VISUAL SHORT-TERM MEMORY DURING SMOOTH PURSUIT EYE MOVEMENTS

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Running Head:

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Abstract

Visual short-term memory (VSTM) was probed while observers performed smooth pursuit eye movements (SPEM). SPEM keep a moving object stabilized in the fovea. VSTM capacity for position was reduced during SPEM compared to a condition with eye fixation. There was no difference between a condition in which the items moved with the pursuit target such that they were stabilized on the retina, and a condition in which the items were stationary such that they moved across the retina. The reduction of SPEM capacity for position was eliminated when miniature items were presented on the pursuit target. Similarly, VSTM capacity for color did not differ between SPEM and fixation. The results suggest that visuo-spatial attention is tied to the target during SPEM such that VSTM for the position of peripheral objects is impaired. Sensory memory during SPEM was intact and allowed for improved performance based on apparent motion cues.

Introduction

The visual world is in motion for two reasons. First, the physical objects around us move and second, we move our eyes. In order to ensure the stability of our perceptual world, we need to store snapshots of objects that go out of sight. This task may be solved by visual short-term memory (VSTM). VSTM stores information for several seconds that is no longer available after an eye or object movement. VSTM has to be distinguished from sensory memory which keeps visual information for less than hundred milliseconds and is far less capacity-limited than VSTM (Sperling, 1960). Most of the research on VSTM has tried to characterize the nature and number of items in VSTM. One important finding was that the entities of VSTM are objects, and not single features (Luck & Vogel, 1997). For instance, short-term memory capacity may be increased from four to eight features if two features are combined to form an object (but see Olson & Jiang, 2002). While the capacity for object features such as color and orientation was determined to be on the order of 4-5 items (Pashler, 1988; Phillips, 1974), it appears that the number of spatial locations is larger (Simons, 1996). In most of the previous studies, VSTM was probed with a change detection paradigm: Observers viewed an array of items for some time, and were asked to memorize these items. The array of items-to-be-memorized will be referred to as <u>memory image</u>. After a blank retention interval, another array of items was shown which will be referred to as <u>probe image</u> and observers were asked to indicate whether there was a change between the memory and the probe image. Performance was found to be stable across a range of memory image presentation times (0.1-0.5 s, Luck & Vogel, 1997; Pashler, 1988) and retention intervals (about 0.07-1s, Pashler, 1988; Sperling, 1960).

Beyond the capacity issue, it was argued that information in VSTM is stored in a relational or configurational manner. Evidence for this view was provided by manipulating the number of items that were present in the probe image (Jiang, Olson, & Chun, 2000). Jiang and Olson either presented the same number of items in the probe as in the memory image (<u>all probes condition</u>), or only a single probe item (<u>single probe condition</u>). In both cases, the critical item was cued by an outline box. Observers' ability to correctly identify a change of the critical item dropped drastically in the single probe condition compared to the all probes condition, indicating that the position or features of an item were coded with respect to the position of other items in the image. That is, the relative position of an item was important for VSTM performance.

In the current study, we investigated contributions of continuous <u>spatial</u> and <u>retinal</u> position changes to VSTM. Spatial position refers to the position of an object with respect to the observer (i.e., the egocentric position), whereas the retinal position is the position with respect to the fovea (i.e., retinotopic position). For instance, if an observer moves the eyes from object A to B, this induces a change in the retinal position of objects A and B while there is no change in their spatial positions (i.e., A and B did not move). If, on the other hand,

object A moved toward B and the observer maintained fixation on the stationary object B, there would be a change in the retinal and spatial position of object A. Finally, if the observer was pursuing the moving object A with the eyes, and object B moved at the same velocity and in the same direction as object A, there would be a change in the spatial position, but the retinal position of the objects would stay the same. The effects of eye and object movements on retinal position are summarized in Table 1.

To disentangle the contribution of spatial and retinal position to VSTM, either the objects or the eyes have to move. Previous work in which spatial and retinal position were manipulated focused on saccadic eye movements. The main question was whether the short-term memory store that preserves information from the interval before a saccade to the interval after a saccade (i.e., transsacaddic memory) is the same as visual-short term memory. The nature of the position changes in studies on transsaccadic memory was abrupt: Saccadic eye movements bring the eyes into a new position within approximately 50 ms and parts of visual input is suppressed during this time (Ross, Morrone, Goldberg, & Burr, 2001). If the objects are stationary, a saccade will produce changes in the retinal position, but leave the spatial positions unchanged. In contrast, if the objects are displaced during the saccade, the retinal position may be the same as before the saccade, but the spatial position has changed. It was observed that memory performance was worse when observers executed a saccade compared to conditions with stationary eyes (Irwin, 1991). This difference was attributed to dual task demands: In the saccade conditions, observers had to simultaneously program a saccade, and encode the memory image. However, the properties of VSTM and transsaccadic memory were remarkably similar: Effects of retention interval and object displacement were small and both VSTM and transsaccadic memory preserved relative position information (i.e., configurational or structural information, Carlson-Radvansky, 1999; Carlson-Radvansky & Irwin, 1995; Irwin, 1991). Therefore, most researchers would agree that VSTM and transsaccadic memory are very similar – if not identical memory stores. One difference between fixation and saccadic conditions concerned the sensory memory store: With retention intervals of less than 100 ms, trials with a change may be detected because of apparent motion between elements in the memory and probe images. That is, observers see the element that undergoes a change to "jump" from one location to another. However, the contents of sensory memory are cleared during a saccade, such that judgments could not be based on apparent motion cues (Irwin, 1991).

In the present study, we investigate visual short-term memory during smooth eye or object motion. To our knowledge, this is the first investigation on this topic. This is peculiar because most of the time, objects around us are in continuous motion (moving cars, people, leaves, etc.), whereas abrupt position changes of real-world objects are infrequent. However, abrupt changes of retinal positions are frequent because saccades occur 3-5 times per second (Rayner, 1978). Therefore, previous research may have focused on abrupt displacements. The purpose of the present study was to investigate how continuous displacement of spatial and retinal position affects VSTM. Continuous displacement of a memory image may be induced by changing the position of the image at a high frequency (typically the refresh rate of the monitor) in small steps. Continuous displacement of the eyes involves smooth pursuit eye movements (SPEM). SPEM keep an object in the fovea by moving the eye at approximately the same velocity as the target (overview in Ilg, 1997). For instance, we may stabilize our fovea on the face of an athlete in a 100 m race. Typically the eye velocity is slightly lower than the target velocity, such that small catch-up saccades are occasionally necessary to bring the target back into the fovea. In contrast to saccades, SPEMs are continuous, may be sustained for variable durations (on the order of seconds or minutes), and cannot be voluntarily produced (Becker & Fuchs, 1985). That is, SPEMs require a moving target object.

Most studies on SPEM have focused on the perception of elementary features such as position (e.g., Honda, 1990; Kerzel, 2000), velocity (e.g., Brenner & van den Berg, 1994), or

contrast (e.g., Flipse, van der Wildt, Rodenburg, Keemink, & Knol, 1988) during smooth pursuit. So far, very little is known about information processing during SPEM. Note that such an investigation would be impossible for saccades, because the duration of a saccade is too short, and visual input is suppressed during a saccade. One study on SPEM indicated that attention is closely tied to the pursuit target, such that perceptual discrimination of letter stimuli that were not part of the pursuit target but presented in close vicinity was impaired (Khurana & Kowler, 1987). At the same time, it is known that smooth pursuit is more accurate when attention is divided between smooth pursuit and a second task (Kathmann, Hochrein, & Uwer, 1999). This suggests that SPEM control operates (best) in an automatic mode. Thus, there is some evidence that perceptual processing suffers during SPEM and that attention plays a role in the control of SPEM (overview in Krauzlis & Stone, 1999), but it is not known whether SPEM will impair cognitive tasks, in particular because SPEMs are partially involuntary, automatic movements.

There are at least three ways in which SPEM could impair VSTM: First, VSTM and eye movement tasks may interfere because of dual task demands. It has been shown that the performance in one task suffers if a different task has to be performed at the same time (e.g., Pashler, 1994). One suggestion was that central resources are limited (Kahneman, 1973) or that the different tasks have to pass a central bottleneck (Pashler, 1994), such that doing two things at a time will impair performance compared to a single task condition. The important point here is that it is a central capacity limitation. For instance, it was shown that dual task interference persists even when the two tasks involve different stimulus and response modalities (Pashler, 1990). Thus, the interference has to arise at a central stage and is independent of sensory processes. The nature of the central "bottleneck" is under debate (Levy & Pashler, 2001; Meyer & Kieras, 1999), however, it is not necessary for the present paper to specify this process in any detail. Second, visuo-spatial attention may be tied to the pursuit target such that processing of peripheral targets is impaired (Khurana & Kowler, 1987). The difference between the first and second alternative is that the first refers to a central resource, which is indifferent to where in space objects are presented. In contrast, narrowing of visuo-spatial attention is linked to particular locations in space. That is, the distribution of attention is such that there is a "lack of attention" in the periphery. Third, it may be that retinal or spatial position is coded in VSTM such that changes in one of these reference frames make encoding or retrieval of information in VSTM more difficult. This would be the case if representations in VSTM were in a retinotopic or spatiotopic format. Finally, it cannot be excluded that VSTM is completely dysfunctional during SPEM because there are no previous studies that looked at this issue.

In Experiment 1, we investigate whether VSTM for the position of peripheral targets is impaired during SPEM. In Experiment 2, we examine whether the performance decrement during SPEM may also be observed for items presented in the fovea. Experiment 3 asks whether retinal motion induced by eye movements differs from retinal motion induced by object motion. In Experiment 4, visual short-term memory during SPEM is compared to sensory memory by manipulating the retention interval. Experiment 5 looks at memory for color during SPEM. Finally, Experiment 6 manipulates SPEM velocity.

Experiment 1a: Memory for Location

In Experiment 1, we tested whether VSTM for position would suffer when the items-to-be-memorized were presented during SPEM. In one condition, the memory image was stationary while the eye moved smoothly. That is, the spatial positions of the items-to-be-memorized did not change while the retinal positions of the items changed continuously because the eyes followed a moving target across the screen (see Figure 1). In another condition, the memory image moved with the same velocity as the pursuit target. In this condition, the spatial position of the memory image changed, but remained stable on the retina (i.e., no retinal motion). If the spatial and retinal position of items was stored in VSTM

and was used to retrieve an item's position from VSTM, a drop in performance would be expected in both conditions.

However, VSTM performance in conditions involving SPEM may not only be governed by spatial or retinal stability. It may be that the execution of SPEM binds resources: First, it may be that processing of the peripheral targets and the execution of SPEM have to pass through the same central bottleneck. Second, it may be that visuo-spatial attention is tied to the target such that processing of peripheral targets is impaired. In both cases, the execution of SPEM would reduce performance, but this reduction would be unrelated to position changes per se. The purpose of Experiment 1a was to establish whether such differences exist, while Experiments 2 and 3 provide more direct tests between these hypotheses.

Further, Experiment 1 varied the stability of relative position information. Similar to Jiang and Olson (2000), we either presented a probe image with the same number of items as in the memory image or only a single item. This manipulation may reveal whether VSTM during SPEM follows the same principles as VSTM during fixation (Jiang et al., 2000) and across saccades (Carlson-Radvansky, 1999; Carlson-Radvansky & Irwin, 1995). In both cases, it was demonstrated that relational information (i.e., the relative position of objects) was important.

Methods

Participants. In all experiments reported in this study, students at the Justus-Liebig-University Giessen participated for pay. Their ages ranged from 19 to 43 years. All had normal or corrected-to-normal visual acuity. The number of participants after exclusion of unusable data sets (see below) was fixed at twelve in all experiments with the exception of Experiment 1d (11 participants). The two authors participated in all Experiments, the remaining participants were naïve. The pattern of DK and NZ's performance was not significantly different from the pattern of naïve observers. Some of the naïve observers participated in more than one experiment, but none of them were aware of the experimental design or hypothesis. Using experienced subjects was preferable because untrained subjects have great difficulty in following a target with their eyes while simultaneously attending to other objects.

In Experiments 1b, 1c, and 3 data from one observer had to be excluded because of chance performance in the detection task. In Experiment 1c, one observer had to be excluded because of poor smooth pursuit eye movements. In Experiment 1d, three observers had to be excluded because of poor smooth pursuit eye movements.

Materials and procedure. The stimuli were presented on a 21 inch CRT display with a refresh rate of 100 Hz and a resolution of 1280 (H) x 1024 (V) pixels. Observers' head position was stabilized with a chin rest at 47 cm from the screen. Eye movements were recorded with a head-mounted, video-based eye tracker (EyeLink II, SR-Research, Osgoode, Ontario, Canada).

On each trial, two images that were separated by a blank interval were presented. The memory image (first image) comprised 3, 6, or 12 squares (memory set size) that were randomly positioned in the stimulus matrix. The probe image (second image) comprised a corresponding number of squares or only a single square. In the probe image, the critical square was cued by a 1.7 x 1.7 deg white outline box. The squares subtended 1.2 x 1.2 deg and appeared in an invisible 10 columns x 12 rows cell matrix that subtended 17° x 20.4° of visual angle. The size of each cell in the matrix was 1.7 x 1.7 deg. The central two rows were always empty to allow for smooth pursuit eye movements through the image. The position of each probe inside one of the cells was somewhat jittered (0.25 deg to the left, to the right, upwards, downwards). The stimuli appeared on a uniform gray background of 32 cd/m². To avoid afterimages, random gray values between black and white were assigned to each pixel in the square (see Figure 2A). Thus, the mean luminance of the squares was approximately

equal to the background, but the spatial frequency content was different. Within a trial, all squares were equal, but the gray values were randomly reassigned between trials.

In the single probe condition, only one square was presented in the probe image. In the all probes condition, the same number of squares was presented in the probe image as in the memory image. The critical probe item in the probe image was cued and appeared either in the same position as in the memory image, or was randomly relocated in the stimulus matrix.

Initially, the black, 0.4 x 0.4 deg fixation cross was presented in the screen center. When observers were ready to begin a trial, they pressed a designated button and the EyeLink II system performed a drift correction to correct for shifts of the head-mounted tracking system. When the drift correction was successful, the fixation cross turned red. In the stationary eye / stationary image condition, the fixation cross stayed at the screen center and observers were instructed to keep fixation on the cross. After the key press, 1200 ms elapsed until the memory image appeared. The memory image was shown for 400 ms, and after a retention interval of 900 ms, the probe image was shown. Observers were instructed to indicate whether the critical probe had changed location. With a stationary image, this judgment could be based on the spatial position of the probe. With a moving image, the judgment could be based on its retinal location.

In conditions with an eye movement, the target jumped 8 deg to the left or right after the initial key press. It stayed in the eccentric position for 700 ms before it started to move. This was sufficient time for observers to refixate the cross at the eccentric position. Then, the cross moved at a velocity of 11.3 deg/s toward the screen center. Observers were instructed to pursue the cross with their eyes. Five hundred milliseconds after motion onset, the memory image appeared and was shown for 400 ms. After offset of the memory image, the cross continued to move for another 500 ms (i.e., during the retention interval). Thus, the trajectory of the fixation cross was symmetrical around the screen center. After a blank interval of 400 ms, fixation cross and probe image appeared in the central position and observers were instructed to refixate the cross. The difference between the stationary and moving image condition was the following: In the moving eye / stationary image condition, the memory and probe images were shown at the central position while the fixation cross moved across the screen. This induced motion of the memory image on the retina. Observers were instructed to judge the spatial position of the critical probe. In the moving eye / moving image condition, the memory image moved at the same velocity as the fixation cross. The relation between fixation cross and image was the same as in the stationary condition. Thus, there was no motion of the memory image on the retina. Observers were instructed to judge whether the critical probe had changed location with respect to the fovea (i.e., the fixation cross). The probe image was presented until a "same" or "different" judgment was given by mouse click. A beep marked an incorrect response. Observers were instructed to respond as accurately as possible.

In 20% of number of experimental trials involving eye movements, no memory or probe image was presented. These blank trials served as baseline trials for the evaluation of smooth pursuit performance. The values thus obtained were compared to the average smooth pursuit gain under experimental conditions.

Design. The single probe and all probes condition were run on different days. The order of probe conditions was balanced across subjects. For each probe condition, the three movement conditions were blocked. The stationary condition, eye movement / stationary image and eye / image movement condition were run in small blocks of 42 trials each. In each block, the conditions resulting from the factorial combination of memory set size (3, 6 or 12 squares) and the presence of a change (yes, no) were randomly interleaved. Before each block, observers were informed about which condition was to be presented. Each eye / image movement condition was run once before the apparatus was recalibrated (i.e., after 126 experimental trials + 16 blank trials). The order of blocks varied according to a latin square

design. Each observer worked through three repetitions of each eye / image movement condition for 426 trials per probe condition and a total of 852 trials.

Results

We calculated several measures for each experimental condition: proportion correct, memory sensitivity, response bias, and smooth pursuit gain.

Proportion correct. Proportions correct were arcsine transformed [transformed proportion correct = 2*arcsine(sqrt(proportion correct))] before inferential statistical analysis (ANOVA, t-test). In the text and graphs, the untransformed means are presented to allow for better comparison across studies. Proportion correct in Experiment 1a-d is plotted in Figure 3. A three-way, repeated-measures ANOVA (probe condition x memory set size x movement condition) on arcsine-transformed proportion correct showed that performance decreased as memory set size increased (.85, .76, .64), $F(2, 22) = 138.34$, $MSE = 3.622E-02$, $p < .001$. The proportion of correct responses was higher when all squares were presented in the probe image (.80) compared to a single square probe image (.70), $F(1, 11) = 57.06$, $MSE = 6.975E-02$, $p < .001$. The main effect of movement condition, $F(2, 22) = 26.25$, $MSE = 3.722E-02$, $p < .001$, showed that proportion correct was highest with stationary image and eyes (.80), and dropped when either the eye (.72), or both eye and image moved (.72). The interaction between probe condition and memory set size, $F(2, 22) = 16.08$, $MSE = 1.763E-02$, $p < .001$, indicated that the performance drop with increasing memory set size was larger with the single probe condition than with the all probes condition. T-tests for each probe condition confirmed that the difference between fixation and SPEM conditions was significant ($ps < .001$), whereas there was no difference between SPEM conditions ($ps > .5$)

Sensitivity and response bias. In the signal detection analysis (Macmillan & Creelman, 1991), the data were collapsed across memory set size. As a measure of sensitivity $d' = z$(proportion Hit) – z(proportion false alarms) was calculated. Response bias was estimated as $c = -0.5*[z$(proportion Hit) + z(false Alarms)]. A positive response bias indicates a tendency to say "same" (i.e., "no change") more often than "different" (i.e., "yes"). Generally, the results of the signal detection analysis mirrored the results of the arcsine-transformed proportion correct.

A two-way, repeated-measures ANOVA (probe condition x movement condition) showed that sensitivity was higher with all squares present in the probe image (1.79) than with a single probe (1.07), $F(1, 11) = 18.31$, $MSE = 0.161$, $p < .001$. Sensitivity was highest with stationary eyes and image (1.79), than with eye movement (1.27) and both eye and image movement (1.25), $F(2, 22) = 27.89$, $MSE = 27.89$, $p < .001$. A second ANOVA on response bias showed that that observers adopted a more conservative criterion for change detection (more "no change" responses) when all squares were shown in the probe image (0.18) than when only a single probe was present (-5.75E-02), $F(1, 11) = 23.34$, $MSE = 4.330E-02$, $p < .001$.

Eye Movements. The eye movement traces were visually inspected. Trials in which the observer blinked during memory image presentation, or was obviously not following the target were excluded from analysis. The rate of rejected trials did not exceed 3% in any of the Experiments. We calculated the average pursuit velocity during memory image presentation after saccades were removed from the eye movement trace. To this end, a rather sensitive acceleration criterion of 3250 deg/s² was used that also detected small jerky movements of the eye. The ratio of smooth pursuit velocity over target velocity is referred to as gain and is often used to characterize the quality of SPEM. A high gain indicates good smooth pursuit performance and is typically accompanied by few catch-up saccades. Mean pursuit gain for all experiments is shown in Table 2. The values in the experimental conditions were compared to each other and the gain in the corresponding interval of the blank trials. Further, we determined the proportion of trials in which a saccade occurred during the presentation of the memory image, and the average number, duration and size of those saccade. For this

analysis, the output of the EyeLink II eye movement parser was used. It classified episodes with acceleration larger than 4000 deg/s² and a velocity larger than 22 deg/s as saccades. These values are reported in Table 3. It is clear from the table that saccades smaller than 1 deg were rather frequent during smooth pursuit (30-50% of the trials). The quality of SPEM was higher (larger gain, fewer saccades) with a moving compared to a stationary background.

To examine the effects of catch-up saccades on the detection task, we reran the ANOVAs on only those trials without saccadic eye movements. In none of the experiments presented here did this alter the results, showing that saccades did not contribute substantially to our findings. This is not surprising because the saccades were small (less than 1 deg) and short (about 20 ms) relative to the presentation time of the memory image (400 ms). Previous research has demonstrated that saccadic suppression does not occur for small saccades (less than 2 deg, see Ross et al., 2001).

Discussion

The results show that VSTM is not dysfunctional during SPEM. Quite to the contrary, performance during SPEM was well above chance. We were able to replicate Jiang and Olson's (2000) finding that elimination of relative position information impairs VSTM for location. When all squares were present in the probe image, performance was better than with a single probe. Thus, VSTM during SPEM may follow the same principles as VSTM with fixation such that there is no reason to believe that VSTM and VSTM during SPEM rely on different stores or operations. Further, performance was best when spatial and retinal positions were stable. Proportion correct decreased by about 8% when either the retinal or the spatial position changed. This result is particularly striking because in the moving eye and moving image condition, the retinal input was about the same as in the stationary eye and stationary image condition: Smooth pursuit gain in this condition was close to unity (0.99) such that the memory image scarcely moved on the retina. Smooth pursuit gain was somewhat lower when the memory image was stationary (.91). The latter situation is similar to smooth pursuit across a stationary background which is known to reduce smooth pursuit gain (Collewijn & Tamminga, 1984).

Overall, the results of Experiment 1a are consistent with the ideas presented in the introduction: First, it may be that the egocentric and retinotopic object position is coded in VSTM, such that motion in one or the other reference frame impaired performance. Second, it may be that SPEM used visuo-spatial or central resources that were not available for the VSTM-task. Experiments 2 and 3 will test these two assumptions.

Before concluding that VSTM capacity is reduced during SPEM, alternative explanations need to be ruled out. In the experimental procedure, observers had to make a saccade back to the screen center before comparing memory and probe image. It may be that this saccade produced the performance decrement. To rule out this alternative explanation, we changed the velocity profile of the trajectory and the position of the probe image in three control experiments (see Figure 1).

Experiment 1b: Eccentric Probe Image Position

To avoid the saccade from the final, eccentric trajectory position to the screen center, the probe image was shown at the end of the trajectory. Further, the velocity of the trajectory was sinusoidal such that the increase from zero velocity and the decrease to zero velocity was smooth. This allows for a smooth transition from SPEM to fixation and thereby avoids saccades (e.g., Collewijn & Tamminga, 1984).

Method

Materials, procedure, and design. The materials and procedure were the same as in Experiment 1a with the following exceptions. The stationary condition and two variants of the eye / image movement condition were run. One variant of the moving eye / image condition was similar to Experiment 1a: After presentation of the memory image, and a retention interval of 500 ms, the fixation cross jumped back to the center of the display and the probe

image was presented around the screen center. In the second variant, the probe image was presented around the final position of the fixation cross. That is, the fixation cross moved from the starting position at 8 deg to the opposite side and stopped at 8 deg on the other side of the screen center. The fixation cross remained there until the response was given. To avoid saccades, onset and offset of the trajectory in the moving image / eye conditions was smoothed. The velocity profile was sinusoidal with an amplitude of 8 deg and a temporal frequency of 0.38 Hz (i.e., one half-cycle took 1300 ms). Only the condition with the critical square in the probe image was run (single probe condition).

The stationary condition, and the two eye / image movement conditions were run in small blocks of 28 trials each. In each block, the conditions resulting from the factorial combination of memory set size (3 or 6 squares) and the presence of a change (yes, no) were randomly interleaved. Each eye / image movement condition was run once before the apparatus was recalibrated (i.e., after 84 experimental trials + 12 blank trials). Each observer worked through three repetitions of each eye / image movement condition for a total of 288 trials.

Results

Data treatment was as in Experiment 1a. Mean proportion correct is shown in Figure 3 and the eye movement data is described in Tables 2 and 3.

Proportion correct. A two-way, repeated-measures ANOVA (memory set size x movement condition) confirmed that performance decreased with increasing set size (.76, .70), $F(1, 11) = 16.79$, MSE = 2.651E-02, $p < .005$. The proportion correct was higher in the stationary condition (.81) than in the moving image / eye condition with probes at the center (.68) and in the moving image / eye condition with probes at the end of the trajectory (.69), $F(2, 22) = 16.82$, MSE = 4.509E-02, $p < .001$. The interaction was not significant ($p > .7$). T-tests confirmed that the difference between fixation and SPEM conditions was significant ($ps < .005$), whereas there was no difference between fixation conditions ($p = .603$)

Sensitivity and response bias. A one-way, repeated measures ANOVA showed that sensitivity was higher in the stationary condition (1.93) than in the moving image / eye condition with probes in the center (.95) and at the end of the trajectory (1.1), $F(2, 22) = 20.19$, MSE = 0.167, $p < .001$. A second ANOVA on response bias did not reveal a significant effect ($p > .609$). Mean response bias was -5.47E-02.

Discussion

Removing the large "back" saccade from the experimental protocol did not change the results. This makes it unlikely that processes related to saccade control or execution interfered with memory performance in the smooth pursuit conditions of Experiment 1a.

Experiment 1c: Moving Probe Image

Another alternative explanation for the results of Experiment 1a would be that the recall context was the same with stationary eyes while it was different in the smooth pursuit conditions: The memory image was shown during SPEM, while the probe image was presented during fixation. In contrast, both memory and probe image were shown during fixation in the stationary condition. The performance decrement in the SPEM conditions may therefore result from the mismatch of cues present at encoding and retrieval. To test this account, the probe image was presented during smooth pursuit. That is, observers pursued the target on its way from one side of the screen to the other and during this initial part of the trajectory, the memory image was shown. Then, the pursuit target reversed direction and moved back to the starting position. During this "return" part of the trajectory, the probe image was presented. The presentation time of the probe image matched the presentation time of the memory image (0.4 s) and was the same across experimental conditions.

Method

Materials, procedure, and design. The materials and procedure were the same as in Experiment 1a with the following exceptions. The fixation condition and two eye / image

movement conditions were run. In all conditions, the retention interval was increased from 0.9 to 1 s and the probe image was presented for 400 ms only. The same smoothed trajectory as in Experiment 1b was used. In one eye / image movement condition, the probe image appeared while the fixation cross remained at the eccentric position. In the other eye / image movement condition, the probe image was presented during smooth pursuit back to the initial starting position. To this end, the same trajectory was presented as in the initial movement of the fixation cross, but the direction was changed. The memory and the probe images were presented from 200 ms before the center of the image passed the center of the screen until 200 ms after it had passed the center. Only the condition with the critical square in the probe image was run (single probe condition).

The stationary condition, and the two eye / image movement conditions were run in small blocks of 28 trials each. In each block the conditions resulting from the factorial combination of memory set size (3 or 6 squares) and the presence of a change (yes, no) were randomly interleaved. Each eye / image movement condition was run once before the apparatus was recalibrated (i.e., after 84 experimental trials + 12 blank trials). Each observer worked through three repetitions of each eye / image movement condition for a total of 288 trials.

Results

Data treatment was as in Experiment 1a. Mean proportion correct is shown in Figure 3 and the eye movement data is described in Tables 2 and 3.

Proportion correct. A two-way, repeated-measures ANOVA (memory set size x movement condition) showed that performance decreased with increasing memory set size (.82, .74), $F(1, 11) = 45.50$, $\underline{MSE} = 1.857E\text{-}02$, $p < .001$. The proportion of correct responses was higher in the stationary condition (.83) than in the moving eye / image condition with static probe image (.75) and moving probe image (.74), $F(2, 22) = 7.58$, $\underline{MSE} = 5.688E\text{-}02$, $p < .005$. The interaction was far from significant ($p > .7$). T-tests confirmed that the difference between fixation and SPEM conditions was significant ($ps < .025$), whereas there was no difference between fixation conditions ($p = .664$)

Sensitivity and response bias. A one-way, repeated-measures ANOVA showed that memory sensitivity was higher in the fixation condition (2.13) than in the eye / image movement condition with a static probe (1.47) and dynamic probe (1.36), $F(2, 22) = 8.44$, $\underline{MSE} = 0.245$, $p < .005$. The ANOVA on response bias did not show a significant effect ($p > .2$). Mean response bias was 0.69E-02.

Discussion

The results obtained mirror those in Experiment 1a and 1b. Therefore, differences in the match between encoding and recall contexts may not explain the difference between smooth pursuit and fixation conditions.

Experiment 1d: Flashed Memory Image

Even if the gain of the smooth pursuit eye movements is high, the variability in the eye velocity will cause the retinal image to slightly move on the retina. Because some jitter of the eye position is also present during fixation, one may argue that the difference in retinal velocity will not be substantial. However, to further rule out the possibility that the higher retinal velocity with SPEM caused the performance drop, we briefly flashed the memory image either during pursuit or during fixation. The memory image was presented for one refresh cycle which will yield a presentation time of less than 10 ms. Thus, the image was effectively stabilized on the retina because the eye could not move a substantial distance during this time.

Method

Materials, procedure, and design. The materials and procedure were the same as in Experiment 1a with the following exceptions. The fixation condition and one eye movement condition were run. The trajectory length (1.4 s) was as in Experiment 1a, but the memory

image was presented for one refresh cycle only. The checkered stimuli used in Experiment 1 were not visible with this presentation duration. Therefore, we used dark gray squares of 2 cd/m².

The moving and stationary eye conditions were run in small blocks of 30 trials each. In each block the conditions resulting from the factorial combination of memory set size (3, 6, or 12 squares) and the presence of a change (yes, no) were randomly interleaved. Each eye movement condition was run once before the apparatus was recalibrated (i.e., after 60 experimental trials + 12 blank trials). Each observer worked through two repetitions of each eye movement condition for a total of 264 trials.

Results

Data treatment was as in Experiment 1a. The gain was calculated for the interval starting 50 ms before until 50 ms after the flashed image. Trials in which a saccade occurred during presentation of the memory image were excluded from the analysis (1.4 %). Mean proportion correct is shown in Figure 3 and the eye movement data is described in Table 2.

Proportion correct. A two-way, repeated-measures ANOVA (memory set size x movement condition) showed that performance decreased with increasing memory set size (.91, .81, .70), $F(2, 20) = 99.39$, $\underline{MSE} = 1.988E\text{-}02$, $\underline{p} < .001$. The proportion of correct responses was higher in the stationary condition (.84) than in the moving eye condition (.76), $F(1, 10) = 15.70$, $\underline{MSE} = 5.224E\text{-}02$, $\underline{p} < .003$. The interaction was far from significant ($\underline{p} > .3$).

Sensitivity and response bias. Memory sensitivity was significantly higher in the stationary condition (2.17) than in the moving eye condition (1.45), $\underline{t}(10) = 4.30$, $\underline{p} < .002$. The ANOVA on response bias did not show a significant effect ($\underline{p} > .1$). Mean response bias was 0.21.

Discussion

The results obtained mirror those in Experiment 1a-c. Therefore, differences in the retinal velocity of the memory image between fixation and pursuit may not explain the performance drop between the two conditions.

Experiment 2: Miniature Image in the Fovea

Experiment 2 was designed to test the different accounts of the performance drop in the SPEM conditions in Experiment 1. To this end, miniature memory and probe images were presented that were fully contained in the pursuit target (i.e., in the fovea). Only the stationary eye / image condition and the moving eye / image condition were run. If SPEM entailed focusing of attention on the pursuit target that impaired processing of the peripheral image, then this performance drop should be eliminated with foveal presentation of the memory image. As outlined in the introduction, there are reasons to believe that visuo-spatial attention during SPEM is tied to the target. If, on the other hand, the change in the spatial position caused the performance decrement in Experiment 1, the difference between SPEM and fixation conditions should persist with the miniature image. Similarly, if central performance limitations were responsible for the performance drop with SPEM, the difference between SPEM and fixation should persist.

Method

Materials, procedure, and design. All aspects of the method were identical to Experiment 1a with the following exceptions. A black 1 x 1 deg square with a 0.4 x 0.4 deg, dark gray fixation cross inside served as fixation target (see Figure 2B). Single white pixels were used as image elements. The pixels were presented on a 10 x 10 grid (0.75 x 0.75 deg) centered on the square. Each cell consisted of one target pixel and 0.5 pixel padding such that the minimum separation between two target pixels was 1 pixel. Only the condition with all elements in the probe image was run. The critical probe item in the probe image was not cued in this experiment. In one condition, the eyes and the image moved (i.e., the observer was pursuing the miniature image), or both the eyes and the image were stationary.

The stationary image and moving image conditions were run in small blocks of 60 experimental trials (+ 12 blank trials, when applicable) each. In each block the conditions resulting from the factorial combination of memory set size (3, 6, or 12 squares) and the presence of a change (yes, no) were randomly interleaved. The order of blocks was balanced across observers. Each observer worked through two repetitions of each movement condition for a total of 264 trials.

Results

Data treatment was as in Experiment 1a. Mean proportion correct is shown in Figure 4 and the eye movement data is described in Tables 2 and 3.

Proportion correct. A two-way, repeated-measures ANOVA (memory set size x movement condition) showed that the proportion of correct responses decreased with increasing set size (.95, .85, .70), $F(2, 22) = 77.10$, MSE = 4.384E-02, $p < .001$. There was no significant difference between stationary eye / image condition (.85) and the moving eye / image condition (.82), $F(1, 11) = 2.01$, MSE = 3.603E-02, $p = .184$. The interaction was far from significant ($p > .5$).

Sensitivity and response bias. Sensitivity did not differ significantly between the stationary eye / image condition (2.10) and the moving eye / moving image condition (1.94), $t(11) = 1.40$, $p = .190$. A second one-way ANOVA on response bias showed a marginally significant difference, $F(1, 11) = 4.86$, MSE = 1.611E-02, $p = .05$. Observers adopted a slightly stricter criterion for reporting a change in the eye / image movement condition (0.24) than in the stationary condition (0.13).

Discussion

With miniature images on the pursuit target, the highly reliable performance drop between fixation and SPEM conditions from Experiment 1 disappeared. This favors an account in terms of attentional focusing: During SPEM, attention may "zoom in" on the pursuit target such that processing of the peripheral image in Experiment 1 was impaired. In contrast, the foveal image in Experiment 2 was contained in the attentional focus such that SPEM had no detrimental effects on VSTM. With respect to the remaining mechanisms that may impair VSTM during SPEM, the following answer may be given: Because the changes in spatial location in the present experiment were the same in the moving eye / moving image condition in Experiment 1, spatial position does not appear to play a major role in VSTM performance. If spatial location was important for the encoding and retrieval of position information in VSTM, performance should have dropped with SPEM and a miniature image in the fovea. This was not the case, at least not when motion was restricted to only one reference frame (spatial position). Similarly, central performance limitations fail to explain why there was no difference between the SPEM and fixation condition.

Experiment 3: Retinal Motion with and without Eye Movements

On the basis of Experiment 2, one may arrive at the conclusion that changes in retinal or spatial position do not affect VSTM. This conclusion would be in line with the importance of relative position in VSTM. Indeed, Irwin (1991) found no detrimental effects of displacing the target arrays on VSTM. To see whether this conclusion was justified for continuous position changes, we compared two conditions that had equal retinal projections. Either the image was stationary and the eye moved through the image, or the eye was stationary and the image moved across the screen (and retina). If VSTM-performance was governed by relative position alone, the condition with a moving image and stationary eyes should be superior to the SPEM condition because it replicates the stationary eye condition from Experiment 1. If, however, spatial and retinal stability was important for VSTM, performance in the condition with stationary eyes should drop to the level of the SPEM condition. The reason is that motion of the image induces changes in both the retinal and spatial reference frames.

Method

Materials, procedure, and design. The materials and procedure were as in Experiment 1a with the following exceptions. The probe image contained all the squares present in the memory image. In one condition, the moving eye / stationary image condition from Experiment 1a was run. In the other condition, the probe image moved at a velocity of 11.3 deg/s while the eye was stationary. The trajectory of the moving probe image was the same as in the moving image / eye condition in Experiment 1a. That is, the probe image moved for 200 ms before it passed the screen center and continued to move for another 200 ms. The retention interval was 500 ms.

The stationary image / moving eye condition, and moving image / stationary eye condition were run in small blocks of 60 trials each. In each block the conditions resulting from the factorial combination of memory set size (3, 6 or 12 squares) and the presence of a change (yes, no) were randomly interleaved. Each eye / image movement condition was run once before the apparatus was recalibrated (i.e., after 60 experimental trials + 12 blank trials). Each observer worked through two repetitions of each eye / image movement condition for a total of 264 trials.

Results

Data treatment was as in Experiment 1a. Mean proportion correct is shown in Figure 4 and the eye movement data is described in Tables 2 and 3.

Proportion correct. A two-way, repeated-measures ANOVA (memory set size x movement condition) showed that performance decreased with increasing memory set size (.87, .79, .64), $F(2, 22) = 125.05$, $\underline{MSE} = 1.591E-02$, $\underline{p} < .001$. The proportion of correct responses was not significantly different with stationary eyes and moving image (.75) than with stationary eyes and moving image (.78), $F(1, 11) = 1.51$, $\underline{MSE} = 7.536E-02$, $\underline{p} = .245$. The interaction was not significant, $F(2, 22) = 1.60$, $\underline{MSE} = 2.880E-02$, $\underline{p} = .225$.

Sensitivity and response bias. A t-test on sensitivity did not reveal any difference between the moving eye / stationary image (1.43) and the stationary eye / moving image (1.71) condition, $\underline{t}(11) = 1.63$, $\underline{p} = .13$. Similarly, there was no difference between the response bias in the stationary and moving memory image. Mean response bias was 0.10.

Discussion

The advantage of the fixation condition was lost when the memory image moved. Thus, retinal and spatial stability do contribute to VSTM. It is interesting to note that conditions with approximately equal retinal input do not always yield similar results: In Experiment 1, the condition with stationary eye / stationary image was retinally equivalent to the condition with moving eye / moving image. However, performance was superior when the eyes were stationary. In contrast, there was no superior performance with stationary eyes and moving image in the present experiment. This discrepancy may only be explained when the number of stable reference frames is considered: With stationary eyes and stationary image in Experiment 1, there was stability of spatial, and retinal position. In contrast, eye movements in Experiment 1 were associated with instability in one reference frame: retinal motion with a stationary image and spatial motion with a moving image. With stationary eyes and moving image in the present experiment, there was only stability of relative position, while spatial and retinal stability were lost. In contrast, the SPEM condition only eliminated stability of retinal position. Thus, loss of stability in more than one reference frame may explain why performance in the stationary eye condition was not superior in the present experiment.

Experiment 4: Sensory Memory

In Experiments 1-3, visual short-term memory during SPEM was explored. We observed that the focusing of visuo-spatial attention and positional stability contribute to VSTM performance. So far, the retention interval was about 1 s, which is well above the temporal limits of the sensory store. With very short retention intervals of less than 100 ms, the sensory store allows for a simple mechanism of change detection: A position change between memory and probe image is perceived as apparent motion between two image

elements. Previous studies on transsaccadic memory have shown that apparent motion is eliminated if a saccade intervenes between memory and probe image (Irwin, 1991). The question is whether the sensory store would be affected by intervening smooth pursuit eye movements. When both the image and the eyes move, the retinal stimulation is approximately the same as with a stationary image and no eye movement. However, it is unknown whether the perception of apparent motion would be suppressed in this condition. In contrast, when the eyes move and the memory image remains stationary, there is strong retinal motion. The question is whether apparent motion detection would still be possible in this case.

Method

Materials, procedure, and design. All aspects of the method were identical to Experiment 1a with the following exceptions (see Figure 5). The stationary eye / image condition and the two eye / image movement conditions were run. As in Experiment 1a, the trajectory was always symmetrical around the central position. However, the trajectory length varied with the retention interval. Four hundred milliseconds of pursuit preceded presentation of the memory image and also followed presentation of the probe image. The memory and probe images were presented for 400 ms. The pursuit target continued to move during the intervening retention interval of either 80 or 900 ms. In the moving image / moving eye condition, the memory image was presented while the target was in one half of the screen and after the target had passed the midpoint of the screen, the probe image was shown in the other half (always centered around the pursuit target). This was done because the short retention interval did not allow for probe presentation in the center position. Probe presentation in the center would have disrupted SPEM and would have produced a saccade. The downside of the manipulation was that memory and probe images were viewed from different angles in the moving eye / stationary image condition. For instance, if the target started on the left and moved to the right, elements on the left would be in foveal view during presentation of the memory image (the first part of the trajectory), but in the far periphery during presentation of the probe image (the second part of the trajectory).

The stationary condition and the two eye / image movement conditions were run in small blocks of 48 trials. In each block, the conditions resulting from the factorial combination of memory set size (3, 6 or 12 squares), retention interval (80 or 900 ms) and the presence of a change (yes, no) were randomly interleaved. Each eye / image movement condition was run once before the apparatus was recalibrated (i.e., after 164 experimental trials + 20 blank trials). The order of blocks varied according to a latin square design. Each observer worked through three repetitions of each eye / image movement condition on two different days for a total of 984 trials.

Results

Data treatment was as in Experiment 1a. Mean proportion correct is shown in Figure 5 and the eye movement data is described in Tables 2 and 3.

Proportion correct. A three-way, repeated-measures ANOVA (retention interval x memory set size x movement condition) showed that proportion correct decreased as memory set size increased (.96, .92, .80), $F(2, 22) = 126.33$, $\underline{MSE} = 4.507E\text{-}02$, $p < .001$. The proportion of correct responses was higher with the short (.94) than with the long retention interval (.84), $F(1, 11) = 158.22$, $\underline{MSE} = 3.761E\text{-}02$, $p < .001$. The main effect of movement condition, $F(2, 22) = 84.24$, $\underline{MSE} = 3.532E\text{-}02$, $p < .001$, showed that proportion correct was highest with stationary image and eyes (.94), and dropped when both the eye and image moved (.91). Performance was worst with stationary image and moving eyes (.82). The interaction between retention interval and memory set size, $F(2, 22) = 12.91$, $\underline{MSE} = 2.815E\text{-}02$, $p < .001$, indicated that the performance drop with increasing memory set size was larger with the long retention interval than with the short retention interval. The interaction between retention interval and movement condition, $F(2, 22) = 8.01$, $\underline{MSE} = 2.469E\text{-}02$, $p < .01$, showed that performance differed more strongly between the three movement conditions with

the long compared to the short retention interval. However, separate t-test confirmed that the difference between the three eye movement conditions was significant for both retention intervals (see Table 4). Finally, the three-way interaction between retention interval, memory set, and movement condition was significant, $F(4, 44) = 3.00$, $MSE = 2.366E-02$, $p < .05$. At first sight, this interaction appears to be due to a larger performance drop with the short retention interval and stationary image / moving eyes. However, two separate two-way ANOVAs (memory set size x movement condition) for each retention interval did not yield a significant two-way interaction [short retention: $F(4, 44) = 1.78$, $MSE = 3.174E-02$, $p = .149$; long retention: $F(4, 44) = 1.54$, $MSE = 2.674E-02$, $p = .206$].

      <u>Sensitivity and response bias.</u> A two-way, repeated-measures ANOVA (retention interval x movement condition) showed that sensitivity was higher with the short (3.37) than with the long retention interval (2.40), $F(1, 11) = 109.47$, $MSE = 0.156$, $p < .001$. Sensitivity was highest with stationary eyes and stationary image (3.52), dropped with moving eyes and moving image (3.03) and was worst with stationary image and moving eyes (2.11), $F(2, 22) = 155.63$, $MSE = 7.876E-02$, $p < .001$. The interaction between retention interval and movement condition was significant, $F(2, 22) = 7.95$, $MSE = 7.417E-02$, $p < .01$, indicating that the performance difference between the movement conditions was smaller with the short retention interval than with the long retention interval. However, Table 4 shows that all pair wise comparisons were significant.

      A second ANOVA on response bias showed that observers adopted a more conservative criterion for change detection (more "no change" responses) with the long retention interval (.38) than with the short retention interval (.14), $F(1, 11) = 17.15$, $MSE = 6.180E-02$, $p < .01$. Observers were more conservative with fixation (.29) and moving eye / moving image (.38) than with moving eye and stationary image (.11), $F(2, 22) = 12.51$, $MSE = 3.544E-02$, $p < .001$. The interaction of retention interval and movement condition, $F(2, 22) = 5.791$, $MSE = 5.813E-02$, $p < .01$, showed that the movement conditions differed only with the long retention interval (stationary eye / image: .47, stationary image / moving eye: 9.556E-02, moving image / eye: .57), but not with the short retention interval (.10, .18, .13).

Discussion

      We replicated the result of Experiment 1 that performance was best when the eye and the image were stationary. In contrast to Experiment 1, however, performance was worse with SPEM and a stationary image compared to SPEM and a moving image. The most likely explanation is that it was more difficult to retrieve the image from VSTM when memory image and probe image were viewed from different angles. As shown in Figure 5, the memory image was viewed while the pursuit target was in one half of the screen, while the probe image was viewed after the pursuit target had moved to the other part. In Experiment 1, the mean viewing angle was the same for probe and memory image.

      Further, memory performance was superior and the effect of memory set size was strongly reduced when the retention interval was shortened to 80 ms. This result indicates that apparent motion was available as a cue in all three conditions. It may be that the cue could not be used as efficiently in the moving eye / stationary image condition due to the retinal motion of the image. However, a larger performance drop with increasing memory set size could not be confirmed in this condition, even if the three-way interaction was (marginally) significant. It may be that the displacement of the image elements was detected by long-range motion processing, whereas the motion of the items induced by the eye movement was processed by short-range motion mechanism (Braddick, 1980; but see Cavanagh & Mather, 1989). Thus, the functional segregation of short- and long-range motion processes may have enabled the detection of abrupt element displacement during the retention interval. Another striking finding was that even with the small retention interval, performance was better in the condition with fixation than with SPEM. This difference was small, but reliable because of the small variability. Therefore, memory for spatial relations is impaired during SPEM even if

15

the situation is retinally equivalent (pursuit gain was 0.99), and if apparent motion may be used as a cue.

<div align="center">Experiment 5: Color</div>

So far, we have demonstrated that VSTM for object position is impaired during SPEM when the location of peripheral targets has to be remembered. Because Experiment 2 showed that this performance decrement was not observed when the stimuli were presented in the fovea, it was argued that attention was tied to the target during SPEM. This is plausible because during SPEM, the visual system has to monitor the positional error between fovea and target in order not to lag behind. That is, each time the difference between fovea and target becomes too large, a compensatory eye movement has to occur. Thus, position may be considered a response-relevant dimension that has to be attended in the region around the fovea. This would explain why SPEM produces a performance drop with peripheral objects, but not with foveal objects. However, there is evidence that attention may operate along more than a single dimension (Folk, Remington, & Wright, 1994; Muller, Reimann, & Krummenacher, 2003). Thus, the question is whether the performance drop during SPEM generalizes to other dimensions. Therefore, we probed observer's memory for color during SPEM.

Method

Materials, procedure, and design. All aspects of the method were identical to Experiment 1a with the following exceptions. The stationary condition and the two eye / image movement conditions were run. Instead of presenting gray squares to the observer, we used eight highly distinguishable, isoluminant color squares. Colors were chosen from a plane of equiluminance of the opponent color space (Krauskopf, Williams, & Heeley, 1982). Eight colors of equal saturation and equal angular distance on the cardinal directions and the main diagonals were selected. C.I.E. xy coordinates were (0.370, 0.312), (0.395, 0.387), (0.374, 0.458), (0.308, 0.444), (0.263, 0.364), (0.264, 0.296), (0.290, 0.266), and (0.330, 0.270). These colors were centered on a neutral white point with C.I.E. coordinates of (0.321, 0.336). All stimuli had a luminance of 32 cd/m². Memory and probe image contained eight items and there were no changes of relative position. In a particular display, repetition of colors (e.g., two instances of red) was allowed with the restriction that the same color could not repeat more than three times on each display and that at least one color was repeated at least once. Observers were instructed to indicate whether the critical probe had changed color in the probe image. Please note that observers so far had to decide whether the critical probe changed location. Memory set size was fixed to 8 items and the number of items was identical for memory and probe image.

The stationary condition and the two eye / image movement conditions were run in small blocks of 42 trials. Each eye / image movement condition was run once before the apparatus was recalibrated (i.e., after 126 experimental trials and 16 blank trials). In each block, the critical probe changed its color in half of the trials. The order of blocks varied according to a latin square design. Each observer worked through three repetitions of each eye / image movement condition for a total of 426 trials.

Results

Data treatment was as in Experiment 1a. The eye movement data is described in Tables 2 and 3.

Proportion correct. A one-way, repeated-measures ANOVA showed that there was no significant difference between the stationary condition (0.65 ± 5.355E-02), moving eye / stationary image condition (0.67 ± 4.304E-02) and moving eye / moving image condition (0.67 ± 6.025E-02), $F(2, 22) = 0.68$, $\underline{MSE} = 7.738E-03$, $\underline{p} = .517$.

Sensitivity and response bias. Memory sensitivity did not differ significantly between the stationary condition (0.84 ± 8.862E-02), the moving eye / stationary image (0.91 ± 7.188E-02) and the moving eye / moving image condition(0.91 ± 9.808E-02), $F(2, 22) = 0.43$,

MSE = 5.469E-02, p = .656. Another one-way ANOVA on response bias did not reveal any significant effects (p > .07). Mean response bias was -0.02.

Discussion

In strong contrast to Experiment 1, there was no difference between the three movement conditions. Performance did not differ between conditions in which the memory image moved with the eye, the memory image was stationary while the eye moved, or was stationary with no eye movement. Thus, performance decrements due to SPEM depend on which dimension is considered. If the position of peripheral objects has to be remembered, performance drops when SPEM are executed. Experiment 2 suggests that this drop results from the narrowing of attention to the target. However, focusing of attention is restricted to information about an object's position. The reason may be that position is important for the control of SPEM: The distance between the fovea and the target has to be monitored in order to allow for accurate pursuit. Therefore, it is difficult to attend to spatial relations or distances among peripheral objects. However, attention to color is not affected by SPEM because it is not response-relevant.

Further, overall performance was somewhat lower than in a comparable condition run by Jiang and Olson (2000): Proportion correct was about .67 in the present experiment, whereas it was about .9 in the previous study. This may be due to the usage of isoluminant color stimuli. In Jiang and Olson, the color stimuli were created by permutation of the three phosphors (red, green, blue) which typically results in changes of color and brightness. As brightness cues were absent in the present task, the task was harder. To check whether the additional cue would alter the results, we ran four observers with combined color and luminance stimuli and found performance to be better (about .77). However, the pattern of results was the same.

Experiment 6: Different Smooth Pursuit Velocities

Finally, we investigated whether the degree to which the image or the eye moved would affect memory performance. To this end, we ran the two eye movement conditions with a stationary and a moving image: Increasing target speed with a stationary image led to increases in retinal speed. Increasing target speed with a moving image did not alter retinal speed, but changed the rate of spatial displacement. The question is whether performance would decrease with increased speed or whether it would remain stable. If it remained stable, the process impairing VSTM for position during SPEM would be discrete in the sense that it only mattered that SPEM were executed and not how fast this occurred. In contrast, a decrease of performance with SPEM would suggest that the process impairing SPEM is affected by the SPEM-task demands. One may assume that increasing SPEM would increase the difficulty of the task. Note that any of the hypotheses outlined in the introduction are compatible with this idea: It may be that changing the retinal or spatial position of the target objects to a larger extent perturbs encoding or retrieval of spatial or retinal position to a larger extend. Similarly, it may be that a faster moving pursuit target requires more visuo-spatial attention around the fovea; and finally, it may be that central processing is more strongly challenged by faster target motion.

Method

Materials, procedure, and design. All aspects of the method were identical to Experiment 1a with the following exceptions. Only the conditions involving smooth pursuit eye movements were presented. The image was stationary or moved with the eye. Memory set size was fixed at 6 probes and the single probe condition was used. The fixation cross (and the memory image, when applicable) moved at 3.7, 11.3, or 22.6 deg/s. Because the temporal parameters were unchanged, the trajectory length increased with velocity.

The three velocities were randomly interleaved. The stationary image and moving image conditions were run in small blocks of 60 experimental and 12 blank trials. In each block, the critical probe changed position in half of the trials. The order of blocks was

balanced across participants. Each observer worked through two repetitions of each movement condition for a total of 288 trials.

Results

Data treatment was as in Experiment 1a. Mean proportion correct is shown in Figure 6 and the eye movement data is described in Tables 2 and 3.

Proportion correct. A two-way, repeated-measures ANOVA (velocity x movement condition) confirmed that proportion correct decreased as velocity increased (.72, .70, .65), $\underline{F}(2, 22) = 5.97$, $\underline{MSE} = 2.604E-02$, $\underline{p} < .01$. None of the other effects reached significance ($\underline{p}s > .3$).

Sensitivity and response bias. A two-way, repeated-measures ANOVA (velocity x movement condition) confirmed that sensitivity decreased with increasing velocity (1.29, 1.09, 0.86), $\underline{F}(2, 22) = 4.17$, $\underline{MSE} = 0.264$, $\underline{p} < .05$. No other effects reached significance ($\underline{p}s > .3$). Another ANOVA on response bias did not reveal any significant effects ($\underline{p}s > .06$). Mean response bias was 0.10.

Discussion

Performance decreased with increasing velocity. Thus, the process that impairs smooth pursuit performance is affected by the extent to which the target moves. Experiment 1-5 suggested that visuo-spatial attention and the stability of spatial references contribute to VSTM for position. Therefore, the present results suggest that increasing target speed puts stronger demands on visuo-spatial attention, and makes encoding or retrieval of spatial or retinal position codes more difficult. Again, it is surprising that the condition in which the image was stabilized on the retina (pursuit gain of .98 and higher) did not produce superior performance compared to the condition with moving eyes and stationary target: The retinal speed of the image's projection increased linearly with target velocity when the image was stationary on the screen. However, there was no interaction of target speed and eye movement condition such that the increasing retinal velocity did not impair VSTM any more than increasing the spatial velocity.

General Discussion

We investigated visual short-term memory (VSTM) during continuous eye and object motion. While there is a large body of studies on abrupt changes in eye (saccades) or object position, studies on continuous changes are missing. The main question we tried to answer was how VSTM would be affected by the concomitant execution of smooth pursuit eye movements (SPEM). Overall, we observed that VSTM capacity during SPEM was reduced in some conditions, but that the performance decrements were moderate. That is, observers were well able to encode and retrieve the position and color of objects during SPEM. When VSTM for object position was probed in Experiment 1, we found that the execution of SPEM produced performance decrements compared to a condition without eye and object motion. This was surprising because in one SPEM condition, the memory image moved with the target such that the retinal input was about the same as with stationary eyes. Experiment 2 showed that the performance decrement with SPEM was absent when the memory image was shown in the fovea. This suggests that attention is tied to the target during SPEM such that processing of peripheral targets is impaired. However, stability of spatial and retinal position is also important because when both spatial and retinal position changed, performance in a condition with stationary eyes dropped to the level of a condition with SPEM (Experiment 3). Experiment 4 examined ultra short-term (sensory) memory during SPEM. Sensory memory allows for the detection of position changes on the basis of apparent motion. Usage of this cue was possible in the fixation and the SPEM conditions. However, the differences between SPEM and fixation conditions persisted even with the small retention interval. Experiment 5 showed that the performance drop with SPEM does not hold for dimensions other than position. VSTM for color was unaffected by the execution of SPEM suggesting that the focusing of attention was restricted to position. Finally, we varied the velocity of smooth

pursuit and found that performance decreased with increasing velocity (Experiment 6). This suggests that increasing the difficulty of the eye movement task aversely affected VSTM.

In sum, the present study shows that VSTM during SPEM only differs in one aspect from VSTM during fixation: Memory for peripheral positions is impaired. Our experiments have demonstrated that the most likely cause for this impairment is a narrowing of the attentional focus to the pursuit target. Our argument was that focusing of attention around the fovea was necessary because of the task-demands during SPEM. Observers have to monitor differences between the target and the fovea and adjust parameters of the eye movement in order to accurately follow the target. Therefore, the current study provides evidence for the close coupling between action, attention, and memory. This is in line with some recent evidence suggesting a close connection between the requirements of an intended or ongoing action (Bekkering & Neggers, 2002) or perception (e.g., Ganel & Goodale, 2003).

One piece of evidence for such a close connection comes from a recent study using a conjunction search task (Bekkering & Neggers, 2002): Observers had to find a target object with a specific orientation and a specific color (e.g., a green rectangular block oriented at 45°) in a number of distractor items (green blocks at 135°, orange blocks at 45° or 135°). Observers were instructed to look at the target and the accuracy and latency of the first saccade was measured. The important manipulation was the manual task that accompanied the eye movement: Either observers were instructed to point to the target or they were instructed to grasp it. These two tasks differ with respect to the response-relevant dimensions. For pointing movements, only the object's position, but not its orientation is response-relevant. In contrast, both position and orientation are response-relevant for grasping movements because the wrist has to be rotated for successful grasping. Participants selected objects with a wrong orientation less frequently when asked to grasp the object compared to pointing to the object. Thus, processing of object orientation was more efficient when it was response-relevant. This finding suggests that attention was allocated preferentially to orientation when grasping movements were required. However, no performance drop was noted for color: Selection of objects with the wrong color occurred about as frequently with grasping as with pointing. Thus, task-specific requirements enhanced attention to the response-relevant dimension.

In contrast, the present study showed that attending to position during SPEM did not enhance performance along this dimension, but rather the opposite was the case: Attention was focused on the foveated pursuit target in the sense that attention was withdrawn from the periphery. In the fovea, the level of performance was about the same as without SPEM, whereas performance was impaired in the periphery. This result supports theories postulating that attention may operate along more than a single perceptual dimension (Folk et al., 1994; Muller et al., 2003). In particular, the present study suggests that attention may be impaired along a response-relevant dimension (i.e., position) while it is unimpaired along another (i.e., color).

Finally, VSTM during short-term memory may be compared to VSTM across saccades ("transsacadic memory"). Irwin (1991) conducted a series of experiments that are most relevant to the present study: First, he noted a marked performance drop of 20-30% correct responses between a condition in which the spatial and retinal position of the target array overlapped and a condition in which observers executed a saccade (spatial, but no retinal overlap). This comparison is similar to the present comparison between stationary eyes and stationary image vs. moving eye and stationary target. Compared to the performance difference in Irwin (1991), the difference in performance that we observed was rather small (on the order of 6-12% correct responses). Although such a comparison across studies is difficult, one may cautiously conclude that the impairment of VSTM for position is larger for saccades than for SPEM. Second, Irwin noted that there was no advantage of short retention intervals over long retention intervals for transsaccadic memory (retention intervals from 40-

5000 ms). In contrast, there was clear advantage of short over long intervals when SPEM intervened. This shows that the sensory store was intact even with strong retinal motion (i.e., the condition with moving eyes and stationary image). One may argue that the distance the eye traversed during the retention interval was smaller in the current (0.08 s * 11.3 deg/s = 0.9 deg) than in Irwin's study (3 deg). One way to test such an alternative explanation would be to increase SPEM-distance by increasing the target velocity. We opted not to perform such a test for two reasons. First, Irwin (1991) reported that a small displacement (0.8 deg) of the memory image during eye fixation eliminated the advantage of the short retention interval. This shows that the magnitude of the displacement does not play a major role. Second, we believe that velocity may affect the condition with retinal motion (i.e., moving eye and stationary image), however, it appears unlikely that this is the case for the condition with no retinal motion (i.e., moving eye and moving image). As Experiment 6 shows, effects of velocity are rather small, even with long retention intervals (decrease of 7% correct responses for an increase in velocity by a factor of about 6).

Finally, we observed in the present that the pursuit target was special in that VSTM for position did not suffer for images presented on the pursuit target. In studies on transsaccadic memory, participants are typically presented with a memory image and make a saccade from a central source to a designated saccade target. It was demonstrated, that neither the saccade source, nor the saccade target played a dominant role in VSTM for object position (Germeys, De Graef, Panis, Van Eccelpoel, & Verfaillie, 2004): Depending on the task demands, both the presence of the saccade source and the target could facilitate change detection in the memory image.

In sum, there are differences between VSTM across saccades and VSTM during SPEM. However, we believe that these differences may reflect different task demands and do not point to different underlying memory systems. Rather, the memory store is identical. The major reason for this assumption is that there is strong agreement across studies that relational information is stored in VSTM (cf. Experiment 1).

Acknowledgements

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Table 1. Absence (no) or presence (yes) of retinal motion as a function of eye and image movement. When physical image and eye move at the same velocity, there is no motion of the image's retinal projection. This situation is similar to the combination of stationary eyes and stationary image. Movement of either eye or image produces retinal motion.

	Moving Image	Stationary Image
Moving Eye	No	Yes
Stationary Eye	Yes	No

Table 2. Smooth pursuit gain (eye velocity divided by target velocity) for each experiment and experimental condition. Means and between-subject standard error are given in the format $\underline{M} \pm \underline{SE}*10^{-2}$. The pursuit gain in the experimental conditions was compared to pursuit gain in trials without a memory image (blank trials) by t-test. The results are indicated in the column "Pursuit Gain (Experimental Conditions)". The difference between experimental conditions was compared to zero by t-test.

	Pursuit Gain (Exp. Conditions)	Difference between Exp. Conditions	Pursuit Gain (Blank Trials)
Exp.1a (All Probes)			
Stationary Image	0.91 ± 1.98**	0.08 ± 1.52**	0.97 ± 1.28
Moving Image	0.99 ± 1.20**		
Exp. 1a (Single Probe)			
Stationary Image	0.93 ± 2.68*	0.06 ± 1.90**	0.97 ± 1.47
Moving Image	0.99 ± 1.46*		
Exp. 1b			
Central Probe	0.96 ± 1.20*	0.01 ± 0.51*	0.93 ± 1.92
Eccentric Probe	0.95 ± 1.04		
Exp. 1c			
Moving Probe	0.94 ± 1.56	0.00 ± 0.73	0.94 ± 1.34
Eccentric Probe	0.94 ± 1.46		
Exp. 1d Flashed Image	0.98 ± 1.13	---	0.98 ± 1.16
Exp. 2 Moving Image	1.00 ± 0.80	---	0.99 ± 0.83
Exp. 3 Stationary Image	0.94 ± 2.54*	---	0.97 ± 2.08
Exp. 4 Stationary Image	0.94 ± 2.13*	0.05 ± 1.24*	0.98 ± 1.38
Moving Image	0.99 ± 1.10*		
Exp. 5 Stationary Image	0.94 ± 2.59**	0.05 ± 1.58**	0.97 ± 1.88
Moving Image	0.99 ± 1.72**		
Exp. 6			
4 °/s Stationary Image	0.99 ± 2.24	0.02 ± 1.24	0.97 ± 2.57
Moving Image	0.97 ± 1.49		
11 °/s Stationary Image	0.98 ± 1.42	0.01 ± 0.86	0.99 ± 1.30
Moving Image	0.99 ± 1.35		
23 °/s Stationary Image	0.95 ± 1.14*	0.03 ±0.91**	0.97 ± 1.42
Moving Image	0.98 ± 1.40		

Note. Significant t-tests are marked by one ($p < .05$) or two ($p < .01$) asterisks.

Table 3. Mean proportion of trials in which a saccade occurred during presentation of the memory image. For trials in which a saccade occurred, the mean number of saccades, the mean saccade duration and the mean saccade amplitude were computed. Means and between-subject standard error are given in the format $\underline{M} \pm \underline{SE}*10^{-2}$. In the fixation condition, between 0 and 3 participants did not make any saccades at all.

	Proportion of Trials	Number of Saccades	Saccade Duration (ms)	Saccade Amplitude (deg)
Exp.1a (all probes)				
Fixation	0.06 ± 1.93	1.27 ± 11.65	22 ± 301	0.53 ± 8.20
Stationary Image	0.55 ± 5.80	1.10 ± 2.39	20 ± 80	0.92 ± 5.66
Moving Image	0.33 ± 4.53	1.13 ± 4.25	19 ± 125	0.76 ± 7.18
Exp. 1a (single probe)				
Fixation	0.07 ± 2.46	1.23 ± 11.07	20 ± 215	0.51 ± 10.25
Stationary Image	0.50 ± 6.06	1.12 ± 3.16	21 ± 98	0.94 ± 8.29
Moving Image	0.30 ± 4.53	1.13 ± 2.94	19 ± 109	0.66 ± 5.91
Exp.1b: Fixation	0.10 ± 3.25	1.09 ± 4.55	18 ± 107	0.45 ± 8.44
Central Probe	0.64 ± 5.14	1.17 ± 3.85	22 ± 110	1.04 ± 7.34
Eccentric Probe	0.60 ± 4.14	1.17 ± 3.14	23 ± 131	1.07 ± 8.32
Exp. 1c Fixation	0.06 ± 1.64	1.07 ± 4.02	17 ± 90	0.70 ± 21.41
Moving Probe	0.57 ± 5.33	1.17 ± 4.13	21 ± 135	0.92 ± 6.27
Eccentric Probe	0.66 ± 4.08	1.12 ± 2.65	20 ± 103	0.90 ± 6.55
Exp. 2 Fixation	0.08 ± 1.92	1.13 ± 4.82	16 ± 128	0.36 ± 3.84
Moving Image	0.34 ± 4.93	1.07 ± 2.42	16 ± 50	0.59 ± 2.32
Exp. 3 Fixation	0.10 ± 2.33	1.03 ± 1.33	17 ± 70	0.52 ± 6.83
Stationary Image	0.53 ± 6.61	1.09 ± 1.91	19 ± 102	0.82 ± 7.12
Exp. 4 Fixation	0.03 ± 0.85	1.13 ± 4.82	18 ± 194	0.41 ± 3.51
Stationary Image	0.48 ± 7.37	1.11 ± 2.00	20 ± 92	0.91 ± 10.01
Moving Image	0.27 ± 5.04	1.05 ± 1.29	17 ± 66	0.60 ± 4.97
Exp. 5 Fixation	0.05 ± 1.51	1.11 ± 4.66	17 ± 160	0.42 ± 7.61
Stationary Image	0.59 ± 7.25	1.08 ± 2.05	19 ± 62	0.86 ± 3.90
Moving Image	0.36 ± 5.28	1.07 ± 1.51	17 ± 48	0.70 ± 3.61
Exp. 6				
Stationary Image	0.47 ± 5.89	1.11 ± 1.79	21 ± 35	1.01 ± 4.01
Moving Image	0.33 ± 2.66	1.13 ± 4.44	20 ± 103	0.81 ± 5.12

Table 4. Pair wise comparisons (t-tests) of mean performance in the movement conditions of Experiment 4 as a function of retention interval. The left lower corners show the differences between movement conditions expressed as percentage correct. The t-tests, however, were run on arcsine-transformed proportion correct. The upper right corners show the differences expressed as d'.

	Stat. Eye / Stat. Image	Mov. Eye / Stat. Image	Mov. Eye / Mov. Image
Short Retention Interval (80 ms)			
Stat. Eye / Stat. Image	-	1.09***	0.35**
Mov. Eye / Stat. Image	6.63%***	-	0.74***
Mov. Eye / Mov. Image	1.49%*	5.14%***	-
Long Retention Interval (900 ms)			
Mov. Eye / Stat. Image	-	1.72***	0.62***
Mov. Eye / Stat. Image	16.81%***	-	1.10***
Mov. Eye / Mov. Image	5.99%***	10.82%***	-

Note: T-values with probabilities less than .0125, .01, .001 are indicated by one, two and three asterisks, respectively.
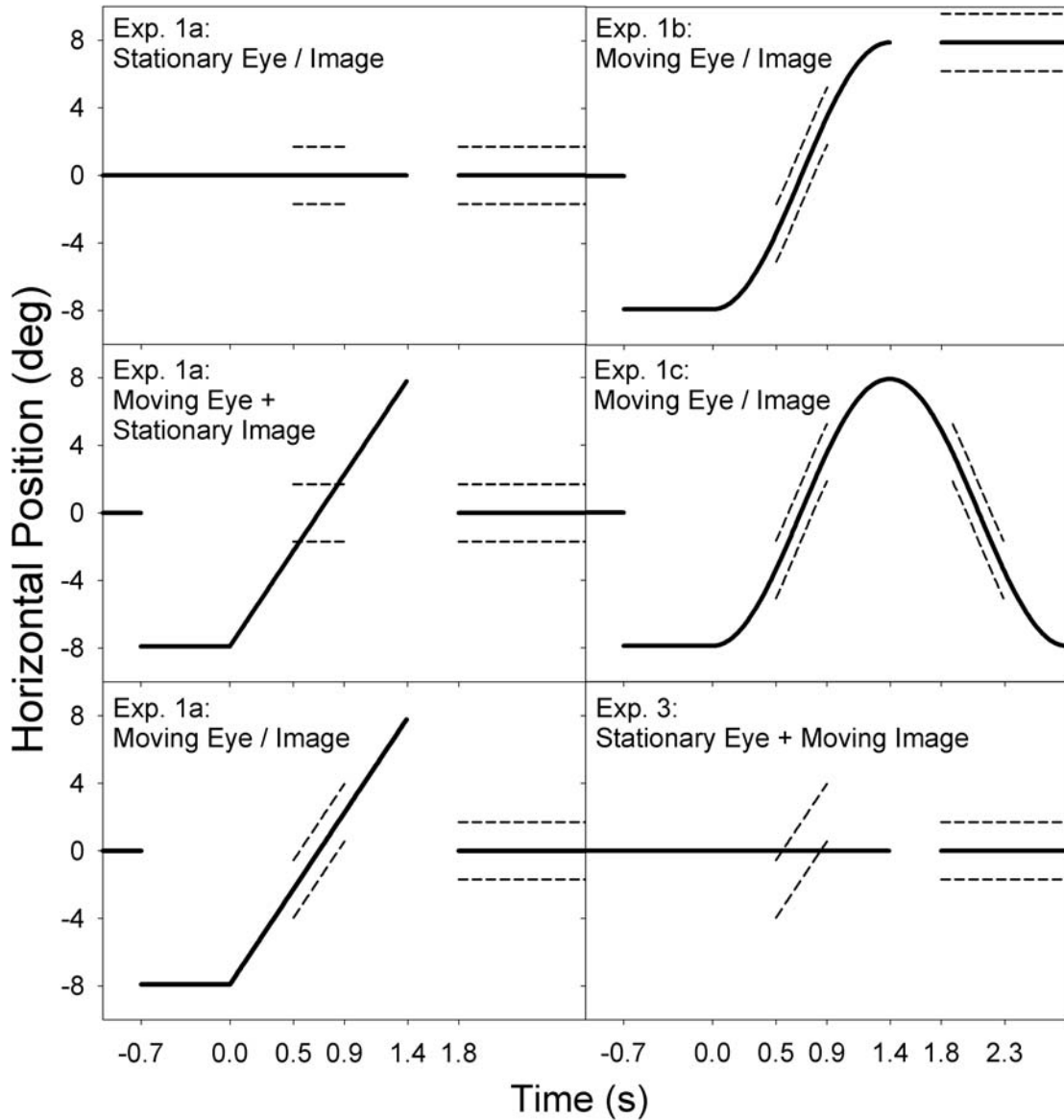
Figure 1. Space-time plots of eye and image movement in Experiments 1 and 3. The thick, solid line indicates the trajectory of the pursuit target (a fixation cross). The thin, dashed lines indicate the trajectories of the memory and probe images. The first set of dashed lines represents the memory image that contains the items-to-be-remembered. The second set of dashed lines represents the probe image that contains the critical probe item. Motion onset was chosen as zero time. The screen center was chosen as zero position and negative positions represent positions on the left. Thus, the target moved from left to right in the current plots.
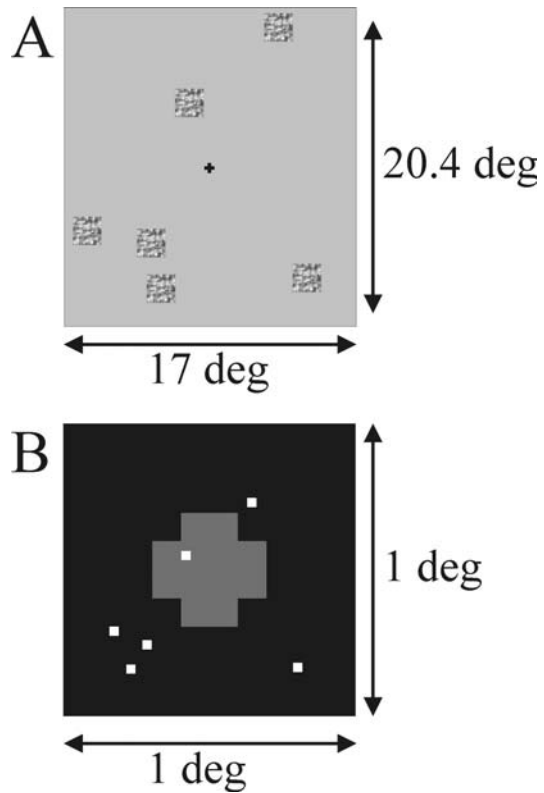
Figure 2. Schematic drawing of the stimuli. In most experiments, the items in probe and memory image were squares which consisted of pixels with random gray values (panel A). Unlike in the graph, the mean luminance of the squares matched the luminance of the background. The extent of the image was 17 x 20.4 deg. The central rows were always empty to allow for smooth pursuit through the image. In Experiment 2, the probe image consisted of single white pixels that were presented on the pursuit / fixation target (panel B).
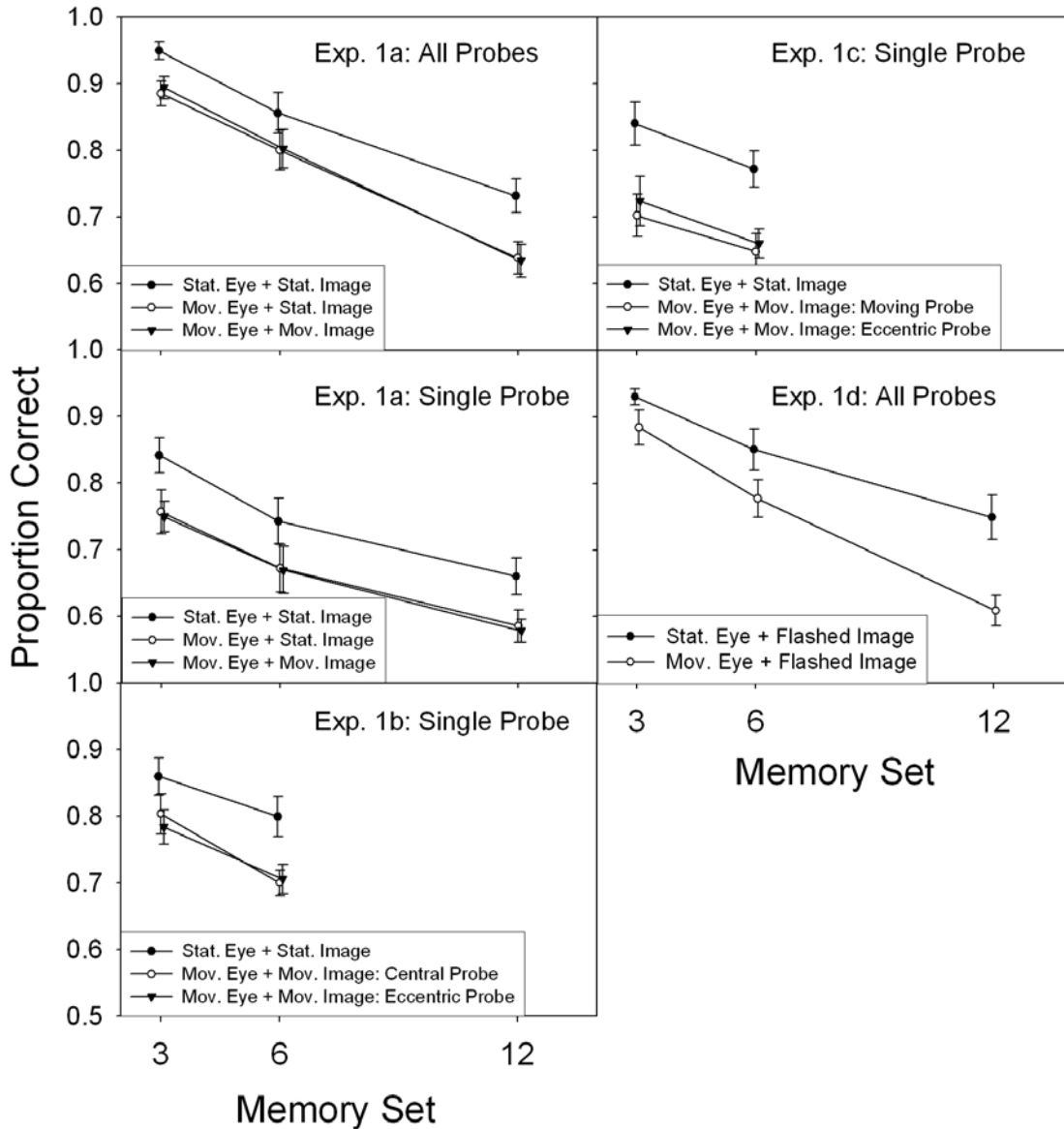
Figure 3. Results of Experiment 1. Mean proportion correct and the between-subject standard error are shown as a function of memory set and movement condition. In Experiment 1b, the probe image was shown in an eccentric position such that no saccade back to the center was necessary. In Experiment 1c, the probe image was shown during smooth pursuit. In Experiment 1d, the memory image was only briefly flashed.
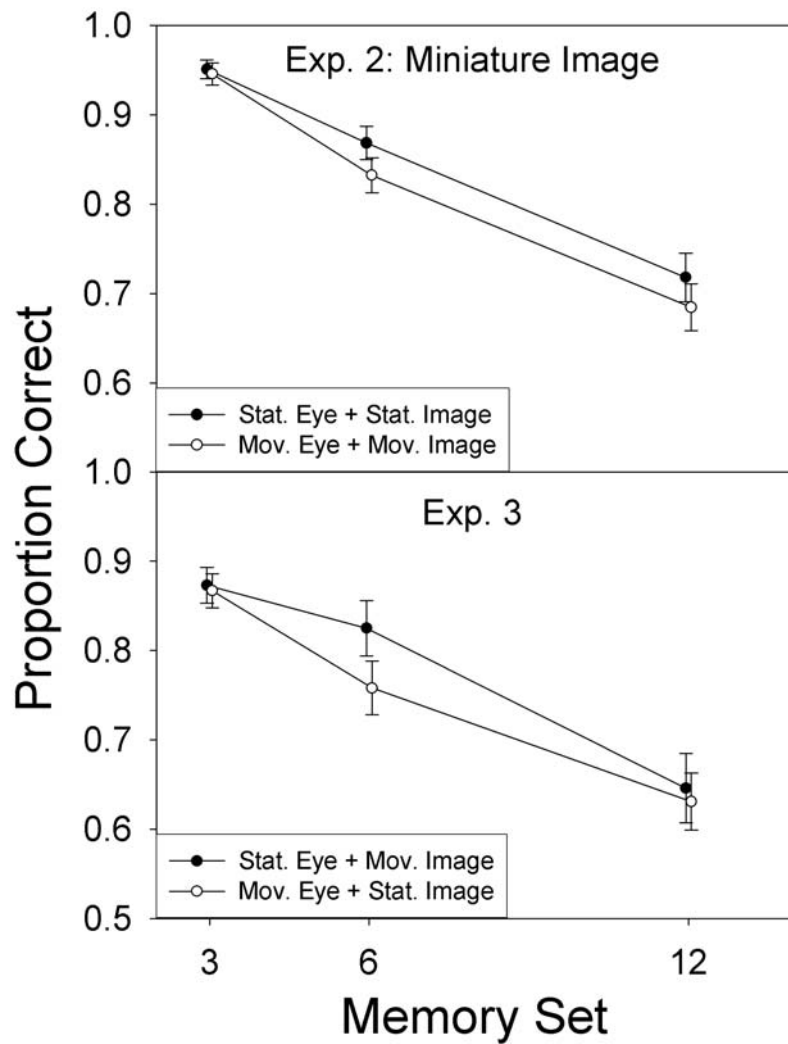
Figure 4. Results of Experiments 2 and 3. Mean proportion correct and the between-subject standard error are shown as a function of memory set and movement condition. In Experiment 2, the image was presented in the fovea. In Experiment 3, the image moved in the condition with stationary eyes.
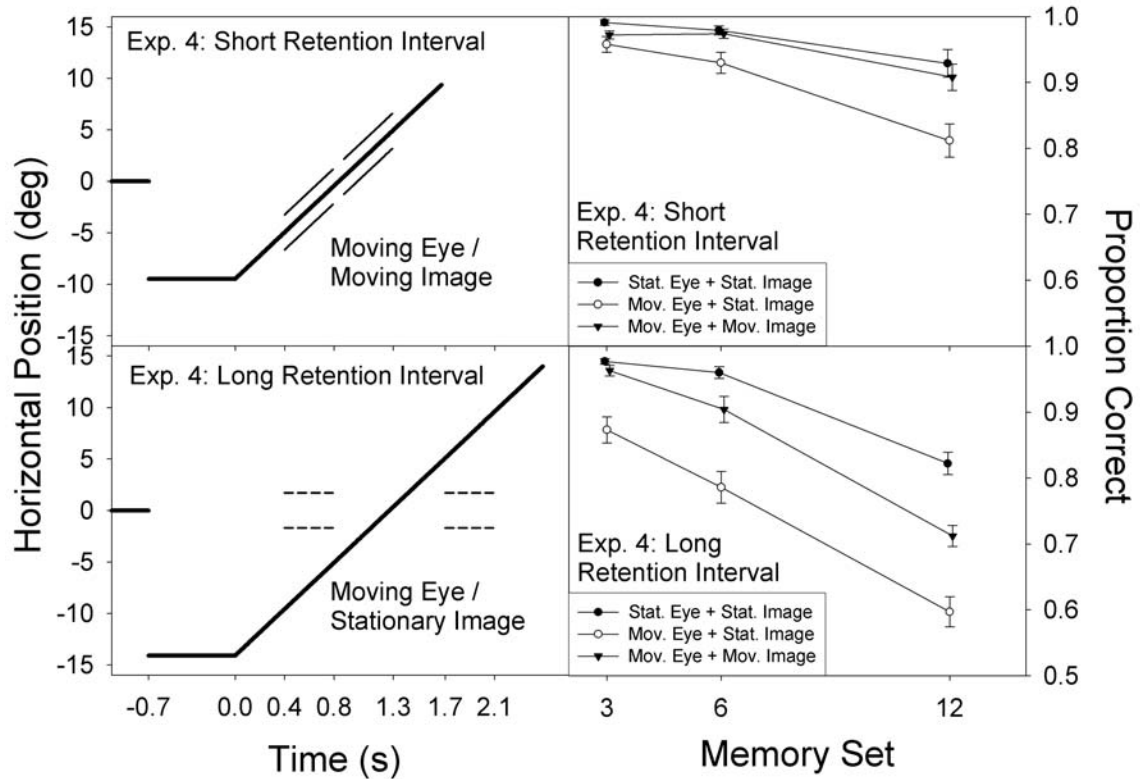
Figure 5. Space-time plots and results of Experiment 4. The left panels show the space-time plots for two sample conditions with short (top) and long (bottom) retention intervals. In contrast to Experiment 1, the mean gaze angle varied between memory and probe image when the eye moved and the image was stationary (left bottom panel). Mean proportion correct and the between-subject standard error are shown as a function of memory set, movement condition, and retention interval on the right. The right top panel shows data from the condition with short retention interval, the right bottom panel shows data from the condition with long retention interval.
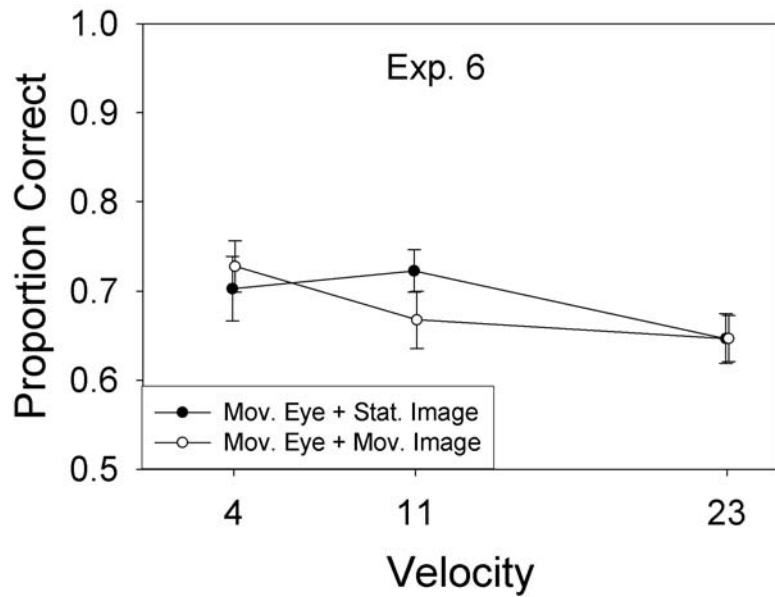
Figure 6. Results of Experiment 6. Mean proportion correct and the between-subject standard error are shown as a function of memory set and movement condition. The target moved at one of three different velocities.