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Updating Visual Memory Across Eye Movements for Ocular and Arm Motor Control

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Thompson AA, Henriques DYP. Updating visual memory across eye movements for ocular and arm motor control. *J Neurophysiol* 100: 2507–2514, 2008. First published September 3, 2008; doi:10.1152/jn.90599.2008. Remembered object locations are stored in an eye-fixed reference frame, so that every time the eyes move, spatial representations must be updated for the arm-motor system to reflect the target's new relative position. To date, studies have not investigated how the brain updates these spatial representations during other types of eye movements, such as smooth-pursuit. Further, it is unclear what information is used in spatial updating. To address these questions we investigated whether remembered locations of pointing targets are updated following smooth-pursuit eye movements, as they are following saccades, and also investigated the role of visual information in estimating eye-movement amplitude for updating spatial memory. Misestimates of eye-movement amplitude were induced when participants visually tracked stimuli presented with a background that moved in either the same or opposite direction of the eye before pointing or looking back to the remembered target location. We found that gaze-dependent pointing errors were similar following saccades and smooth-pursuit and that incongruent background motion did result in a misestimate of eye-movement amplitude. However, the background motion had no effect on spatial updating for pointing, but did when subjects made a return saccade, suggesting that the oculomotor and arm-motor systems may rely on different sources of information for spatial updating.

INTRODUCTION

We maintain a perception that the world around us is visually stable despite the fact that our eyes are almost constantly moving. Since the retinal location of world-fixed objects changes with each eye movement, retinal information alone is insufficient to maintain a stable visual percept. In fact the brain uses multiple sources of information, such as efferent signals and proprioception, to maintain this spatial constancy. For instance, neurons in the macaque posterior parietal cortex (PPC) fire preferentially for both retinal target direction and for positions of the eyes within their orbits using gain fields (Andersen et al. 1985). Further, neurons like those in the lateral intraparietal area (LIP), the frontal eye fields (FEF), and the superior colliculus (SC) also have access to corollary discharge, or efference copy, allowing them to modify firing rates in anticipation of a saccade that will bring a target into, or out of, the receptive field (Duhamel et al. 1992; Sommer and Wurtz 2002). This creates a dynamic link between retinal images across the eye movement, allowing for the continuous remapping of visual space and

visuospatial memory required for the stable representation of the visual world just described.

The remembered location of a pointing target has also been shown to be remapped following an intervening eye movement (Henriques et al. 1998). When subjects made intervening saccades between viewing a central target and pointing to its remembered location, they overestimated the location of the remembered target relative to gaze (i.e., consistent with the retinal magnification effect reported by Bock 1986). That is, subjects had the same pattern of errors when they foveated the target and remapped its remembered location to the periphery after moving their eyes (as in Henriques et al. 1998) as they did when pointing to a remembered target seen only peripherally (as in Bock 1986). These results suggest that remembered target locations are stored and updated in an eye-fixed reference frame, and not converted to a head-centered or hand-centered frame—at least until the decision to generate an action toward that target is made. Gaze-dependent updating has also been shown for auditory and proprioceptive pointing targets (Pouget et al. 2002), for pointing to remembered target locations at different distances relative to the body (Medendorp and Crawford 2002), for both explicit and implicit targets (Poljac and van den Berg 2003), when shifts in gaze are produced by translating the entire body (Van Pelt and Medendorp 2007), and when start positions of the seen or unseen hand are varied (Beurze et al. 2006). Updating of visuospatial memory relative to gaze has even been shown for repeated arm movements made to the same location, seen only once, but with gaze in different directions (Sorrento and Henriques 2008). Using fMRI, Medendorp et al. (2003) showed that remapping of remembered saccade and pointing targets as a function of gaze occurs in the PPC.

As mentioned earlier, retinal (i.e., visual) and extraretinal (i.e., proprioception and efference copy) information must be combined for the accurate remapping of visual targets. The combination of the remapped target location (reflected in the shift of parietal activity) with peripheral visual information of the target postsaccade, results in a significant decrease in the variability of pointing errors (Vaziri et al. 2006). So, retinal information (pre- and postsaccade) and knowledge of eye position or motion (i.e., from proprioception and efference copy) are optimally combined to locate the remembered target for pointing. However, some retinal information, such as visual background motion, can lead to misestimates of eye-movement direction or magnitude when combined with efferent signals

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for updating visuospatial memory (Somers et al. 2000; Zivotofsky et al. 1996).

As retinal information is suppressed during saccades, the influence of retinal motion on perceived movement amplitude would be present only during slower eye movements (Wurtz 2008). During smooth-pursuit eye movements there is an inherent movement of the visual scene across the retina in the opposite direction of the eye movement. Therefore induced background motion opposite to the direction of the eye movement leads to a misperception of the eye's velocity and, thereby, the movement amplitude (Lindner et al. 2001; Zivotofsky et al. 2005). In addition to illusory retinal motion seeming to override accurate efference-copy signals of eye movements, it has also been shown to influence goal-directed reaching endpoints (Whitney et al. 2003). This suggests that retinal information may be weighted more heavily than efferent signals in some cases.

It is not known what the contribution of visual information is to estimating how much the eyes have moved (i.e., the magnitude and direction by which targets would be remapped) for directing pointing movements. The primary goal of this study was to determine the extent of the role of retinal motion information in estimating eye movements for updating the remembered location of saccade and pointing targets. Since retinal information is suppressed during saccades, we examined updating following smooth-pursuit. However, although previous studies have investigated how the brain updates spatial memory following saccadic movements, it is unknown whether it does so for smooth-pursuit. So, we first determined whether remembered locations of visual targets are updated following a smooth-pursuit eye movement, as they are following a saccade.

METHODS

Participants

Participants ($n = 8$; 6 male, 2 female) included healthy right-handed individuals between the ages of 20 and 33 yr (mean: 23.9 ± 4.2 yr). All participants were prescreened verbally for self-reported handedness and history of visual, neurological, and/or motor dysfunction. All participants had normal or corrected-to-normal vision, with four requiring glasses or contact lenses. Participants were recruited by word of mouth and received no compensation for their participation in the study. All provided informed consent and were treated in accordance with the ethical guidelines of York University's Human Participants Review Subcommittee.

Apparatus

Eye movements of the right eye only were recorded by infrared pupil identification with the EyeLinkII eye tracker (SR Research, Osgoode, ON, Canada) at a sampling rate of 250 Hz. At the start of each testing session, the apparatus was calibrated for each participant within the parameters specified by SR Research to ensure reliability of measurement.

The three-dimensional (3D) position of the upper arm and fingertip were recorded at 125 Hz during the pointing tasks using the OPTOTRAK Certus (Northern Digital, Waterloo, ON, Canada) 3D motion capture system. Position and orientation of the upper right arm was marked by a rigid body containing three infrared emitting diodes (IREDs) of fixed distance from each other. The fingertip was marked with two single IREDs for the sake of redundancy to prevent lost data points (note there was no missing marker signal during data

collection so all measurements of finger position were taken from the same IRED). To ensure that there was no head movement, head position was measured throughout the experiment by a four-IRED rigid body attached to the EyeLinkII. Recordings from the EyeLinkII and the OPTOTRAK were simultaneously controlled by The Motion-Monitor (Innovative Sports Training, Chicago, IL), ensuring a common temporal and spatial reference between the two data sets.

Stimuli

All visual stimuli were generated by an Optikon XYLP-C Laser Projector (Optikon, Kitchener, ON, Canada) and rear projected onto a 178-cm matte display surface situated 150 cm from the participants' eyes. The stimuli used in the study consisted of an array of fixation crosses and pointing targets (diamonds), as shown in Fig. 1. Diamonds spanned 1.25 cm or 0.48° , whereas the crosses spanned 2 cm or 0.76° . The center pointing target (diamond) was located right in front of the participant's right eye, whereas the other two targets were located 5° to its left and right. Crosses were located 0 , 5 , and 10° both left and right of center. All stimuli were at the same elevation as the eye (Fig. 1). Some conditions also included a background array of 50 dots (each dot ~ 0.2 cm in diameter, and an average density of 1 dot per 4°) 5° above and below the target spanning 20° of the visual field horizontally as shown in Fig. 2.

Experimental procedures

In the main task, participants pointed to a briefly flashed target after moving their eyes in some eccentric direction. Participants were seated in complete darkness with their right eye aligned with the central target location and their heads fixed by a bite bar. We recorded movements only from the right eye and patched participants' left eyes to ensure that the subjects' pointing was based on vision from the recorded eye. Patching also ensured that participants aligned the finger with a line joining the target and the viewing eye, even if it was not the dominant eye (Henriques and Crawford 2002; Khan and Crawford 2001).

For the pointing experiments, each trial began with participants pressing down on a single-button mouse (Apple Canada, Markham, ON) located to the right of the body and within comfortable reach of the participants. The button press was used as a release switch for the display (targets appeared only when participants had their reaching hand at the start position) and to mark movement onset and the end of the pointing movement. If the mouse was released at the wrong time (during the target display), that is if participants moved their hand too soon, the trial was aborted and repeated at a later time. Thus the mouse ensured that participants began each trial with their right hand at the same start position and that they

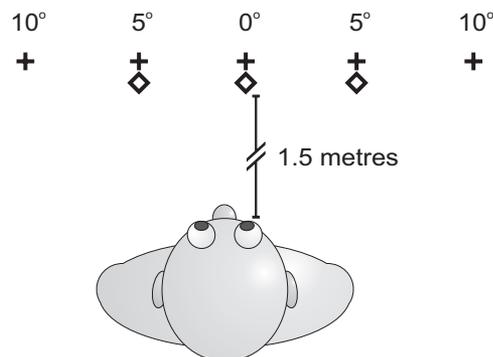


FIG. 1. Display and experimental setup for all conditions. The 3 pointing targets (diamonds) were located directly in front of the right eye (0°), and 5° to the left and right of center. The five fixation crosses were located 10° , and 5° to the left and to the right of the central fixation cross (0°). The left eye was patched and the head was fixed by a bite bar.

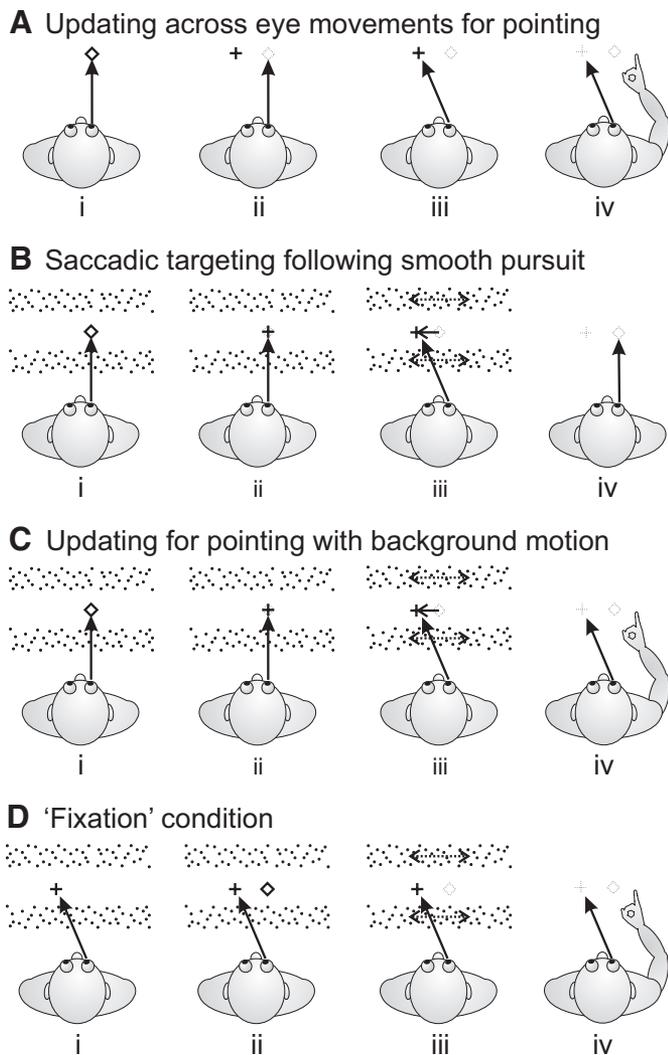


FIG. 2. Sequence of events for trials in all 4 conditions. A: “spatial updating for pointing following saccades vs. smooth tracking” condition: In this condition subjects briefly viewed the target (*i*) until the target disappeared (demonstrated by the faded dashed representation of the target) and a fixation cross appeared (*iii*). They then performed a saccade (*iii*) or a smooth-pursuit (as depicted in *Biii*) to the fixation cross, and pointed to the remembered location of the target when instructed (*iv*). B: “spatial updating for saccadic targeting with background motion” condition: in this condition subjects briefly viewed the target and a background array (*i*) until the target disappeared and a fixation cross appeared (*ii*). They then performed a smooth-pursuit (*iii*) with the fixation cross as the background moved in either the same or opposite direction as the eye movement, or remained static. Following completion of the eye movement the background and fixation cross disappeared and subjects would then saccade back to the remembered location of the target (*iv*). C: “spatial updating for pointing with background motion” condition: As in A except with the presence of the background stimulus as in B. D: “fixation” condition: Subjects would maintain fixation on a cross presented in the background array (*i*) as a target was presented and the background moved either to the left or to the right, or remained static (*ii*). Both stimuli and the background were then extinguished while fixation was maintained (*iii*). Subjects then pointed to the remembered location of the target when instructed. All movements to the remembered target locations were made in complete darkness, with no visual stimuli of any kind, in all conditions.

did not prematurely begin a pointing movement. To prevent dark adaptation a halogen lamp was illuminated for 4 s at the end of each trial (i.e., during the intertrial interval). The end of a trial occurred when participants depressed the mouse on returning their hand following their pointing movement. When the lamp was

turned off the next trial began immediately. Experiments were otherwise performed in complete darkness.

Each participant performed three conditions involving memory-guided pointing following movements of the eyes and one condition where only the eyes moved. These conditions were run across eight sessions on separate days.

Spatial updating for pointing following saccades versus smooth tracking condition

In this task, we wanted to compare how well subjects updated the location of the remembered pointing target following either a saccade or a smooth-tracking movement to some eccentric direction. The pointing target (diamond) was presented for 1 s at one of the three locations (Fig. 2*Ai*), followed by the appearance of the fixation cross (Fig. 2*Aii*) once the target disappeared. For smooth-pursuit trials, the cross appeared in the same spot as the pointing target (as in Fig. 2*Bii*) and then moved to one of the seven locations (in addition to the fixation locations in Fig. 1 this condition also had fixation cross locations at 15° to the left and right of center) at a constant velocity of 10°/s, eliciting a smooth-pursuit (for a movement time of 0.5 s for each 5° traversed). The cross disappeared 1 s after reaching its final location. For saccade-updating trials, the cross would appear at one of the seven locations to elicit a saccade in that direction (Fig. 2*Aiii*). The cross for these saccade-updating trials was on for the length of time it would have taken for the moving cross to reach its final destination in the tracking trials. After the cross disappeared, participants received an auditory command to point to the remembered location of the pointing target without moving their eyes from the final location of the cross (Fig. 2*Aiv*). Participants pointed to the remembered target location with their arm and index finger fully extended. The trial ended when they returned their hand to the mouse. The combination of targets and crosses was randomized across trials. The central target was combined with all seven fixation sites; the 5° targets were combined with only six of them, so that the maximum retinal eccentricity was 15° from center. These 19 target–fixation combinations were repeated four times for pointing movements following both an intervening saccade and a smooth-pursuit movement, for a total of 152 trials. To reduce fatigue, this condition was split in two sessions (each with two repetitions of each possible combination for a total of 76 trials) run on separate days.

Spatial updating for saccadic targeting with background motion condition

To induce misestimates of eye motion we had participants slowly move their eyes (smooth-pursuit) in one direction while an array of moving dots (the background) moved at an equivalent speed in either the same direction or opposite direction. Participants then returned their eyes back to the original location after the background disappeared. Each trial began with participants looking at the diamond target as in the previous condition in one of three target locations (Fig. 2*Bi*). Then the fixation cross appeared in place of the diamond (Fig. 2*Bii*) and moved slowly (10°/s) to elicit a pursuit movement (Fig. 2*Biii*) to one of the five final locations (Fig. 1). We did not run an equivalent condition for outbound saccades with a moving background because any changes in visual background would not be detected during the saccade as a result of saccadic suppression (Wurtz 2008). Since there was no expectation, then, that the background would influence the estimate of outbound saccadic movements, there was no expectation that the return saccade should be influenced.

For this condition, we removed the 15° fixation crosses to reduce the overall target–fixation combinations from 19 to 15 combinations, again with four repetitions per background motion direction. In 25% of the trials (60 trials) no background was displayed as before, but in 75% of trials (180 trials), the background appeared at the onset of the

diamond (Fig. 2*Bi*). In 33% of these trials (60 trials) the background remained stationary and was extinguished at the same time as the fixation cross. In the remainder of trials where the background was displayed the background moved at a velocity of 10°/s, in the same direction as the motion of the cross and gaze or in the opposite direction, at the same velocity (Fig. 2*Biii*). The background motion halted and disappeared after the cross reached its final location. This cued participants to saccade back to the initial gaze location in complete darkness, in the absence of any visual stimuli (Fig. 2*Biv*). All possible combinations were presented in a single session of 240 trials.

Spatial updating for pointing with background motion condition

After establishing that participants' estimates of their eye movements were influenced by the direction of background motion, we introduced background motion when the eyes were moving in our original pointing task. In this condition the background array was displayed statically with the pointing target (Fig. 2*Ci*). When the target disappeared and the fixation cross appeared, the background began to move in either the same or opposite direction as the fixation cross and resulting eye movement (whether a saccade or a smooth-pursuit). For the pursuit movement, both the cross and the background moved at a velocity of 10°/s (Fig. 2*Ciii*). The background was then removed simultaneously with the cross and participants maintained their gaze in the final direction of the cross while pointing to the remembered location of the target in complete darkness (Fig. 2*Civ*). The velocity of the background remained at 10°/s during saccadic movements and persisted for an equivalent amount of time as would have taken a pursuit movement to land at that location. Background velocity was not tied to the saccadic velocity because there is no expectation that the background would influence estimation of saccadic movement amplitude due to saccadic suppression. The background was used to maintain consistency across the tasks.

For trials in which the cross and target appeared in the same location, the background remained stationary since no eye movement was required. All other aspects of this condition were identical to the first condition, except we further reduced the target–fixation combinations so that the central target was combined with five fixation crosses, whereas the 5° targets were combined with the three more proximal fixation crosses for a total of 11 target–fixation combinations. This was done to reduce the overall length of the experiment given the number of different background motions. The combination of targets and crosses, and background motion direction, were randomized across trials and each combination was repeated twice, for each eye movement type, for a total of 88 trials. This set of 88 trials was repeated four times (30-min sessions) on separate days.

“Fixation” condition

This condition served as a control, to ensure that the background motion was causing misestimates of eye motion rather than final gaze position (for the purpose of updating the pointing target location). In this condition, the eyes did not move during the background motion. The cross and the background were displayed first (Fig. 2*Di*). While participants continued to look at the cross, one of the three pointing targets appeared after 500 ms for 1 s (Fig. 2*Dii*). After the peripherally viewed target disappeared, the background began to move either to the right or to the left, at a velocity of 10°/s (Fig. 2*Diii*). Participants did not move their eyes from the cross. After 1 s the background and the cross were simultaneously extinguished and participants (signaled by an auditory command) pointed to the remembered location of the target in complete darkness (Fig. 2*Div*). All possible target–cross combinations (as in the previous condition) were presented in a single session of 88 trials.

Data reduction

Kinematic data of the eye, head, and arm were exported from the MotionMonitor and combined with the command file of the laser projector, allowing the data to be temporally aligned with the appropriate stimulus and background motion combination. These integrated files were then viewed in a graphical user interface (GUI) custom developed and executed in MatLab 7.1 (The MathWorks, Natick, MA). Arm and eye data were then manually selected at time periods when the pointing target and fixation cross were each displayed and during stable pointing (i.e., when maximal amplitude was reached and velocity appeared to be 0 mm/s in the GUI; cf. Sorrento and Henriques 2008). Trials in which the eye moved inappropriately (i.e., at the wrong time or to the wrong location) were discarded. A custom MatLab routine was then used to identify potential gaze or arm outliers ($\pm 2SD$ the respective mean). The identified outliers were then examined to determine whether they were due to a misselection of the data point or a mistrial to be removed from analysis (data removed as outliers accounted for about 6% of all data collected). Pointing errors for each movement were calculated by subtracting the arm direction and finger position during pointing from those in baseline testing conducted at the conclusion of each block of trials (i.e., normal pointing to the three target locations with full vision of the arm, target, and surrounding environment). We were specifically interested in horizontal angular errors as a function of horizontal movement of the eyes.

Data analysis

Repeated-measures (RM) ANOVAs were then performed in SPSS for each condition. For the “Spatial updating for pointing following saccades versus smooth tracking” condition the RM ANOVA was 2 (eye movement type: saccade, smooth-pursuit) \times 5 (retinal error: $-10, -5, 0, 5, 10$). For the “Spatial updating for pointing with background motion” condition the RM ANOVA was 2 (condition: background, no-background) \times 2 (eye movement type: saccade, smooth-pursuit) \times 3 (background direction: same, no movement, opposite) \times 5 (retinal error: $-10, -5, 0, 5, 10$). For the “Fixation” condition the RM ANOVA was 3 (background direction: same, no movement, opposite) \times 5 (retinal error: $-10, -5, 0, 5, 10$). All omnibus effects were evaluated with an alpha level of 0.05. Appropriate post hoc comparison procedures were used to further explore significant main effects (Tukey's LSD) and interactions (i.e., simple-effects ANOVA followed by Tukey's LSD) as necessary.

RESULTS

Spatial updating for pointing following saccades versus smooth-pursuit

Our first aim was to investigate updating of spatial memory for pointing targets as a function of different types of eye movements. Although several studies have shown that remembered pointing targets are updated across saccadic eye movements, here we test whether similar updating occurs following smooth-pursuit movements away from a briefly flashed pointing target. Thus in this condition, we had subjects point to the remembered target location following either a saccade or pursuit movement away from the briefly displayed target.

In Fig. 3, we plot horizontal pointing errors (averaged across subjects) as a function of all gaze eccentricities relative to the target (i.e., the amplitude of the required eye movement from the target). Here the pointing errors are systematically directed to the opposite side of the target relative to the final position of the eye (i.e., looking left resulted in rightward pointing error and vice versa) for both saccadic movements

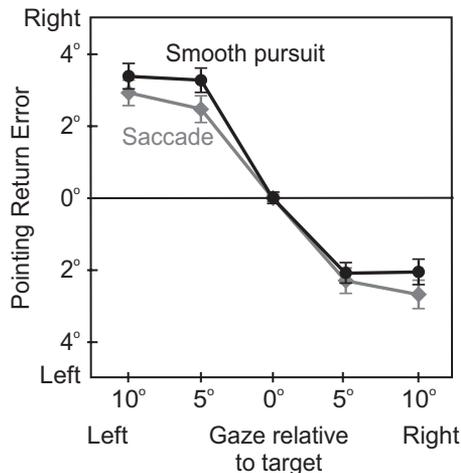


FIG. 3. Horizontal pointing errors following saccades (diamonds) and smooth-pursuit (circles), with no background stimulus, averaged across all subjects as a function of gaze direction relative to the target. The horizontal line at 0° represents accurate pointing and error bars represent SE.

(diamonds) and smooth-pursuit movements (circles), consistent with the retinal magnification effect. The effect of retinal error (i.e., gaze direction relative to target), was significant [$F(4,28) = 38.6$, $P < 0.001$]. There was no significant difference in pointing error across the two types of eye movements [$F(1,7) = 0.343$, $P > 0.05$] (i.e., the pattern of horizontal pointing errors as a function of gaze relative to target was the same following a saccade or a smooth-pursuit away from the target, as illustrated by the largely overlapping curves). These results suggest that the locations of the pointing target are updated in eye-centered coordinates following smooth-pursuit eye movements just as they are following saccades.

Spatial updating for saccadic targeting with background motion

Our next aim was to determine whether misestimates in the amplitude of the eye movement away from the target location would affect the magnitude by which the remembered pointing target was remapped. To do this, we first measured the extent to which a moving visual background would induce misestimates in the size of eye movements. We did this by having subjects make a return saccade to the initial starting point after the eyes had pursued a cross moving out to the periphery while a background array of dots moved either in the same direction or in the opposite direction.

Figure 4A plots horizontal saccadic return errors (averaged across subjects) as a function of all gaze eccentricities relative to the target. The return saccade error was larger when the background velocity was opposite to that of the pursuing eye motion compared with when background velocity was the same and even when the background was stationary or there was no background at all [$F(5,35) = 323.9$, $P < 0.001$]. That is, errors were significantly greater when the saccades were made following a smooth-pursuit against oppositely moving background motion. This is further exemplified in Fig. 4B where saccadic return error following pursuit movements through a moving background is plotted with saccadic return error when there was no background motion representing zero error. When we compared across the

six final gaze directions relative to the target, we found that this background motion effect for opposite moving background arose for five of the six final gaze amplitudes ($P < 0.05$, simple-effect analysis) and for four of the six eccentricities ($P < 0.05$, simple-effect analysis) when comparing opposite background velocity with zero background velocity. There was no significant difference in saccadic amplitude when the background moved in the same direction, when there was no background, and when there was a static background ($P > 0.05$), except when the saccadic target was 5° right. As expected, there were no significant differences between the static background and the absent background conditions. The larger return saccades suggest that while pursuing the cross, the peripheral stimuli moving in the opposite direction across the retina led subjects to overestimate how far their eyes had moved.

Spatial updating for pointing with background motion

After confirming that the direction of background motion did influence estimates of pursuit eye-movement amplitude for updating saccade targets, we then tested whether these misestimates affect the extent to which pointing targets were updated. Figure 4, C and E shows horizontal pointing errors following pursuit (circles) did not vary as a function of the background motion [$F(2,14) = 0.12$, $P > 0.05$], nor did pointing errors following saccades (diamonds) [$F(1,7) = 0.807$, $P > 0.05$]. So, there was no significant influence of the background motion on pointing error following either type of eye movement. Whereas pointing errors varied significantly as a function of gaze direction relative to target [$F(4,28) = 38.46$, $P < 0.001$], the direction of the background motion had no significant effect on pointing errors following either smooth-pursuit or saccades. Figure 4, D and F plots the pointing error following eye movements through a moving background relative to the pointing error when there was no background motion. There were no significant differences in pointing error across these conditions.

“Fixation” condition

This condition served as a control to ensure that background motion was affecting the misestimate of eye-movement amplitude and not causing a misestimate of final gaze position. In this condition, the eyes did not move during the background motion. Given that we found no effect of background motion during eye movement on pointing, it is not surprising that we also found no effect when the background moved after the eyes had saccaded to the periphery [$F(1,7) = 0.807$, $P = 0.399$]. Although retinal error did show a significant effect [$F(4,28) = 4.047$, $P < 0.01$], as would be expected (i.e., normal pointing error relative to gaze), there was no interaction effect between retinal error and direction of background motion [$F(4,28) = 0.606$, $P > 0.662$].

DISCUSSION

We first wanted to determine whether the remembered locations of pointing targets were updated following smooth-pursuit eye movements, as they are following saccades. If this was the case, our next goal was to determine the extent of the role of visual information in updating spatial memory. Our

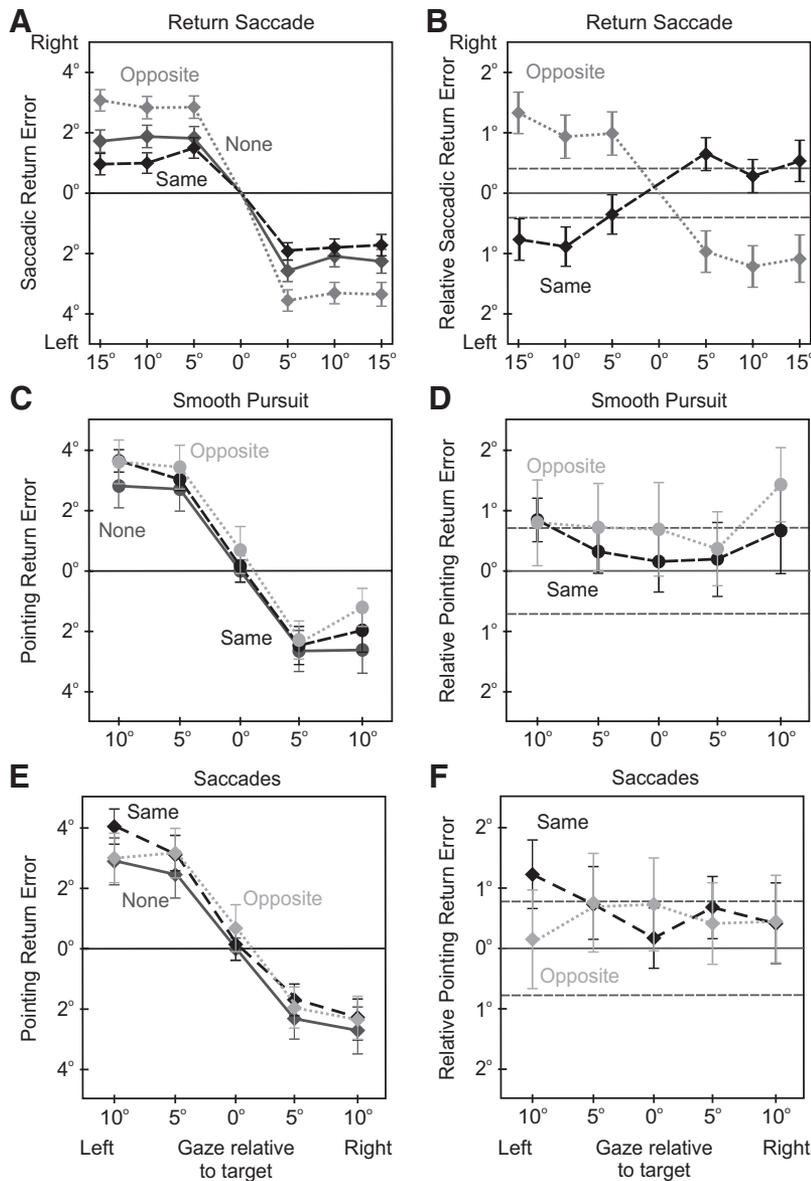


FIG. 4. Horizontal errors for pointing or saccading back to the remembered target location. *A*: return saccade errors following a smooth-pursuit movement away from the target with a background moving in the same direction (black dashed), in the opposite direction (light gray dotted), or not moving (dark gray solid). *C* and *E*: pointing errors following smooth-pursuit (*C*, circles) and saccadic (*E*, diamonds) movements made when the background moved in the same direction (black dashed), in the opposite direction (light gray dotted), or not at all (dark gray solid). The horizontal line at 0° represents accurate pointing or accurate return saccades. *B*: return saccade errors following a smooth-pursuit movement away from the target with a background moving in the same direction (black dashed), or in the opposite direction (light gray dotted) relative to the return error when the background did not move. *D* and *F*: pointing errors following smooth-pursuit (*D*, circles) and saccadic (*F*, diamonds) movements made when the background moved in the same direction (black dashed), or in the opposite direction (light gray dotted) relative to pointing errors when the background did not move. In *B*, *D*, and *F* the horizontal line at 0° represents mean error when the background did not move, with the parallel dashed lines representing SE. In each panel, error bars represent SE.

findings suggest that the locations of pointing targets are updated across different types of eye movements. However, although visual information influences estimates of eye-movement amplitudes (of smooth-pursuit movements) for updating remembered saccade targets, this misestimate does not influence the updating of visuospatial memory for pointing movements.

We found that horizontal pointing error systematically varied following the final gaze direction after smooth-pursuit eye movements, which indicates that visuospatial memory of pointing target locations is updated relative to gaze following smooth-pursuit eye movements as it is following saccades (cf. Henriques et al. 1998). Despite the fact that the movement parameters and the internal copy of the oculomotor command likely differ between saccades and pursuit movements—the error signals are different (i.e., retinal error vs. velocity of retinal slip, respectively)—the magnitude of the gaze modulation on pointing endpoints did not significantly differ between the two types of eye movements. This similarity in spatial updating across the two different eye

movements is consistent with recent evidence from neurophysiological recordings in primates that have identified that saccade and pursuit systems are controlled by some of the same neural substrates (Krauzlis 2005; Stone and Krauzlis 2003). It is possible that the copy of the efferent signals produced by these common neural substrates may be used for updating space across movements of the eyes.

Since it is difficult to identify efference signals in the primate brain (Wurtz and Sommer 2004), most studies of this nature have investigated efferent signals associated with saccadic movements rather than with smooth-pursuit. It has been demonstrated that neurons in the mediodorsal (MD) thalamus, which link the SC and FEF, carry the necessary corollary discharge for spatial updating following saccades in monkeys (Sommer and Wurtz 2002). By temporarily disabling this SC–FEF pathway via MD the authors found some disruption to sequential eye movements with no disruption to single eye movements, suggesting that this pathway carries efference copy signals. However, substantial updating still occurred, so these efferent signals are not the sole source of information.

Other sources of extraretinal information beyond efference copy are also likely to be involved in updating spatial memory as a function of gaze direction (e.g., proprioceptive information from the ocular musculature) for both types of eye movements described here (van Donkelaar et al. 1997). As described earlier, the retinal signal of a peripherally visible target following a movement away from it is optimally combined with the efference copy signals of the movement to produce less variable pointing movements (Vaziri et al. 2006). Given that pointing errors following intervening eye movements are similar to those made to peripherally viewed targets—where the eyes do not move following seeing the target—it also seems logical that both retinal and extraretinal information may be used when calculating the target's remembered location relative to gaze.

To investigate the contributions of retinal (i.e., vision) and extraretinal (i.e., efference copy and proprioception) information we used a moving background to elicit misestimated eye-movement amplitudes. Visual stimuli that move across the retina while the eyes are in smooth-pursuit of a target (i.e., reafference) may provide a cue about how far or how fast the eyes have moved (cf. Lindner et al. 2001). If the magnitude of the eye movements was misestimated due to external visual cues, then it is possible that the remembered target could also be updated by an incorrect magnitude. This would be revealed by errors in pointing. In other words, we wanted to test whether spatial memory was updated by the *perceived* eye-movement amplitude rather than the actual eye-movement amplitude. We found that a background moving in the opposite direction of the eye during smooth-pursuit movements consistently resulted in return saccadic amplitudes of significantly greater magnitude than that of those produced following pursuit when the background was static, or moved in the same direction as the eye. This finding suggests that the oppositely moving background significantly influenced the perceived motion of the eye at the completion of the smooth-pursuit or, at least, the estimated amplitude of that movement, indicating that background motion successfully produced a misestimate of final eye position. In fact, the return saccades were approximately 16% larger, on average, when the direction of the background movement was opposite to pursuit movements versus when it was the same (or stationary), despite other sources of information about eye motion such as efferent signals and proprioception remaining constant. This finding is consistent with Somers et al. (2000) who reported that saccades to the remembered locations of visual and auditory targets were influenced by moving background stimuli. Verbal reports of estimated eye-movement amplitude are also larger when gaze pursues a target against an oppositely moving background despite the pursuit movement being accurate (i.e., uninfluenced by the moving background). This suggests that perception of movement amplitude was influenced by the background motion despite the availability of proprioceptive and efferent signals (Schweigart et al. 2003). Erroneous return saccades following pursuit during background motion have also been shown in nonhuman primates (Zivotofsky et al. 2005).

Receptive fields of neurons in macaque LIP that code for the location of remembered visual and auditory stimuli tend to be altered when a target is presented with background motion (Somers et al. 2000), a change that is reflected both by perceptual reports of target motion and by return saccades in

macaque (Zivotofsky et al. 2005). LIP neurons have also been shown to be involved in updating visuospatial memory relative to gaze (Duhamel et al. 1992; Wardak et al. 2002) and the human analogue of LIP has been shown to be involved in updating remembered target locations for both reaching and eye movements (Medendorp et al. 2003). When this is taken with the finding that perceived motion of smooth-pursuit can be affected by background motion (Soechting et al. 2001; Wyatt and Pola 1979; Zivotofsky 2005; Zivotofsky et al. 2005), it seems plausible that pointing targets would be misestimated as the result of a misestimated pursuit command.

After confirming that we could induce misestimates of smooth-pursuit eye-movement amplitudes with the background array, we incorporated this background motion in our initial pointing task to test whether misestimates in eye motion resulted in misestimates in spatial updating for pointing. In our "Spatial updating for pointing with background motion" condition, we found that pointing errors made in complete darkness did not differ when the background remained stationary or moved in the opposite or same direction of the eye movement prior to pointing. Given the increased estimate of pursuit eye-movement amplitudes, we expected that the background moving in the opposite direction of the eye would lead to an increase in pointing error (i.e., the overestimate of eye-movement amplitude should lead to remapping the target location by a greater amplitude, shifting the representation of the remembered target farther away from final gaze). For example, if subjects estimated that they had moved their eyes 12° leftward following the pursuit of a cross 10° to the left against opposite background motion, then the target would be remapped 12° to the right of final gaze location. We would then expect a 2° rightward error on top of the error produced by the retinal magnification effect, although we did not see this. This suggests that although background motion did influence estimates of pursuit eye-movement amplitude and influenced spatial updating for saccade targets (as measured by errors in the return saccade), these misestimates did not translate to errors in updating visuospatial memory for pointing. If eye motion was sufficiently misestimated so as to affect the error signal used by the oculomotor system to plan and execute the return saccade, how was the updating mechanism for the arm-motor system able to filter the influence of the background motion and update the pointing target location relative to the *actual* distance the eyes traveled?

The actual saccadic or pursuit movements of the eyes were not disturbed in this experiment, but the estimated magnitude of the eye movements was. Eye movement parameters were unaffected likely because the fixation cross was always visible during saccading or tracking. If the target had disappeared beneath a field of moving dots (as in the Duncker illusion), we would likely have found an effect of the moving background on both the actual and perceived movements of the eyes (Soechting et al. 2001). Both Soechting et al. (2001) and Whitney et al. (2003) reported reaching errors consistent with the direction of background motion. However, Whitney et al. (2003) reported that reaching motion was affected by the flanking background motion only when the target duration was brief (<600 ms) and occurred during the movement of the arm. Studies by Gomi and colleagues (Gomi et al. 2006; Saijo et al. 2005) suggest that this manual following (i.e., reaching end-point errors consistent with the direction of background motion),

like ocular following, is reflexive rather than voluntary, and the magnitude of this reflexive behavior is different from perception effects caused by the same visual motion. More recently it has been reported that following a target through background motion with the unseen finger is not influenced by background motion (Zivotofsky et al. 2008). As such, although background motion (i.e., retinal motion) does affect the concurrent movements of the eyes and arm whereas there is no salient target to keep the effectors on "track," it does not seem to affect the updating mechanism when pointing to remembered targets in complete darkness, without any background, as shown here. It may be that the functionally different roles of the arm-motor and the oculomotor systems result in processing illusory stimuli differently for the purpose of updating spatial goals and generating eye movements versus arm movements (Thompson and Westwood 2007). The brain may weight the inputs for the oculomotor and arm-motor systems differently. That is, the medial intraparietal area and the parietal reach region may place more weight on efference copy signals (i.e., accurate information regarding the distance traveled by the eye) than visual motion signals for updating arm-movement goals. The oculomotor system, however, when combining efference copy signals of the outbound pursuit movement and input from visual-motion areas, may rely more proportionally on the latter compared with the reach-related parietal areas. Given that the errors for updating the saccade target were relatively small, however, the proportional contribution of efferent signals to estimating eye amplitude for updating space is likely larger than the visual motion signals overall.

In any case, our results indicate that retinal information (i.e., the moving background) is used for guiding movements of the eyes, but it does not influence spatial updating of visual memory for pointing. This suggests that spatial updating of visual memory in eye-fixed coordinates is far more reliant on extraretinal information than on retinal information. In sum, gaze-dependent pointing errors are similar following smooth-pursuit and saccades, misleading retinal information during smooth-pursuit leads to misestimates of eye movement amplitudes, but background motion has no effect on spatial updating for pointing.

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