$ ).

**PURSUIT/MOVING BACKGROUND.** Horizontal saccadic errors were greatest (Fig. 4A), but vertical saccadic error was only greater than during the FSB paradigm in *subject 4* ( $P < 0.003$ ). The magnitude of the horizontal saccadic error was unrelated to whether the location of the secondary target was central or in one of the eccentric positions ( $P > 0.05$ ). Horizontal saccadic errors were significantly greater than during either FSB or PSB for all subjects ( $P < 0.0001$ ). Horizontal errors were also greater than during FMB, although only statistically so in *subject 1* ( $P < 0.0001$ ). Thus the illusory trials (FMB and PMB) produced significantly larger horizontal errors in all four subjects when compared with the nonillusory (FSB and PSB) paradigms.

We also examined the distribution of positive/negative (overshoot/undershoot) errors during the PMB paradigm. The respective distributions of the initial and final errors for the four subjects were 53/54 and 59/48 (*subject 1*), 30/32 and 30/32 (*subject 2*), 33/25 and 29/29 (*subject 3*), and 28/24 and 31/21 (*subject 4*).

To relate the magnitude of the errors shown on Fig. 4A to the required saccade needed to foveate the target, we replot the data for *subject 3* in Fig. 5 showing the actual versus the required horizontal saccade size during the PSB and PMB paradigms. The only difference between these two paradigms was background motion, yet saccades were inaccurate during the latter, indicating that the presence of background motion, not vertical smooth pursuit, was responsible for the large horizontal errors.

**PURSUIT/MOVING-STATIONARY BACKGROUND.** In this paradigm, in which the background stopped after the secondary target was flashed, vertical saccadic errors were no different from any other paradigm. Horizontal saccadic errors were no different from those during FSB or PSB but were significantly less than during PMB in all four subjects ( $P < 0.0001$ ), and for *subjects 2–4* were significantly less than during FMB ( $P < 0.0001$ ).

**FIXATION/STATIONARY BACKGROUND CONTROL PARADIGM.** All subjects showed smaller saccadic errors, both horizontally and vertically, during this paradigm, in which saccades were made to visual targets, than for memory-guided saccades; this difference was significant for *subjects 2 and 4* ( $P < 0.0001$ ).

**PURSUIT/MOVING BACKGROUND CONTROL.** All subjects showed significantly smaller horizontal saccadic errors during this control ( $P < 0.0001$ ), during which saccades were made to visual targets in the presence of background motion, compared with memory-guided saccades under similar conditions.

### *Comparison of initial and final errors*

In most trials, for all paradigms, more than one saccade was made to the remembered target location while in darkness. The accuracy of the initial and final eye positions in darkness are statistically compared in Table 1. In general,

# A HORIZONTAL SACCADIC ERRORS

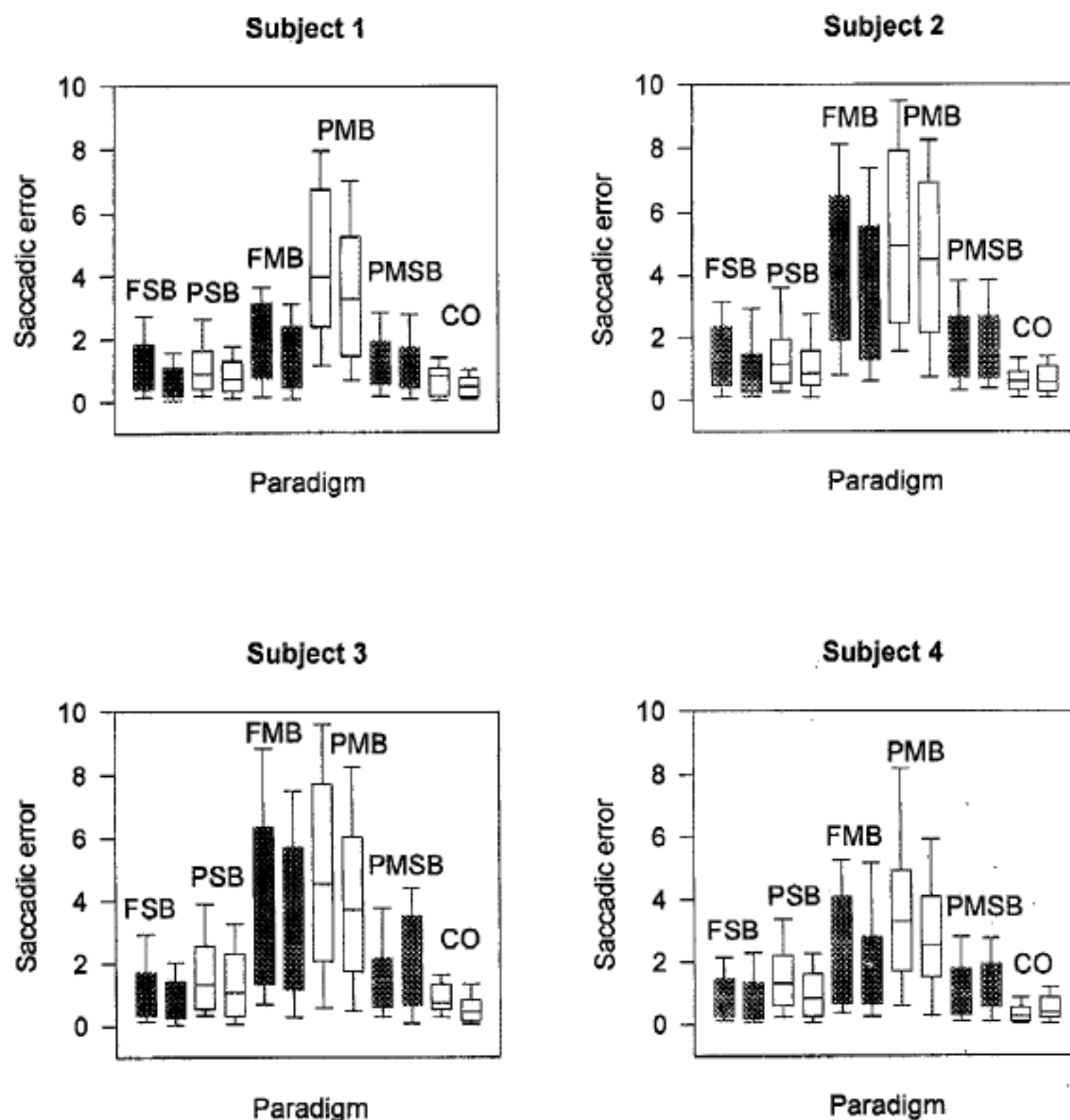


FIG. 4. Tukey box plots of median, 25–75% and 10–90% of absolute errors for in all paradigms for all 4 subjects. Horizontal saccadic errors are shown in A and vertical saccadic errors in B. Pairs of columns correspond, respectively, to initial and final errors for fixation/stationary background (FSB), pursuit/stationary background (PSB), fixation/moving background (FMB), pursuit/moving background (PMB), and pursuit/moving-stationary background (PMSB). Initial saccadic error is shown for fixation/stationary background control and pursuit/moving background control, respectively (CO).

the additional saccades made in darkness brought the eye nearer to the target. However, during the PSB, FMB, and PMB paradigms, final eye position was usually more accurate horizontally but not vertically. During the PMSB paradigm, final eye position was no more accurate horizontally than initial eye position, but two subjects showed improved accuracy of final vertical eye position.

## Vertical retinal error versus spatial error in PSB and PMB

During the PSB and PMB paradigms, the eye continued to smoothly track vertical target motion between the time the secondary target was flashed and the onset of the saccade to the remembered target location. It is in these trials that spatial error and retinal error differ significantly. Figure 6 shows the plots of actual saccade size against either retinal or spatial error in the vertical plane for *subject 1*. A linear regression, performed on both initial and final saccades, showed that all subjects under all conditions showed a high correlation with spatial error ( $r$  values  $> 0.9$ ) and a low

correlation with retinal error ( $r$  values  $< 0.15$ , for 15 of the 16 values).

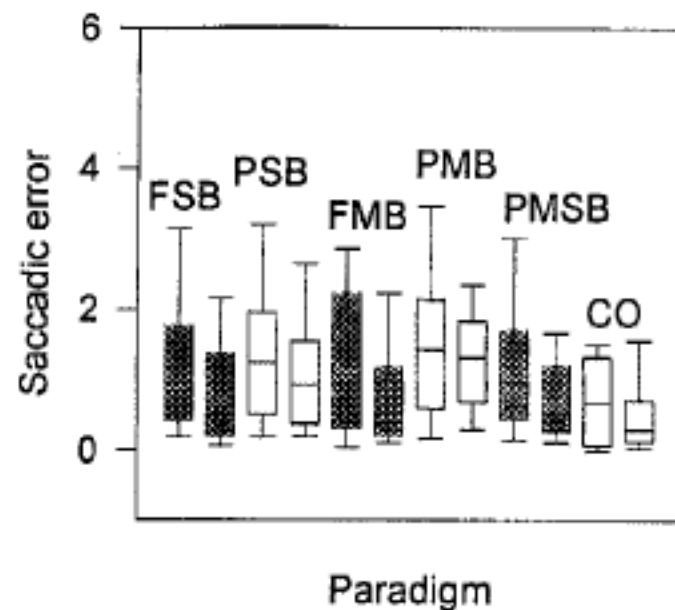
## Study 2

Both subjects reported a strong illusion of diagonal motion of the target during all trials, and both subjects made relatively large errors when compared with their earlier performance when illusory stimuli were not applied. Furthermore, although  $>650$  trials were conducted for each subject over the course of numerous sessions, no “learning effect” was evident: errors were as conspicuous at the end of the study as at the beginning. We confirmed that, during the portion of each trial in which subjects were required to pursue the vertically moving target, their horizontal eye excursions were small despite the diagonal trajectory of illusory stimulus motion (Zivotofsky et al. 1995a). During the stimulus and memory periods, change in horizontal eye position (expressed, in deg, as mean/10th to 90th percentile range) was  $0.02/-0.75-0.85$  for *subject 1* ( $n = 664$ ) and  $-0.03/-1.11-1.02$  deg for *subject 2* ( $n = 683$ ). On the other hand,

B

## VERTICAL SACCADIC ERRORS

Subject 1



Subject 2

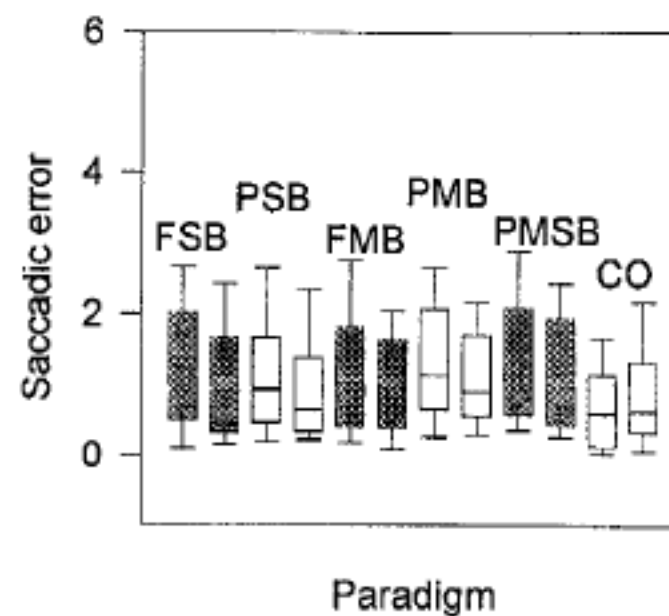
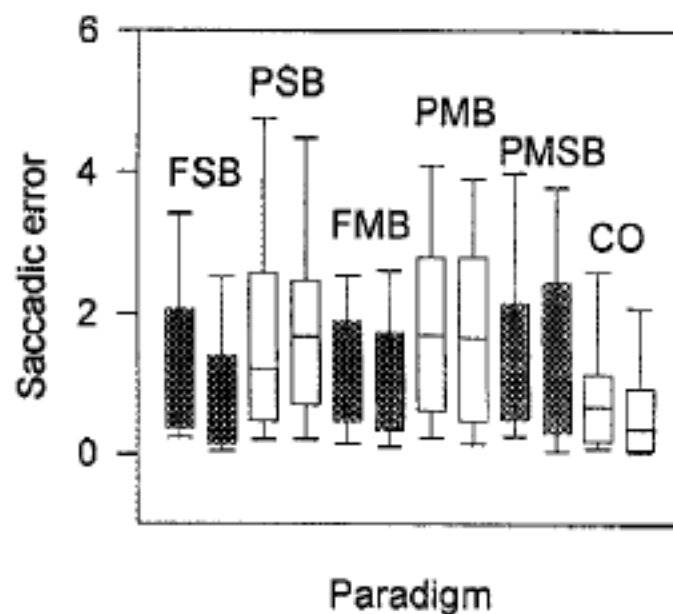
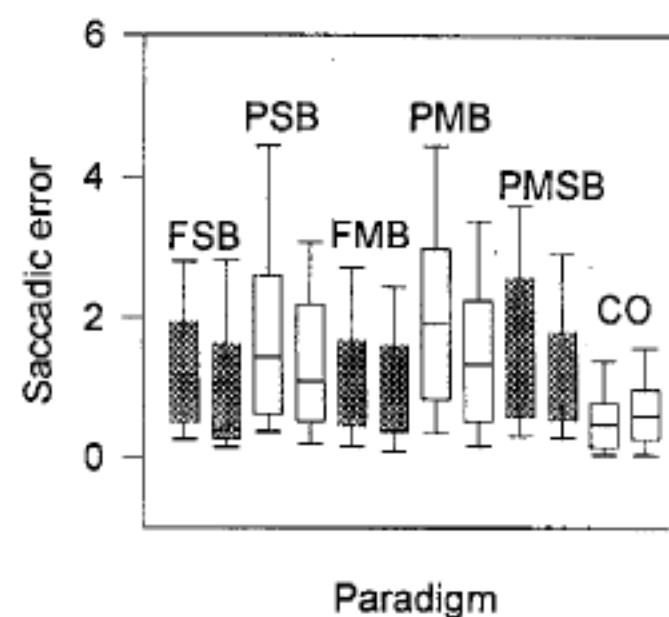


FIG. 4. (continued)

Subject 3



Subject 4



background movement during the corresponding periods was  $-0.06/-9.59-9.71$  and  $0.04/-9.76-9.90$ .

Comparison of horizontal saccadic errors in those trials in which the secondary target flashed when the background was at 0 and subsequently moved right with those in which the background subsequently moved left showed no significant difference for either the initial ( $P = 0.56$  for *subject 1* and  $0.16$  for *subject 2*) or final error in darkness ( $P = 0.90$  for *subject 1* and  $0.23$  for *subject 2*). Thus results from these trials were combined. For reasons concerning relationships between the two stimuli that are explained below, we first present results relating saccadic error to the movement of the background during the memory period, and then describe the effects of the position of the background at the time that the secondary target was flashed.

#### *Relationship between saccadic error and movement of the background during the memory period*

The relationship between saccadic error and the magnitude of movement of the background (in cycles) during the memory

period is plotted for *subject 1* in Fig. 7; data shown are for trials in which the secondary target was always flashed when the background position was at left 9 deg and the primary target was at down 9 deg (corresponding to illusory position down and to the right). It can be seen that as the distance the background moved increased toward its peak, at 0.5 cycles (1.67 s), corresponding to a net movement of 18 deg of visual arc, the error also increased to its maximum value. Saccadic error decreased to a minimum at 1.0 cycle (3.3 s), corresponding to a net movement of 0 deg of visual arc, and increased again thereafter. This relationship is present for both initial and final saccadic error. Thus saccadic error was related to *net movement* of the background during the memory period; this relationship, for *subject 1*, is plotted in Fig. 8 for the same background position at the time of secondary target flash as Fig. 7. Results of linear regression analysis for both subjects and all three "background-at-flash" positions are summarized in Table 2. These results showed a significant correlation between the saccadic error and the net movement of the background ( $P \leq 0.001$ ). The slopes (gains) in Table 2, particularly for those with higher  $r$  values, provide a measure of how strong an influence movement of the background during the memory



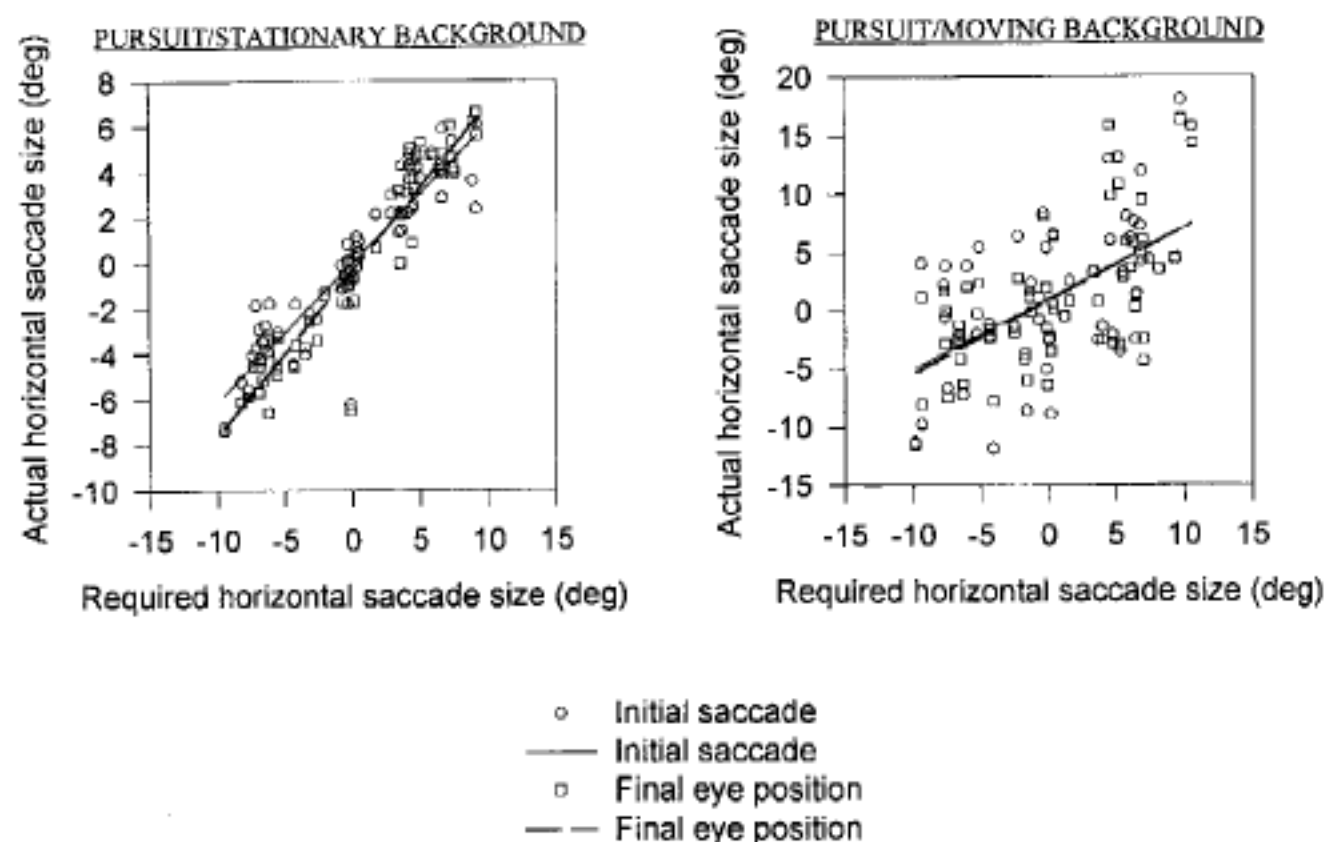


FIG. 5. Plots of required saccade size vs. actual saccade size for the PSB paradigm (A) and PMB paradigms (B) for subject 3. Open circles and solid linear regression are initial saccade and open squares and dashed linear regression are for final eye position in darkness. Left regressions have  $r^2$  values of 0.84 and 0.90; right regressions have  $r^2$  values of 0.29 and 0.40.

period had on saccadic error. In all cases, the slope was less, usually by about half, for the error of final eye position compared with initial saccadic error. This correlation had a gain of 0.2–0.4 for the error of the initial saccade and 0.1–0.2 for the error of the final position.

As a further test of this correlation, each of the six rows in Table 2 can be subdivided based on secondary target position. Thus for each subject, there were 28 varieties of trials in which the secondary target flashed in a fixed location and always flashed when the primary target and thus, presumably, the eye, were in fixed locations. In each of these 28 cases, the only variable was the distance that the background moved during the memory period. For subject 1, initial saccades from all but seven types of trials showed a significant correlation between the size of error and background movement ( $P \leq 0.025$ ), and for final eye position, all but 10 types of trial showed a significant correlation between the size of its error and background movement ( $P \leq 0.025$ ). For subject 2, initial saccades showed a highly significant

correlation between the size of their errors and background movement ( $P < 0.001$ ) for all but two trials. For the final position in darkness, subject 2 showed a significant correlation on all but 4 of the 28 trials ( $P \leq 0.025$ ).

Table 2 shows that the intercepts of the regression lines had different values depending on the location of the background (right, center, or left) at the time the secondary target was flashed. When the background was at left 9 deg there was a positive intercept, whereas when the background was at right 9 deg, there was a negative intercept. When the secondary target was flashed with the background close to 0, the intercept was near zero. These differences are apparent in Fig. 9, in which the relationship between movement of the background and saccadic error is plotted for data from two sets of trials (secondary target flashed with background at right and left). In the two sets of data in these plots, everything was identical except for the position of the background at the time of secondary target flash. A discontinuity is apparent at the point corresponding to a 0 value for net background movement. This suggests that the position of the background at the time that the secondary target is flashed exerts an influence above and beyond that of background movement during the memory period; this effect is examined next.

TABLE 1. Comparison of first saccade versus final eye position in dark

| Subject | FSB     | PSB     | FMB     | PMB     | PMSB                |
|---------|---------|---------|---------|---------|---------------------|
| 1       |         |         |         |         |                     |
| H       | <0.001  | <0.0001 | 0.0548  | <0.0001 | 0.622               |
| V       | 0.0067  | 0.084   | <0.0001 | 0.221   | 0.0085              |
| 2       |         |         |         |         |                     |
| H       | <0.0001 | 0.0087  | 0.0026  | 0.0027  | 0.951               |
| V       | 0.0099  | 0.0984  | 0.145   | 0.0642  | 0.113               |
| 3       |         |         |         |         |                     |
| H       | 0.0238  | 0.0166  | 0.0184  | <0.0001 | 0.0146 <sup>+</sup> |
| V       | 0.0028  | 0.643   | 0.476   | 0.938   | 0.857               |
| 4       |         |         |         |         |                     |
| H       | 0.577   | 0.0204  | 0.0011  | 0.0079  | 0.174               |
| V       | 0.0012  | 0.0617  | 0.0330  | 0.0254  | 0.0092              |

Results of comparison of errors of the 1st saccade vs. the final saccade for each test paradigm, using the rank sum test. Only subject 3 during pursuit/moving-stationary background (PMSB) showed a decrease in error for the final saccade (indicated by +). FSB, fixation/stationary background; PSB, pursuit/stationary background; FMB, fixation/moving background; PMB, pursuit/moving background.

#### Relationship between saccadic error and position of background at time of presentation of secondary target

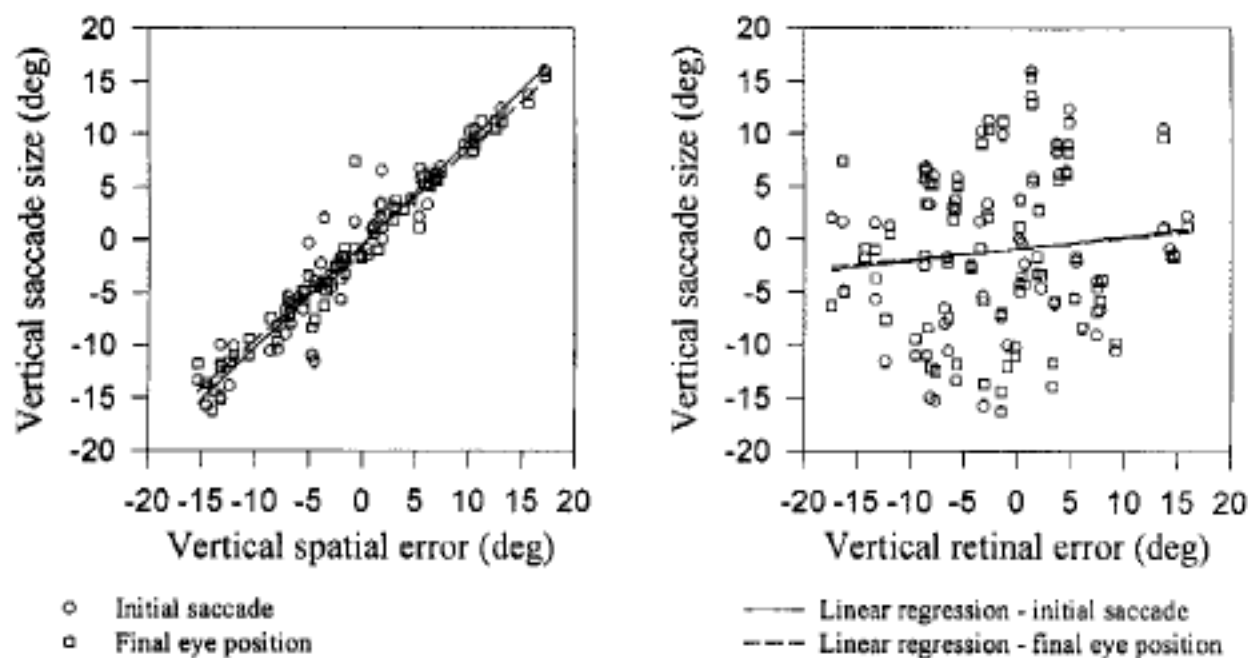
Fewer comparisons were possible between saccadic error and the position of the background at the time of flash with fixed values of background movement than were possible between saccadic error and movement of the background during the memory period. This was because, for example, if the secondary target flash occurred as the background was at the right (primary target at top), every subsequent movement was to the left (and down) whereas when the target flashed when the background was at the left, all subsequent movements were to the right. Because the goal was to use fixed values of background movement, the above two examples share no overlapping values.

Comparisons between horizontal saccadic error and the



## COMPARISON OF RETINAL AND SPATIAL ERRORS

## PURSUIT/STATIONARY BACKGROUND



## PURSUIT/MOVING BACKGROUND

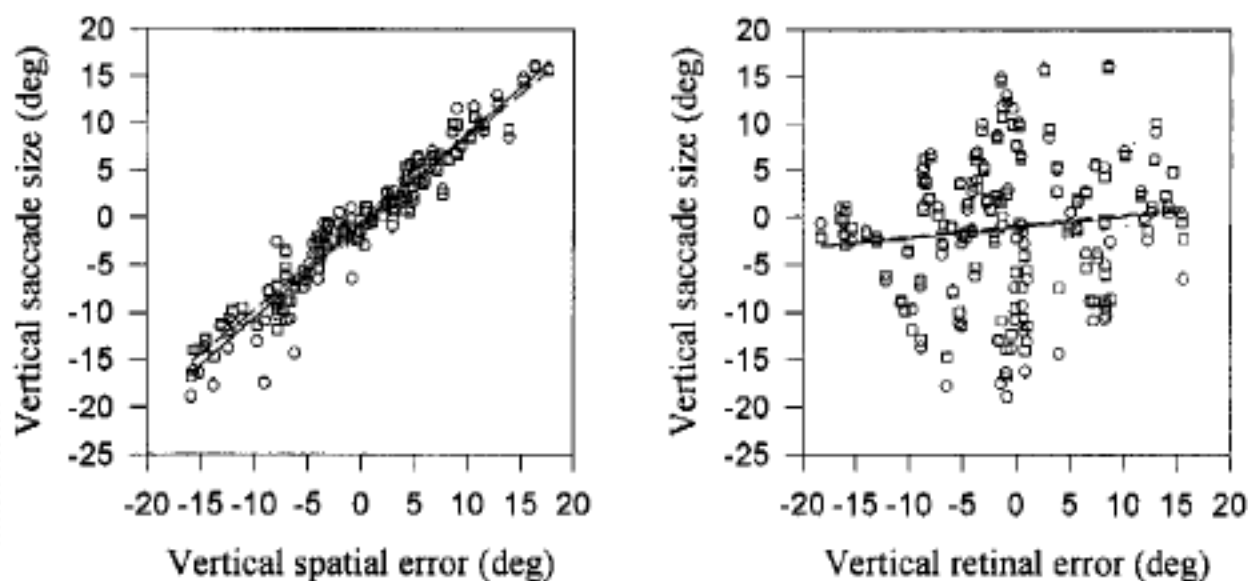


FIG. 6. Plots showing relations of size of vertical component of saccades during PSB (*top*) and PMB (*bottom*) to spatial error (*left*) and retinal error (*right*) in *subject 1*. Positive numbers are upward saccades, negative are downward. Open circles, values for initial saccades; open squares, final eye position. Lines are best linear curve fit for each data set. *Left* regressions all have  $r^2 \geq 0.92$  and  $P < 0.0001$ ; *right* regressions all have  $r^2 \leq 0.018$  and  $P > 0.17$ .

position of the background at the time that the secondary target was flashed, with background movement during the memory period held constant at  $\pm 0.5$  deg of a specific value, are summarized in Table 3 and an example, for *subject 2*, is plotted in Fig. 10. Table 3 shows that for all fixed values of background movement during the memory period, there was a significant correlation between the position of the background at the time that the secondary target flashed and horizontal saccadic error size. Table 3 also provides an estimate of the gain of this relationship, as measured by the slope of the regression line. These data differ from those of Table 2, in that the gain for final position error was not less than for initial eye position.

## DISCUSSION

We have studied the effects of illusory motion of targets, induced by moving the visual background (Duncker 1929), on the accuracy of saccades made to remembered locations. We found that horizontal background motion, either during fixation of a stationary target or during smooth pursuit of a vertically moving target, caused a threefold increase in the inaccuracy of the horizontal component of memory-guided saccades. Final eye position attained in darkness was generally closer to the required location, but it too was inaccurate.

To interpret these findings, we relate our findings to prior studies of saccades to remembered target locations and then examine the mechanisms by which the illusory stimulus may have caused the observed behavior.

*Comparison with prior studies of memory-guided saccades*

Our results using stimulus paradigms that did not induce illusory target motion are generally in accord with prior studies of memory-guided saccades. However, we did not find a systematic error with an upward bias, such that upward saccades are hypermetric and downward saccades are hypometric. This effect is reported to be more marked in monkeys than humans, not all of whom exhibit it (Gnadt et al. 1991; White et al. 1994).

We confirmed prior reports (Ohtsuka 1994; Schlag et al. 1990) that saccades made to remembered targets while performing smooth pursuit corresponded to spatial rather than retinal error (Fig. 6); i.e., the brain takes into account movement of the eye during the memory period. Reports suggesting that such saccades correspond to retinal error (McKenzie and Lisberger 1986) have been attributed to brief (10-ms) flash duration (Schlag et al. 1990). The duration of our target flashes (75 ms) corresponded to those found in prior studies, by Schlag et al. (1990) and Ohtsuka (1994),

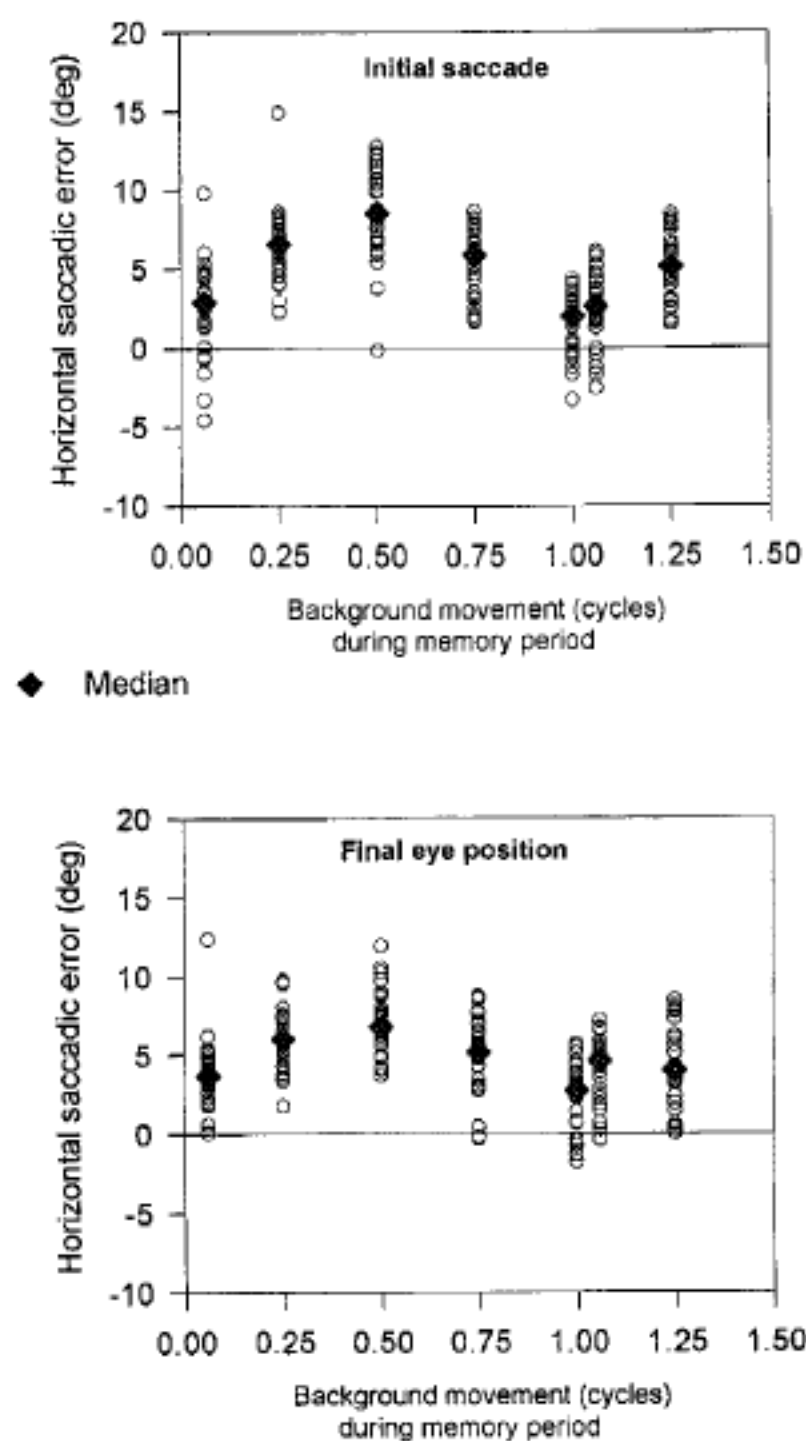


FIG. 7. Plot of background movement in cycles during memory period vs. horizontal saccadic error. Large diamonds are median. Data shown here are from trials in which primary target was at bottom and background was at left when secondary target flashed. Thus after a quarter cycle, both primary target and background were at center. As background movement increased, error increased to a peak at a half cycle, at which time background had moved maximally, decreasing again to a minimum at 1 cycle and then starting to increase. Note that even at 1 complete cycle, the median error is not 0.

to induce saccadic responses corresponding to spatial error. Although it generally is assumed that eye position is monitored during the memory period from an extraretinal signal such as efference copy (Schlag et al. 1990), our results obtained during illusory target motion bring into question this idea (see below).

A consistent finding was that final eye position in darkness was almost always more accurate than initial eye position, and this was especially true horizontally during the illusory paradigms (FMB and PMB). In prior studies of saccades to remembered locations, Becker and Fuchs (1969) found that most large gaze shifts ( $>40$  deg) are composed of two saccades. They hypothesized that large fixation changes are preprogrammed as a package composed of two smaller movements. Our findings suggest that the brain continues to reestimate the remembered location of a target in darkness, even without new visual cues. During our illusory paradigms, the initial saccade appeared to be more influenced by recent visual experience, whereas final eye position more accurately reflected the true location of the target.

TABLE 2. Saccadic error versus net background movement during memory period

| Subject | $B_H$  | $n$ | Slope | Intercept | $r^2$ | $P$      |
|---------|--------|-----|-------|-----------|-------|----------|
| S1      | Left   | 137 | 0.19  | 3.3       | 0.25  | $<0.001$ |
|         |        |     | 0.09  | 3.4       | 0.07  | 0.001    |
|         | Right  | 164 | 0.19  | -2.1      | 0.17  | $<0.001$ |
|         |        |     | 0.12  | -2.4      | 0.12  | $<0.001$ |
|         | Center | 363 | 0.2   | 0.91      | 0.23  | $<0.001$ |
|         |        |     | 0.12  | 0.78      | 0.16  | $<0.001$ |
| S2      | Left   | 216 | 0.37  | 2.2       | 0.51  | $<0.001$ |
|         |        |     | 0.19  | 3.3       | 0.25  | $<0.001$ |
|         | Right  | 190 | 0.25  | -1.1      | 0.25  | $<0.001$ |
|         |        |     | 0.12  | -2.6      | 0.07  | $<0.001$ |
|         | Center | 277 | 0.28  | 1.01      | 0.43  | $<0.001$ |
|         |        |     | 0.17  | 0.82      | 0.24  | $<0.001$ |

Results of linear regressions with net background movement during the memory period as the independent variable and saccadic error as the dependent variable. Each row corresponds to a different background position at the time of secondary target flash ( $B_H$ ). For each position of the background at target flash, 2 values are given: the top one is for the initial saccade, the bottom for the final position in darkness. The slope is a measure of the gain, or the level of effect, of net background movement on saccadic error. The intercept is the theoretical value of the error when net background movement is 0.

(Background-at-flash at fixed position - far left)

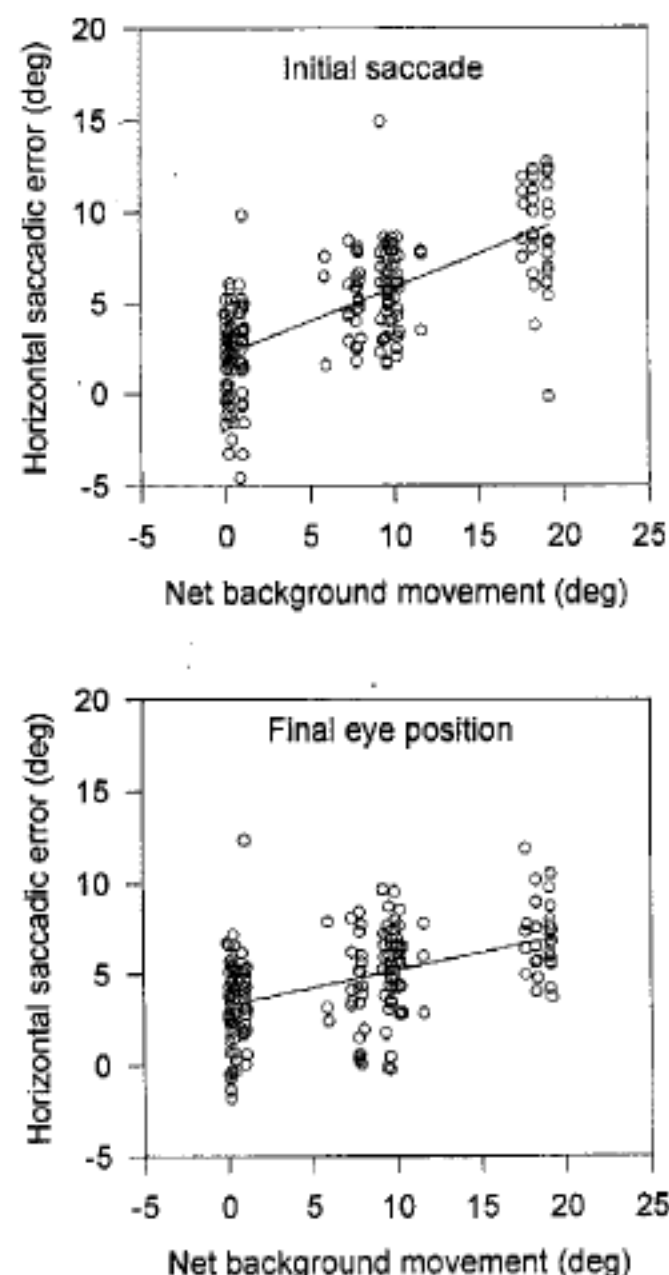


FIG. 8. Plot of net distance the background moved during memory period vs. horizontal saccadic error for a fixed location of background (far left) at time that secondary target was flashed. Data are from subject 2. This figure corresponds to data in Fig. 7 "folded over" at 0.5 and 1.0 cycles. Note that saccadic error and net background movement are correlated ( $P < 0.001$ ).



### Possible mechanisms by which the illusory stimuli caused memory-guided saccades to become inaccurate

Several factors may have contributed to the inaccuracy of memory-guided saccades during the two illusory paradigms. First the location of the secondary target was considered as a factor but was found to have no significant influence on the magnitude of errors. Second the horizontal position of the eye during stimulus presentation and the memory period might have influenced the subsequent saccade. However, as discussed below, it remained close to zero throughout. Third because the horizontal saccadic error was much greater during the two illusory paradigms (FMB and PMB) than any other, and their common denominator was horizontal movement of the background, then some aspect of background motion would seem to be the culprit; two possible mechanisms are considered.

One possibility is that illusory target motion caused the brain to misinterpret the location of the secondary target at the time that it was flashed, so that an inaccurate retinal

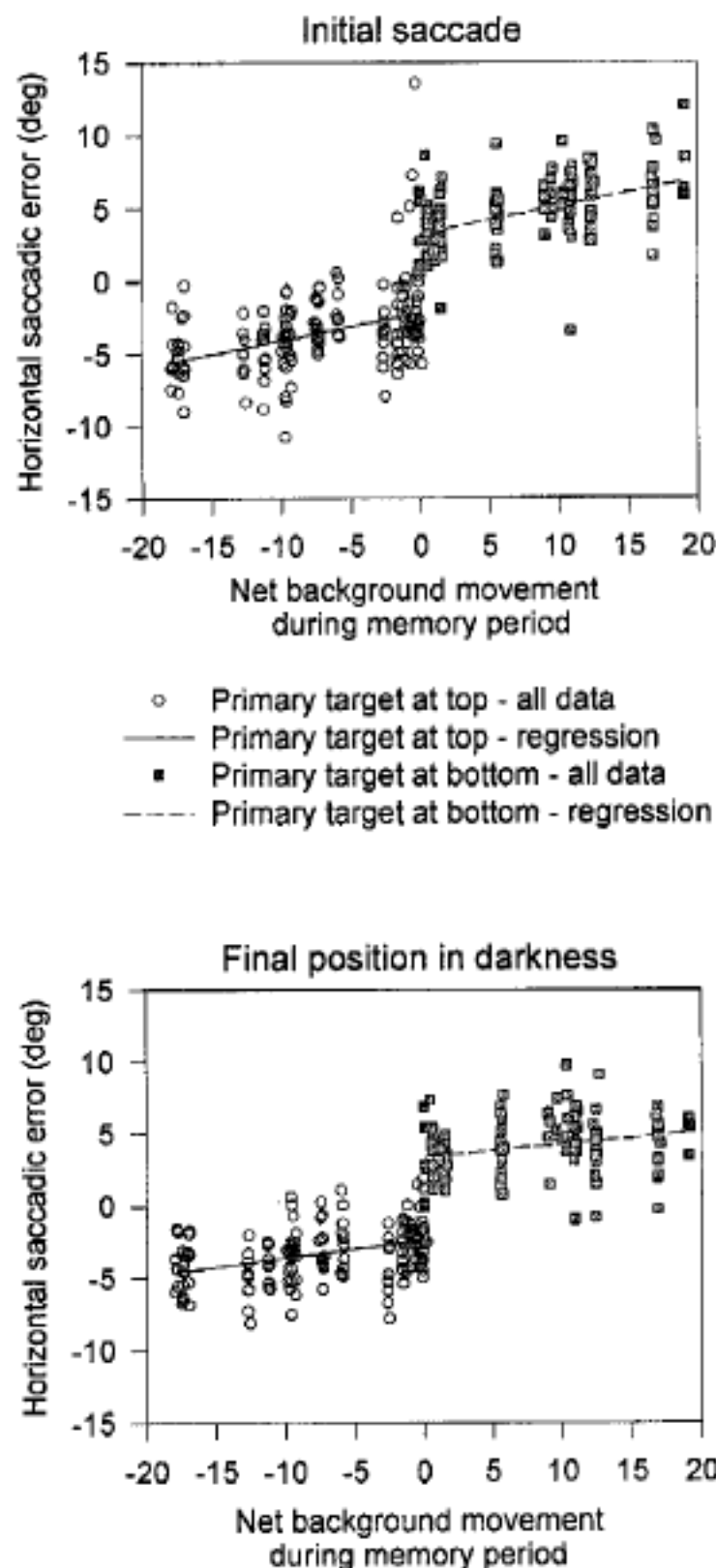


FIG. 9. Combined plot of net background movement during memory period vs. saccadic error for 2 locations of background at time that secondary target was flashed. Open circles, those trials in which background was at right; filled squares, background at left. Top: initial saccade; bottom, final position in darkness. Note offset of regression lines and discontinuity that occurs where net background movement is 0.

TABLE 3. Saccadic error versus mean background position at time of secondary target flash

| Subject   | $\Delta B$ ( $\pm 0.5$ ) | n   | Slope | Intercept | $r^2$ | P      |
|-----------|--------------------------|-----|-------|-----------|-------|--------|
| <b>S1</b> |                          |     |       |           |       |        |
| Initial   | -9.4                     | 61  | -0.34 | -1.3      | 0.26  | <0.001 |
| Final     |                          |     | -0.31 | -0.52     | 0.31  | <0.001 |
| Initial   | -1.6                     | 57  | -0.35 | 0.36      | 0.37  | <0.001 |
| Final     |                          |     | -0.33 | 0.44      | 0.42  | <0.001 |
| Initial   | 0.0                      | 65  | -0.27 | 1.1       | 0.19  | <0.001 |
| Final     |                          |     | -0.31 | 0.65      | 0.45  | <0.001 |
| Initial   | 1.5                      | 41  | -0.18 | 1.8       | 0.17  | 0.008  |
| Final     |                          |     | -0.22 | 1.3       | 0.41  | <0.001 |
| Initial   | 9.4                      | 62  | -0.35 | 2.1       | 0.23  | <0.001 |
| Final     |                          |     | -0.34 | 1.6       | 0.35  | <0.001 |
| <b>S2</b> |                          |     |       |           |       |        |
| Initial   | -9.4                     | 51  | -0.25 | 0.80      | 0.24  | <0.001 |
| Final     |                          |     | -0.36 | 0.16      | 0.37  | <0.001 |
| Initial   | -1.6                     | 61  | -0.30 | -0.082    | 0.28  | <0.001 |
| Final     |                          |     | -0.42 | -0.10     | 0.52  | <0.001 |
| Initial   | 0.0                      | 124 | -0.13 | 0.87      | 0.18  | <0.001 |
| Final     |                          |     | -0.28 | 0.55      | 0.52  | <0.001 |
| Initial   | 1.5                      | 33  | -0.18 | 1.2       | 0.14  | 0.029  |
| Final     |                          |     | -0.33 | 0.73      | 0.34  | <0.001 |
| Initial   | 9.4                      | 77  | -0.23 | 3.7       | 0.19  | <0.001 |
| Final     |                          |     | -0.28 | 2.1       | 0.27  | <0.001 |

Results of linear regressions with position of background at the time that the secondary target is flashed as the independent variable and saccadic error as the dependent variable. Each row corresponds to a different, narrow range of net background movement ( $\Delta B$ ) during the memory period. For each value of background movement, 2 values are given, the top one is for the initial saccade, the bottom for the final position in darkness. The slope is a measure of the gain, or the level of effect, of background at flash on saccadic error. The intercept is the theoretical value of the error when background position at the time of secondary target flash is 0.

error or spatial location was consigned to working memory. This mislocalization could be due to background motion causing misinterpretation of current eye position or, perhaps, of the retinal error. The only information available to the brain regarding target location was acquired during the flash of the secondary target, and because there was an illusion of diagonal pursuit at that time, it seems that error could be introduced then.

A second possibility is that illusory target motion corrupted the internal record of eye position during the memory period. We have confirmed the findings of Schlag and colleagues (1990) and Ohtsuka (1994) that the brain does indeed take into account eye movements during the memory period when generating saccades to remembered locations (Fig. 6). The question then is: how is this achieved? We considered the possibility that the brain calculated eye movements based on the perceived trajectory of the target. Because the perceived trajectory of target motion was diagonal and smooth pursuit of the target was accurate, then the brain might have deduced that the eyes also were moving diagonally. Thus our stimulus may have dissociated the brain's estimates of the direction of gaze based on either visual or extraretinal signals. During illusory trials there was little actual horizontal eye motion during the memory period, but there was a great deal of perceived horizontal motion, and it is possible that this perceived motion was monitored rather than eye movement signals.

As an initial attempt to differentiate between these two possibilities, we introduced a controlled illusion paradigm,

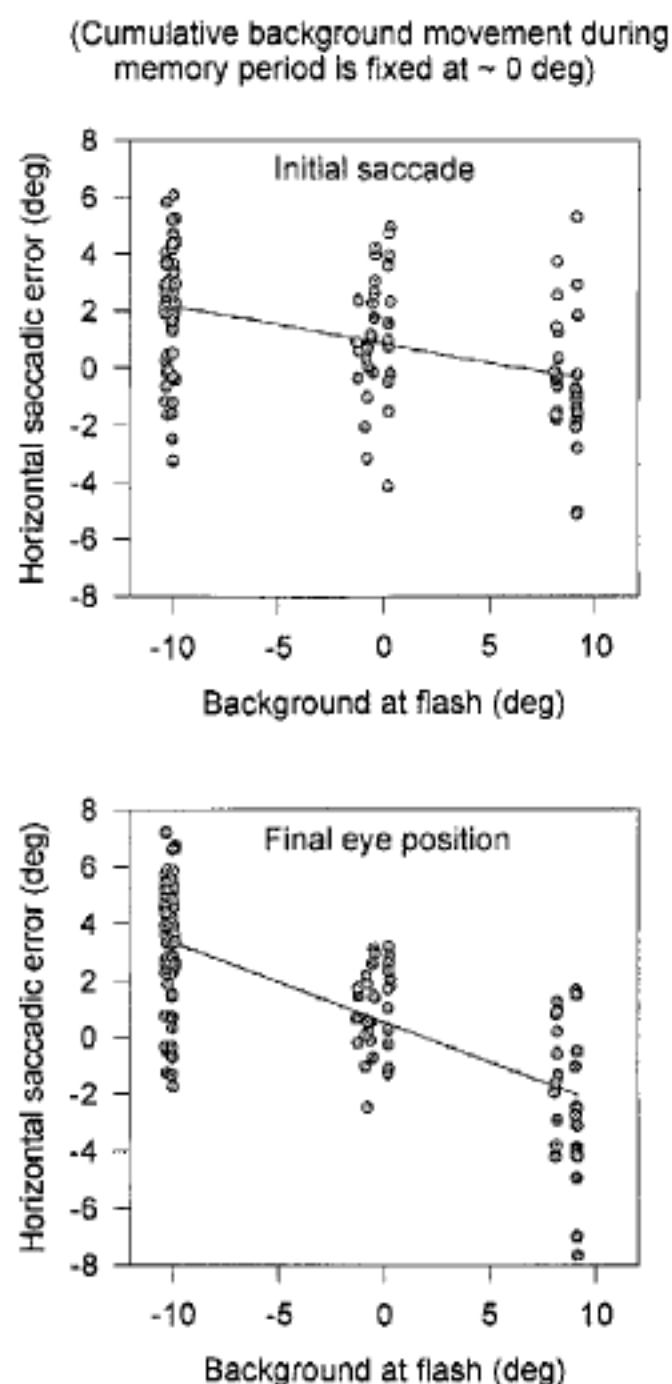


FIG. 10. Plots of background position at time secondary target was flashed vs. horizontal saccadic error for trials in which net movement of background during memory period was ~0. Data from *subject 2*.

PMSB. When motion of the target and background ceased after the secondary target flashed, saccadic error was smaller and more similar to nonillusion than to illusion paradigms. This finding seemed to point to illusory target motion *after* the flash as a major cause for saccadic inaccuracy. However, one potentially confounding factor was present: not only was the illusion stopped at the time of the flash, but the stationary background was also visible during the memory period. Such a "nontarget" cue is known to improve performance significantly (Gnadt et al. 1991) and its presence also may erase the effects of the earlier illusion by "recalibrating" the system. In other words, the PMSB paradigm was equivalent to the FSB paradigm with the whole background offset. This would explain why the errors during PMSB are statistically indistinguishable from the errors during FSB.

We then went on to a second set of experiments in which the position of the background at the time of the secondary target flash and the movement of the background during the memory period were both controlled. Our results indicate that both factors did indeed contribute to the magnitude of the error. To interpret the findings of these experiments, we developed simple models for how the brain programs memory-guided saccades based on current neurophysiological data.

At the time that the stimulus for a memory-guided saccade flashes, the brain receives visual information that is initially in retinal coordinates. Studies in monkeys indicate that this

information is passed to a number of secondary visual areas, including posterior cortex—area 7a and the lateral intraparietal area (LIP) (Barash et al. 1991)—and dorsolateral prefrontal cortex (DLPC) (Friedman and Goldman-Rakic 1994; Funahashi et al. 1990). The latter is especially important, and lesions here severely disrupt the ability to make accurate saccades to remembered target locations (Funahashi et al. 1993). If the brain memorizes target location in craniotopic coordinates, then it must also monitor eye position, possibly from extraretinal sources, such as efference copy. Andersen et al. (1990) have presented evidence that eye position has significant effects on light-sensitive, memory, and saccade responses in parietal areas and this also has been reported in some neurons in other cortical areas, including DLPC (Funahashi et al. 1985; O Scalaidhe and Goldman-Rakic 1993).

#### *Formulation and testing of a model for saccades to remembered targets*

Here we formulate simple linear models to test specific hypotheses regarding the brain's calculation of the required saccade size in our illusory paradigms. We have not attempted to describe the dynamic properties of saccades using the principles of control systems but, rather, to describe algebraically the relationship between the initial and final saccades and the horizontal positions of the secondary target, the eye, and the background of the visual stimulus at the time of target presentation and the end of the memory period. Thus for example, the retina and all other pertinent signals will be treated as one dimensional because our interest lies purely in the horizontal plane. Another simplification in constructing our models involves using either efference copy of eye position or position of the background at each stage. The justification for this is that horizontal eye position was close to 0 both at the time of secondary target presentation and when the memory-guided saccade was generated. In contrast, perceived target location often changed by large amounts during the memory period. We did consider the influence of efference copy in those versions of our model in which we did not include an effect due to background motion. However, in those versions in which the effect of background motion was included, its effect was assumed to greatly overshadow that of efference copy, and the efference copy component was removed to simplify calculations.

Three specific pieces of information are required to make an accurate saccade to a remembered location: retinal error ( $e_r$ ), which is the angular distance on the retina between the flashed target and the fovea (acquired at the time of secondary target flash); eye position at the time of secondary target flash ( $E_i$ ); and eye position at the time that the memory-guided saccade is generated ( $E_f$ ). For the memory-guided saccade to be accurate, the brain must, at some point, make the following calculation to arrive at saccade size ( $E_s$ )

$$E_s = e_r + E_i - E_f \quad (1)$$

If the brain was able to access the three variables on the right side of Eq. 1, it would be able to generate accurate saccades. This might be achieved by monitoring efference copies of the respective eye positions  $E_i'$  or  $E_f'$ . However, our experiments suggest that the brain might use a visual



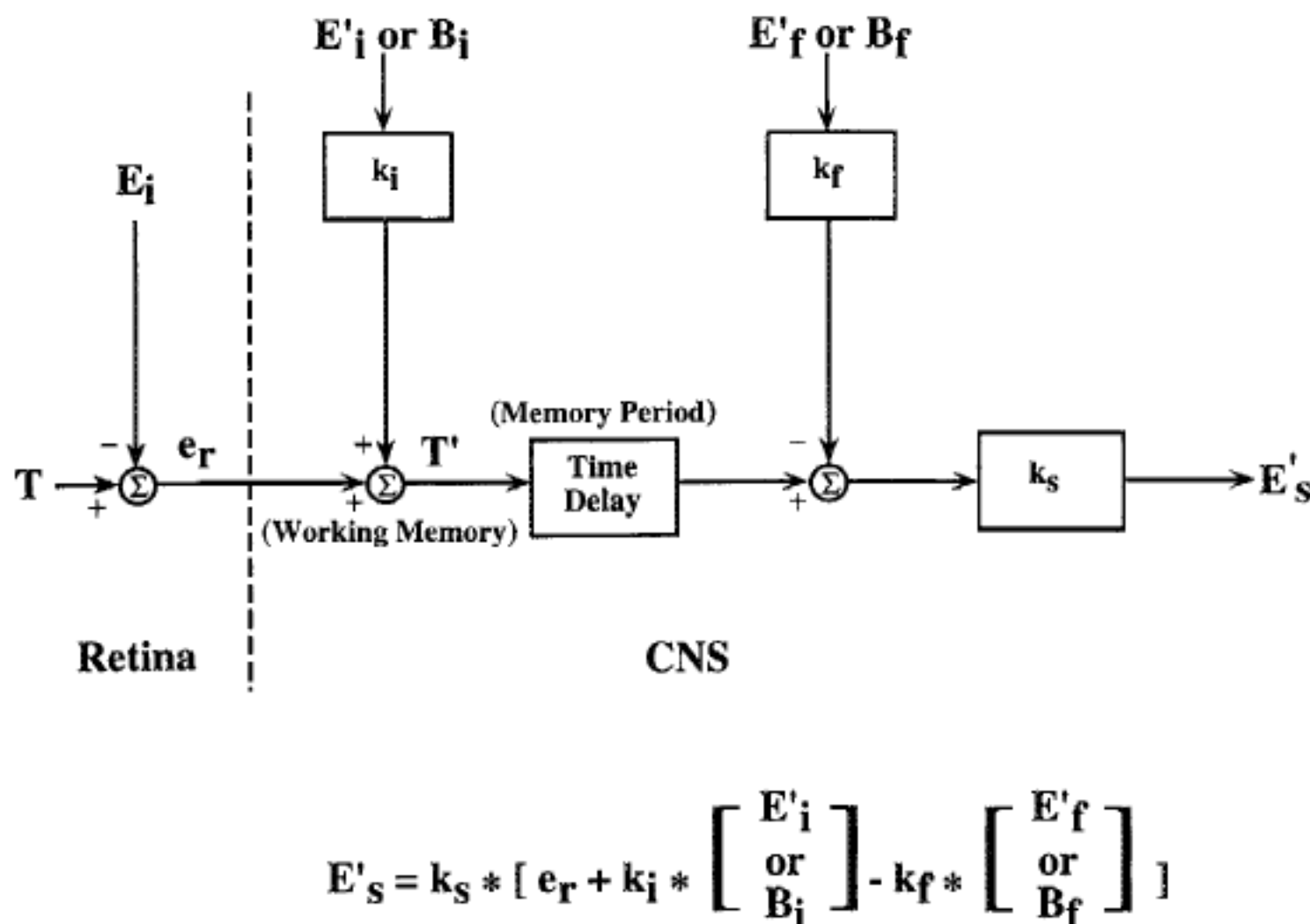


FIG. 11. Simple, linear models representing 4 possible combinations of steps in programming of a memory-guided saccade during tracking of illusory target motion. Retinal error ( $e_r$ ) is sampled as difference between initial eye position ( $E_i$ ) and target position at time that secondary target is flashed at position  $T$ . Brain combines  $e_r$  with an estimate of initial eye position to generate an internal representation of craniotopic location of the flashed target,  $T'$ , which is stored in "working memory" (probably in dorsolateral prefrontal cortex). We model 2 possibilities of how eye position is estimated: based on an efference copy of eye position,  $E'_i$ , or based on illusory position of pursuit target, which is determined by position of background,  $B_i$ ;  $k_i$  is a gain common to either. At end of memory period, brain subtracts current eye position from  $T'$  to program command for a memory-guided saccade,  $E'_s$ , which is governed by gain  $k_s$ . Again, we model 2 possibilities of how eye position is estimated: based on an efference copy of eye position,  $E'_f$ , or based on illusory position of pursuit target, which is determined by position of background,  $B_f$ ;  $k_f$  is a gain common to either. Four combinations of model are summarized by equation at bottom, which is derived in APPENDIX.

estimate of eye position that is influenced by the position of the background at the time of the secondary target flash,  $B_i$ , and at the end of the memory period,  $B_f$  (Fig. 11). The relative influence of each of these factors is postulated to be governed by scaling factors,  $k_i$ ,  $k_f$ , which can be directly related to experimental results (see below);  $k_s$  is an overall scaling factor. The four possible models are summarized in Fig. 11 and a more complete development is presented in the APPENDIX.

To test the four possible equations, nonlinear estimations were performed using the Marquardt-Levenberg algorithm (SigmaStat) to calculate the optimum values for  $k_f$ ,  $k_i$ , and  $k_s$  for the data from each of the two subjects ( $n = 664$  for subject 1 and 683 for subject 2). The predicted horizontal sizes of the initial and final saccades, calculated from the corresponding measured values of  $e_r$ ,  $E_i$ ,  $E_f$ ,  $B_i$ , and  $B_f$ , using each equation with optimized values were then compared with measurements of saccades the subjects actually produced, by performing linear regression analysis. Table 4 presents the result of this analysis and Fig. 12 shows plots of predicted versus observed final saccadic size for each of the four equations for subject 1. Of the four equations, Eq. A8 produced the best predictions of initial and final saccadic size for both subjects as judged by calculated  $r$  values and the predicted residual sum of squares (Stevens 1992) (Table 4).

As an additional test of Eq. A8, we compared the calculated values of the gains  $k_f$ ,  $k_i$ , and  $k_s$  (Table 4) with values derived from the observed relationship between saccadic error and background motion, summarized in Tables 2 and 3. It can be shown (see APPENDIX) that the values of  $k_f * k_s$  are given by corresponding values of the slopes in Table 2, which relate saccadic error to background movement during the memory period. Thus for subject 1, the average value of the slope from Table 2 was 0.19 for the initial saccade and 0.11 for final position; the corresponding calculated val-

ues for  $k_f * k_s$  from Eq. A8 were 0.16 and 0.07 (Table 4). For subject 2, the average value of the slope from Table 2 was 0.30 for the initial saccade and 0.16 for final position; the corresponding calculated values for  $k_f * k_s$  from Eq. A8 were 0.24 and 0.10 (Table 4). It also can be shown that the

TABLE 4. Evaluation of predictions of four models

| Subject   | Model | $k_e$   | $k_i$   | $k_s$  | PRESS | $r$   |
|-----------|-------|---------|---------|--------|-------|-------|
| <i>S1</i> |       |         |         |        |       |       |
| Initial   | A     | -1.1    | -0.486  | 0.935  | 8,587 | 0.839 |
|           | B     | 0.563   | 0.443   | 0.9296 | 4,575 | 0.918 |
|           | C     | -0.0863 | -0.0938 | 0.938  | 9,034 | 0.829 |
|           | D     | -0.167  | -0.48   | 0.926  | 4,058 | 0.927 |
| Final     | A     | -1.1    | -0.536  | 0.825  | 5,479 | 0.863 |
|           | B     | -0.249  | -0.448  | 0.825  | 2,259 | 0.946 |
|           | C     | -0.0143 | -0.157  | 0.833  | 5,689 | 0.857 |
|           | D     | -0.0914 | -0.469  | 0.823  | 2,129 | 0.949 |
| <i>S2</i> |       |         |         |        |       |       |
| Initial   | A     | -1.1    | -1.1    | 0.764  | 6,938 | 0.834 |
|           | B     | -1.1    | -0.49   | 0.730  | 3,641 | 0.917 |
|           | C     | -0.128  | -1.1    | 0.746  | 7,269 | 0.825 |
|           | D     | -0.337  | -0.6115 | 0.7087 | 2,540 | 0.943 |
| Final     | A     | -1.1    | -1.1    | 0.779  | 6,791 | 0.841 |
|           | B     | 0.883   | -0.516  | 0.746  | 2,801 | 0.938 |
|           | C     | 0.0495  | -1.1    | 0.776  | 7,169 | 0.831 |
|           | D     | -0.132  | -0.558  | 0.743  | 2,620 | 0.942 |

Comparison of the 4 equations for generation of memory-guided saccades under illusory conditions shown in Fig. 11.  $k_e$  is the gain governing the brain's estimate of eye position based on either efference copy or background position at the end of the memory period.  $k_i$  is the gain governing the brain's estimate of initial eye position based on either efference copy or position of the background.  $k_s$  is the gain of the overall saccade generation system. The  $r$  values are for correlations between the predicted saccade sizes from each model and the actual saccade size. The PRESS statistic is the predicted residual sum of squares (Stevens 1992). It is a gauge of how well a regression model predicts new data. It is computed by summing the squares of the prediction errors for each observation. The smaller the value, the better the predictive ability of the model. Note that model D always made the best predictions of saccade size.

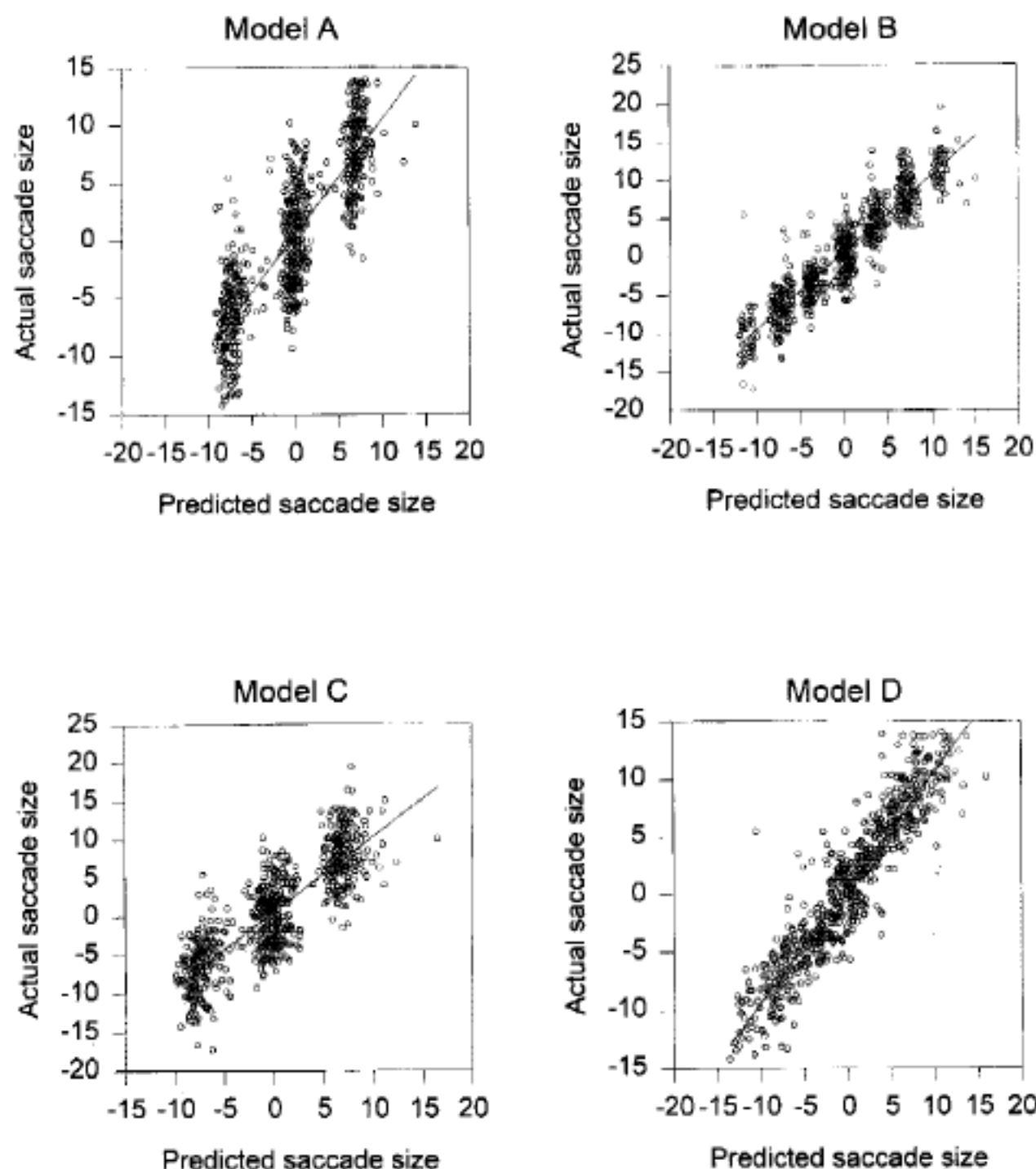


FIG. 12. Plots of predicted saccade size vs. actual saccade size for 4 simple models (equations) of saccade generation described in Fig. 11 after calculation of optimal values of parameters. See text for discussion.

values of  $k_i * k_r$  are given by the difference between the slopes in Tables 2 and 3. For *subject 1*, the average value of the difference of the slopes (Table 3 slope minus Table 2 slope) was 0.49 for the initial saccade and 0.41 for final position; the corresponding calculated values of  $k_i * k_r$  for Eq. A8 were 0.45 and 0.39 (Table 4). For *subject 2*, the average value of the difference of the slopes (Tables 3 slope minus Table 2 slope) was 0.52 for the initial saccade and 0.49 for final position; the corresponding calculated values of  $k_i * k_r$  for Eq. A8 were 0.43 and 0.41 (Table 4).

In using the above models, we have assumed that the brain stores the location of the secondary target in craniotopic coordinates. However, the brain might use retinotopic coordinates and store  $e_r$  and  $E_i$  separately at the time of the secondary target flash and, at saccade initiation, subtract  $E_i$  from  $E_r$ , to yield a net change in eye position during the memory period. These two alternatives are algebraically equivalent and can be distinguished only by electrophysiological studies.

#### *Relative roles of visual and extraretinal signals in programming saccades to remembered target locations*

Our analyses suggest that the illusory nature of our visual stimulus, specifically movement of the background, was principally responsible for the errors that our subjects made. Thus the brain appeared to choose a visual estimate of gaze

over one based on efference copy. For example, when the pursuit target moved up, subjects pursued it closely, holding the image of the primary target close to the fovea. Because subjects perceived that their eye was on the target and, furthermore, (incorrectly) that the target's trajectory was diagonally, they concluded that their eyes were pointing at the illusory position of the target, up and to the left; in fact there was essentially no horizontal deviation of gaze. We postulate that this flawed estimate of gaze occurred at both the time of the target flash and at saccade initiation. The use of perceived eye movement rather than efference copy in estimating eye position might raise the question: what is the evidence that visual areas in cerebral cortex have access to extraretinal signals, such as efference copy for smooth pursuit eye movements? Israël (1992) presented evidence indicating that information acquired retinally was more accurate in guiding memory saccades than internally generated information, such as efference copy, but nonetheless, efference copy did play a role. Evidence to support the idea that an efference copy of smooth pursuit eye movements reaches the medial superior temporal visual area (MST) in monkey was provided by Newsome and colleagues (1988). They found that neurons in MST remained active during smooth pursuit, even if the target disappeared transiently. Recently Assad and Maunsell (1995) have provided evidence to suggest that such sustained activity, when the moving target transiently disappears from view might, instead, be related



to the animal's presumption that the target is still moving rather than, or in addition to, an efference copy. In the experimental paradigm that we used, it seems that if an efference copy of pursuit eye movements was used by the brain in programming memory-guided saccades, then it was subservient to visual cues about the direction of gaze, even if these were flawed. Future studies of the activity of neurons in areas such as DLPC and functional imaging studies in humans may help to clarify this issue.

It is worth noting that an entirely different model could be proposed to account for our findings. At the time of target flash, it is possible that the information on retinal error is either accurate or it is corrupted by the effects of the visual illusion. Our model (Fig. 11) makes that assumption the retinal error is correctly encoded by the brain. However, it has recently been demonstrated (Colby et al. 1995; Duhamel et al. 1992; Kusunoki et al. 1994) that, immediately preceding a saccade, cells respond to future as well as current gaze direction. Certain cells therefore are responding to more than one retinal location, causing an ambiguity as to the true retinal error that is detected. In an alternative scheme, misrepresentation of both eye position and retinal error could contribute to the inaccuracy of memory-guided saccades. Such a possibility could not be resolved by the present experiments and would require electrophysiological investigation.

## APPENDIX

The model will be developed by first describing the two possibilities that exist at each of the two significant points in time. These possibilities are summarized in Fig. 11. These then will be combined to yield the four model equations. In this development, it is assumed that at the time of the secondary target flash, the brain normally stores target position in craniotopic coordinates. An independent storage of retinal error and initial eye position also could have been used.

The target position in craniotopic coordinates,  $T'$  is calculated from the sum of the angular distance between the fovea and the flashed target position on the retina,  $e_r$ , and the estimate of current eye position,  $E_i'$ . This may be performed accurately using an efference copy of eye position,  $E_i'$ , thus

$$T' = e_r + k_i * E_i' \quad (A1)$$

where  $k_i$  is a gain factor used to weight the brain's perception of eye position, be it real or illusory, at the time of secondary target presentation.

Or it is possible that this equation is modified under illusory conditions to include a term that incorporates the position of the background at the time of target flash. The brain may mislocalize the current eye position and use the perceived target location as the current eye position. The estimate of current eye position then would be related to the background at the time of the flash  $B_i$ , such that

$$T' = e_r + k_i * B_i \quad (A2)$$

At the time of saccade generation, the brain must use the stored target location,  $T'$ , be it correct or incorrect, and modify it by the current eye position at the end of the memory period. Here too, final eye position may be determined from efference copy,  $E_f'$ , or it may be corrupted by the illusion. If it is based on efference copy, then the size of the memory-guided saccade is

$$E_s = T' - k_f * E_f' \quad (A3)$$

where  $k_f$  is a gain factor used to weight the brain's perception of eye position, be it real or illusory, at the end of the memory period.

Alternatively, the estimate of current eye position might be corrupted by the illusory trajectory of eye movements due to movement of the background and may be related to background position at the end of the memory period,  $B_f$ . The command for the memory-guided saccade then might be

$$E_s = T' - k_f * B_f \quad (A4)$$

In either of the two equations for  $E_s$ , Eqs. A3 and A4, the stored value for target position,  $T'$ , can be from either Eq. A1 or A2, giving a total of four possible models. In general, saccades to remembered targets under nonillusory conditions are not perfectly accurate (Becker and Fuchs 1969) and therefore in our model, the final value of  $E_s$  was multiplied by a gain factor,  $k_s$ .

Substituting Eq. A1 or A2 into Eqs. A3 and A4 provides us with the four possibilities. Using Eq. A1 in Eq. A3 is the equivalent of using the correct spatial error and yields a saccade size,  $E_s$ , of

$$E_s = k_s * (e_r + k_i * E_i' - k_f * E_f') \quad (A5)$$

If instead of Eq. A1, Eq. A2 is used in Eq. A3, that is equivalent to having an error in the storage of, or conversion to, craniotopic coordinates due to a mislocalization of the eye due to the position of the background when the secondary target was flashed but using the correct eye position at the time of saccade generation. That yields

$$E_s = k_s * (e_r + k_i * B_i - k_f * E_f') \quad (A6)$$

Using Eq. A1 in Eq. A4 is the equivalent of using correct craniotopic coordinates but mislocalizing the direction of gaze at the end of the memory period. That yields

$$E_s = k_s * (e_r + k_i * E_i' - k_f * B_f) \quad (A7)$$

If instead of Eq. A1, Eq. A2 is used in Eq. A4, that is equivalent to having an error in both the storage of, or conversion to, craniotopic coordinates due to a mislocalization of the eye due to the position of the background when the secondary target was flashed as well as mislocalizing the direction of gaze at the end of the memory period. The generated saccade size then would be

$$E_s = k_s * (e_r + k_i * B_i - k_f * B_f) \quad (A8)$$

For Eq. A8, the gain values for  $k_i$ ,  $k_f$ , and  $k_s$  can be related to the data presented in Tables 2 and 3, assuming that  $E_i$  is  $\approx 0$  deg (in which case,  $e_r \approx T$ ) and that the size of saccadic error is independent of secondary target location (both these assumptions are supported by the results of the present study). Then, it can be shown that  $k_f * k_s$  is equivalent to the values given by the slopes in Table 2 and that  $k_i * k_s$  is equal to the difference between the gains in Tables 2 and 3. Note that the values of  $k_i$  and  $k_f$  in Table 4 are negative because the model (Fig. 11) uses a sign convention appropriate to model A, which bases estimates of gaze position on efference copy ( $E_i'$  and  $E_f'$ ). However, model D bases estimates of gaze on the position of the visual background ( $B_i$  and  $B_f$ ), and these are opposite in direction to estimates of eye position based on efference copy.

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