

Visual Short-Term Memory During Smooth Pursuit Eye Movements

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Visual short-term memory (VSTM) was probed while observers performed smooth pursuit eye movements. Smooth pursuit keeps a moving object stabilized in the fovea. VSTM capacity for position was reduced during smooth pursuit compared with a condition with eye fixation. There was no difference between a condition in which the items were approximately stabilized on the retina because they moved with the pursuit target and a condition in which the items moved across the retina because they were stationary in space. The reduction of capacity for position was eliminated when miniature items were presented on the pursuit target. Similarly, VSTM capacity for color did not differ between smooth pursuit and fixation. The results suggest that visuospatial attention is tied to the target during smooth pursuit, which impairs VSTM for the position of peripheral objects. Sensory memory during smooth pursuit was only slightly impaired.

To ensure the stability of their perceptual world, humans need to integrate visual information across eye movements. Otherwise, vision would have to start anew with each saccade, and people would see a new scene 3–5 times per second (i.e., with each saccade). In principle, this integration could be achieved by using one of two visual stores that are also available during fixation (Phillips, 1974): First, visual information may be kept for about 100 ms in a short-lived, high-capacity store that is strongly related to sensory processes. Second, visual information may be kept for intervals on the order of seconds in a limited-capacity store that is related to cognitive processing. The latter store is often referred to as *visual short-term memory* (VSTM).

Most of the previous research in this area has focused on the question whether one of these two memory stores (sensory or short-term) is used to integrate information across saccadic eye movements. Saccadic eye movements bring the eyes into a new position within approximately 50 ms, and visual sensitivity is reduced during this time (see Ross, Morrone, Goldberg, & Burr, 2001, for an overview). In contrast, the present study focuses on visual integration across continuous displacement of the eye, smooth pursuit eye movements (*smooth pursuit*, for short). Smooth pursuit keeps an object in the fovea by moving the eye at approximately the same velocity as the target (see Table 1; for an overview, see Ilg, 1997). For instance, an observer may stabilize his or her 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, smooth pursuit is continuous, may be sustained for variable durations (on the order of seconds or minutes), and cannot be voluntarily produced (Becker & Fuchs, 1985). That is, smooth pursuit requires a moving target object. Because most of the research on visual integration across eye movements has focused on saccades, we review the literature on this topic first.

Transsaccadic Memory

Because the retinal position of objects in the world changes with each movement of the eye, visual integration across eye movements has to operate in viewer-centered (spatial) coordinates. If it operated in eye-centered (retinotopic) coordinates, the world would appear to move with each movement of the eye. It has been suggested that transsaccadic integration of visual information is accomplished by a limited-capacity store that may in fact be identical to VSTM: First, it was demonstrated that the high-capacity sensory store operates not in spatial but in retinotopic coordinates. Two patterns presented at the same spatial position and separated by a short time interval (<100 ms) may be perceived as a combined visual pattern if eye fixation is maintained. If a saccade is executed that brings the second pattern to a new retinal position after the blank interval, the perception of a combined pattern is eliminated (Irwin, Yantis, & Jonides, 1983). Similarly, a sine-wave grating may mask a subsequent grating if the two overlap in spatial and retinal coordinates. When a saccadic eye movement intervenes between successive presentations of the stimulus, masking is eliminated (Irwin, Zacks, & Brown, 1990). More recently, however, it was been demonstrated that transsaccadic integration does occur for motion (Melcher & Morrone, 2003): Thresholds for the detection of motion direction were lower when two consecutive motion pulses were presented with a brief temporal separation, even when a saccade placed the second stimulus in a different retinal position. In sum, it appears that for most

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Table 1
Absence (No) or Presence (Yes) of Retinal Motion as a Function of Eye Movement and Image Movement

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

Note. When a physical image and the 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 eye and stationary image. Movement either of eye or image produces retinal motion.

attributes and tasks, there is very little evidence for spatiotopic integration across saccades in the sensory store, but there may be some exceptions.

Second, it was demonstrated that transsaccadic memory shares many characteristics with VSTM. The capacity of VSTM was shown to be around four or five items (Pashler, 1988; Sperling, 1960), and it may be larger for the spatial configuration of objects than for the identity of single items (Simons, 1996). The capacity of VSTM changes very little across time (Phillips, 1974). Essentially the same pattern was observed for transsaccadic memory (Irwin, 1991). Also, simple patterns were easier to retain than complex patterns, regardless of whether the eye moved during the retention interval (Carlson-Radvansky, 1999; Carlson-Radvansky & Irwin, 1995; Irwin, 1991). Thus, transsaccadic memory may in fact be the same as VSTM. Further, there is evidence that VSTM is strongly influenced by saccadic eye movements. In free viewing conditions, the items in VSTM are determined by the preceding fixations (Irwin & Zelinsky, 2002). In particular, memory for the last three objects that were foveated or about to be foveated is very accurate. Similarly, objects presented close to the saccade target before saccade initiation are remembered better than are other objects in the scene (Irwin, 1992; Irwin & Zelinsky, 2002; but see Germeys, De Graef, Panis, Van Eccelpoel, & Verfaillie, 2004), presumably because attention moved to the saccade target prior to the eye movement (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995). Finally, it was observed that fewer items are remembered if a saccade is executed compared with a condition in which the saccade-induced retinal changes are mimicked on a computer monitor during fixation (Irwin, 1991). This drop in performance was attributed to dual-task demands in the saccade condition.

Sensory Memory During Smooth Pursuit

In comparison with the large number of studies on transsaccadic memory, very few studies have looked at visual memory during smooth pursuit eye movements. One study exists that examined whether sensory memory during smooth pursuit was spatiotopic or retinotopic (Sun & Irwin, 1987). As outlined above, only a spatiotopic organization ensures perceptual stability in the face of eye movements. During smooth pursuit, successive presentation of a stimulus at the same spatial position will stimulate different positions on the retina. If sensory memory operates in spatiotopic

coordinates, discrimination of a target should deteriorate if it is followed by a mask that is presented at exactly the same spatial position. In contrast, if sensory memory is retinotopic, masking would be expected if the second stimulus is presented at a position that is shifted in the direction of motion according to the movement of the eye and stimulates the same retinal position. The latter result was observed by Sun and Irwin, arguing in favor of a retinotopic organization of sensory memory during smooth pursuit. Consistent with this notion, it is possible to perceive the 2-D shape of an object that is drawn on the retina by dots of light moving up and down at the same horizontal position while the eyes move horizontally (Morgan, Findlay, & Watt, 1982): Across time, the pursuit-induced horizontal position shifts and the vertical stimulus motion "paint" a 2-D shape on the retina. If the shape is completed in less than 150 ms, the successively stimulated positions are integrated in sensory memory and the painted 2-D shape is accurately perceived.

VSTM During Smooth Pursuit

In the current study, we investigated VSTM for position and color during smooth pursuit. To this end, we used a retention interval far beyond the limits of sensory memory (0.9–1.0 s). We varied the spatial and retinal stability of the stimuli to investigate whether VSTM during smooth pursuit operates in a retinotopic or spatiotopic reference frame. We mainly ran two smooth pursuit conditions and one fixation condition. In one of the smooth pursuit conditions, the items to be remembered (*memory image*) moved at the same velocity as the smooth pursuit target across the screen, resulting in approximate retinal stability and spatial motion. In the second smooth pursuit condition, the memory image remained stationary on the screen while the target moved through the items. This resulted in strong retinal motion and spatial stability. If VSTM for position during smooth pursuit is spatiotopic, improved performance would be expected in the condition with retinal motion and spatial stability; if it is retinotopic, however, performance should be better in the condition with retinal stability and spatial motion. Consistent with a retinotopic organization of VSTM, a recent study of memory-guided saccades in monkeys demonstrated that after a slow displacement of the eye, saccades to the spatial position of a flash presented before the eye displacement are more variable than are saccades to the flash's retinal position (Baker, Harper, & Snyder, 2003). Finally, if VSTM during pursuit is an abstract memory store that is neither strictly spatiotopic nor retinotopic, the two conditions would not be expected to differ. For saccades, the latter conclusion has been favored (e.g., Irwin, 1991; Pollatsek, Rayner, & Henderson, 1990; Rayner, McConkie, & Zola, 1980).

Further, comparison of the conditions with smooth pursuit and the condition with eye fixation may show whether there is an impairment of VSTM due to the execution of the eye movement. There are at least three ways in which smooth pursuit could impair VSTM: First, VSTM and eye movement tasks may interfere with each other 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 explanation for the decrement in performance with two tasks was that central

resources are limited (Kahneman, 1973) or that the different tasks have to pass through a central bottleneck (Pashler, 1994). Therefore, a requirement to do two things at a time will impair performance compared with a single-task condition. The important point here is that it is a central capacity limitation. For instance, it has been 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 it is independent of sensory processes or spatial positions. The nature of the central bottleneck is under debate (Levy & Pashler, 2001; Meyer & Kieras, 1999); however, it is not necessary for the present article to specify this process in any detail.

Second, visuospatial attention may be tied to the pursuit target (see Krauzlis & Stone, 1999, for an overview), thereby impairing processing of peripheral targets. However, this impairment may depend strongly on the task and stimuli involved. On the one hand, it has been demonstrated that visual search for a briefly presented number in a letter string is superior when the pursuit target contains the target number compared with when a nearby distractor that moves at a different velocity contains the target number (Khurana & Kowler, 1987). This suggests that visuospatial attention is tied to the pursuit target and cannot be allocated to the distractor. On the other hand, studies of the perception of contrast (Flipse, van der Wildt, Rodenburg, Keemink, & Knol, 1988; Murphy, 1978), motion (Heidenreich & Turano, 1996), and shape (Morgan et al., 1982) have provided little evidence for the view that perception is impaired during smooth pursuit. Typically, attention enhances perception (e.g., Carrasco, Penpeci-Talgar, & Eckstein, 2000; Yeshurun & Carrasco, 1998), which should lead to perceptual impairment if it is impossible to allocate attention to nontarget stimuli during pursuit. Further, 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 smooth pursuit control operates (best) in an automatic mode. Thus, it is an open question whether VSTM during smooth pursuit would suffer because of pursuit-related limitations in visuospatial attention.

Third, it may be that retinal or spatial position is at least partially coded in VSTM. In this case, changes in one of these reference frames would be expected to impair VSTM for position. That is, compared with a condition in which retinal and spatial positions overlap, VSTM for position during smooth pursuit should be impaired. No such effects would arise if the representation were abstract and contained only relational information between the elements. Finally, the possibility that VSTM is completely dysfunctional during smooth pursuit cannot be excluded, because no previous studies have looked at this issue.

Overview of Experiments

To test these different predictions, we ran a series of experiments using the following paradigm. Observers were presented with an array of items that were to be kept in memory (*memory image*). After a retention interval of ~ 1.0 s, a second array (*probe image*) was presented, and observers were asked to indicate whether the two arrays were the same or different. In most experiments, one critical item in the probe image was cued and observ-

ers were asked to judge changes of this item only. The items used were well above detection threshold, with a maximal contrast of 100%.

In Experiment 1a, we investigated VSTM for the position of peripheral targets. Three control experiments (Experiments 1b–1d) ruled out alternative explanations in terms of saccadic eye movements, context effects, and retinal jitter. In Experiment 2, we examined VSTM for the position of items presented in the fovea. Experiment 3 asked whether retinal motion induced by eye movements differs from retinal motion induced by object motion. In Experiment 4, we compared VSTM for position during smooth pursuit with sensory memory by manipulating the retention interval. Experiment 5 looked at memory for color during smooth pursuit. Finally, Experiment 6 evaluated effects of smooth pursuit velocity on VSTM for position.

Experiment 1a: Memory for Position

In Experiment 1a, we tested whether VSTM for position would suffer when to-be-memorized items were presented during smooth pursuit and whether there was evidence of an advantage for spatiotopic stability. If VSTM for position during smooth pursuit is spatiotopic, performance should be better when the memory image is spatially stable while the eye moves compared with a condition in which both the eye and the memory image move (see Figure 1). Comparison of conditions with smooth pursuit and fixation may show whether smooth pursuit binds central or visuospatial attention and whether the spatial or retinal position of items is stored in VSTM. The purpose of Experiment 1a was to establish whether such differences exist, whereas Experiments 2 and 3 provided more direct tests between these hypotheses.

Further, Experiment 1a varied the availability of relative-position information during recall. It has been demonstrated that information in VSTM is stored in a relational or configurational manner: Jiang, Olson, and Chun (2000), who manipulated the number of items present in a probe image. Jiang et al. presented either the same number of items in the probe as in a memory image or only a single probe item. 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 with the all-probes condition, indicating that the position or features of an item in VSTM were coded with respect to the position of other items in the image.

Similar to Jiang et al. (2000), we presented either a probe image with the same number of items as there were in the memory image (*all-probes condition*) or a single item only (*single-probe condition*). This manipulation may reveal whether VSTM during smooth pursuit follows the same principles as VSTM during fixation (Jiang et al., 2000) and across saccades (e.g., Carlson-Radvansky, 1999; Carlson-Radvansky & Irwin, 1995). In contrast to previous studies, however, there were a minimum of two items on the monitor: one probe item and the fixation cross. Presentation of the fixation cross was necessary because smooth pursuit cannot be maintained without a moving object. Therefore, relational information was never completely absent, even in the single-probe condition. The item could always be located with respect to the fixation mark.

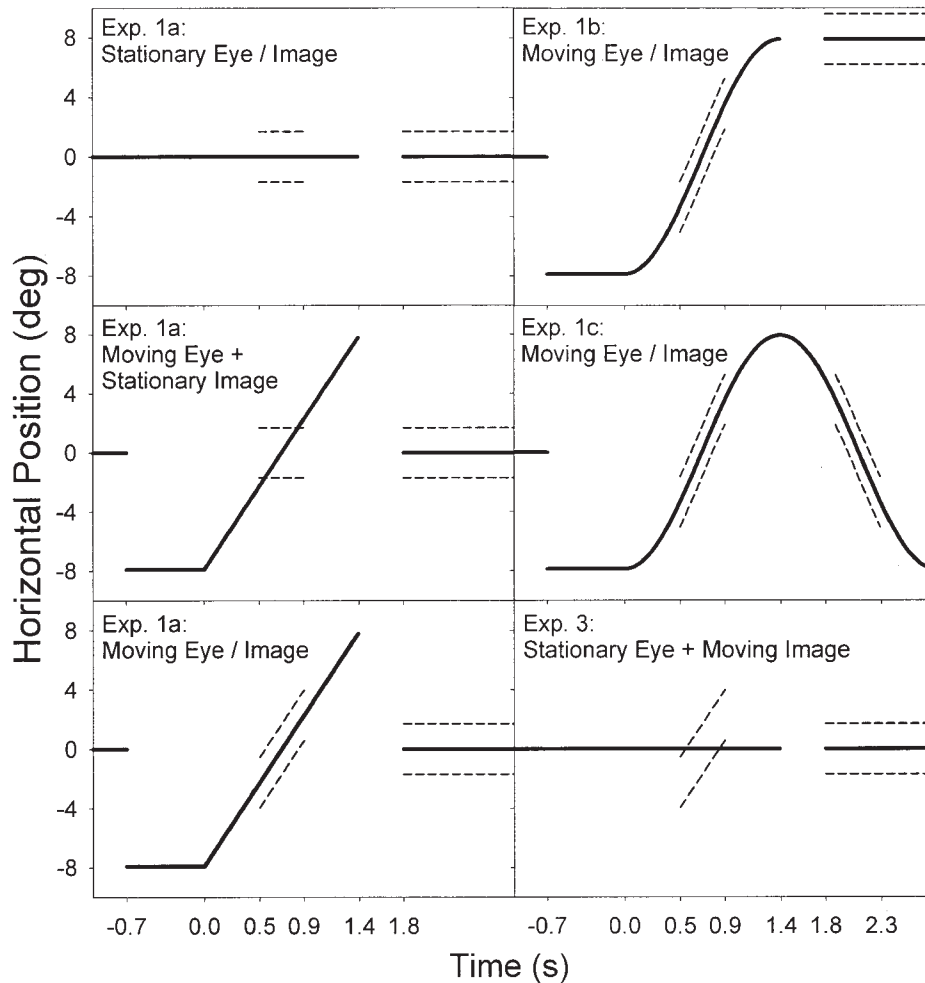


Figure 1. Space-time plots of eye and image movement in Experiments 1a–1c and 3. In each graph, the thick, solid lines indicate the trajectory of the pursuit target (a fixation cross), and the thin, dashed lines indicate the trajectories of the memory and probe images. The set of dashed lines on the left side of each graph represents the memory image, which contains the to-be-remembered items. The set of dashed lines on the right side of each graph represents the probe image, which contains the critical probe item. Motion onset was chosen as time 0. Screen center was chosen as position 0, and negative positions represent positions on the left. Thus, the target moved from left to right in the current plots. Exp. = experiment; deg = degrees.

Method

Participants. In all of the experiments reported in this study, students at the Justus-Liebig-Universität Gießen, Gießen, Germany, participated for pay. They ranged in age 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 12 in all experiments (with the exception of Experiment 1d, which had 11 participants). The 2 authors participated in all experiments; the remaining participants were naive. The pattern of the authors' performance was not significantly different from the pattern of naive observers. Some of the naive observers participated in more than one experiment, but none were aware of the experimental design or hypothesis. Using experienced observers was preferable because untrained observers have great difficulty in following a target with their eyes while simultaneously attending to other objects.

In Experiments 1b, 1c, and 3, data from 1 observer had to be excluded because of chance performance in the detection task. In Experiment 1c,

data from 1 observer had to be excluded because of poor smooth pursuit eye movements. In Experiment 1d, data from 3 observers had to be excluded because of poor smooth pursuit eye movements.

Materials and procedure. The stimuli were presented on a 21-in. (53.34-cm) CRT monitor with a refresh rate of 100 Hz and a resolution of 1,280 (height) \times 1,024 (width) 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, Ltd., Mississauga, 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 1.7×1.7 degrees (deg) white outline box. The squares subtended 1.2×1.2 deg of visual angle and appeared in an invisible 10

(columns) \times 12 (rows) cell matrix that subtended 17.0×20.4 deg of visual angle. The size of each cell in the matrix was 1.7×1.7 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, upward, and downward). The stimuli appeared on a uniform gray background of 32 cd/m^2 . To prevent afterimages, we assigned random gray values between black (0 cd/m^2) and white (64 cd/m^2) to each pixel in the square (see Figure 2A). Thus, the mean luminance of the squares was approximately equal to the background, and the maximal contrast was 100%. Because the overall size of each square was rather large (1.2×1.2 deg) and was made up of 0.03×0.03 -deg pixels, the stimuli were composed of both high and low spatial frequencies. 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 either appeared in the same position as in the memory image or was randomly relocated in the stimulus matrix.

Initially, the black 0.4×0.4 -deg fixation cross was presented at screen center (see Figure 1). 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 screen center, and observers were instructed to maintain fixation on the cross. After a keypress, 1,200 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 position. 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 the probe's retinal position.

In conditions with an eye movement, the target jumped 8.0 deg to the left or right after the initial keypress. 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 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 screen center. After a blank interval of 400 ms, the fixation cross and the probe image appeared in the central position, and observers were instructed to refixate the cross. The difference between the stationary-image and moving-image conditions was as follows: 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 position with respect to the fovea (i.e., the fixation cross). The probe image was presented until an observer gave a *same* or *different* judgment by a mouse click. A beep marked an incorrect response. Observers were instructed to respond as accurately as possible.

In 20% of the 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 with the average smooth pursuit gain under experimental conditions.

Design. The single-probe and all-probes conditions were run on different days. The order of probe conditions was balanced across observers. For each probe condition, the three movement conditions were blocked. The stationary, moving-eye/stationary-image, and moving-eye/moving-image conditions 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 and 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—a total of 852 trials.

Results

Initially, we calculated the following measures for each experimental condition: proportion correct, memory sensitivity, and response bias. Because the inferential statistics computed for proportion correct mirrored those for memory sensitivity (d') and there were no consistent effects of response bias, only proportion correct is reported here. Further, we computed several measures characterizing the eye movements: Smooth pursuit gain, instantaneous eye velocity, spatial lag, and standard deviation of the eye position. These eye movement data are presented in Appendixes A and B.

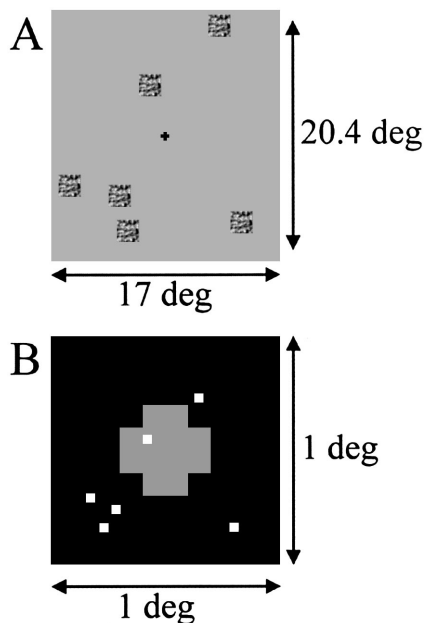


Figure 2. Schematic drawing of the stimuli. In most experiments, the items in probe and memory images were squares consisting of pixels with random gray values (A). Unlike in this representation, the mean luminance of the squares matched the luminance of the background. The extent of the image was 17×20.4 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 (B). deg = degrees.

Proportion correct. Proportions correct were arcsine transformed (transformed proportion correct = $2 * \arcsine \sqrt{\text{proportion correct}}$) before inferential statistical analysis (analysis of variance [ANOVA], *t* test). In the text and figures, the untransformed means are presented to allow for better comparison across experiments. Proportions correct in Experiments 1a–1d are plotted in Figure 3. A three-way (Probe Condition \times Memory Set Size \times Movement Condition), repeated measures ANOVA on arcsine-transformed proportion correct showed that performance decreased as memory set size increased (.85, .76, and .64 correct for 3, 6, and 12 squares, respectively), $F(2, 22) = 138.34$, $MSE = 3.622E-02$, $p < .001$. The proportion of correct responses was higher when all squares were presented in the probe image (.80) compared with 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 higher with stationary image

and stationary eyes (.80) and dropped when either the eye (.72) or both the eye and image moved (.72). The Probe Condition \times Memory Set Size interaction, $F(2, 22) = 16.08$, $MSE = 1.763E-02$, $p < .001$, 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 smooth pursuit conditions was significant ($ps < .001$), whereas there was no difference between smooth pursuit conditions ($ps > .5$).

Eye movements. The eye movement traces were visually inspected. Trials on which an observer blinked during memory-image presentation or was obviously not following the target were excluded from analysis. The number 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. We used a rather

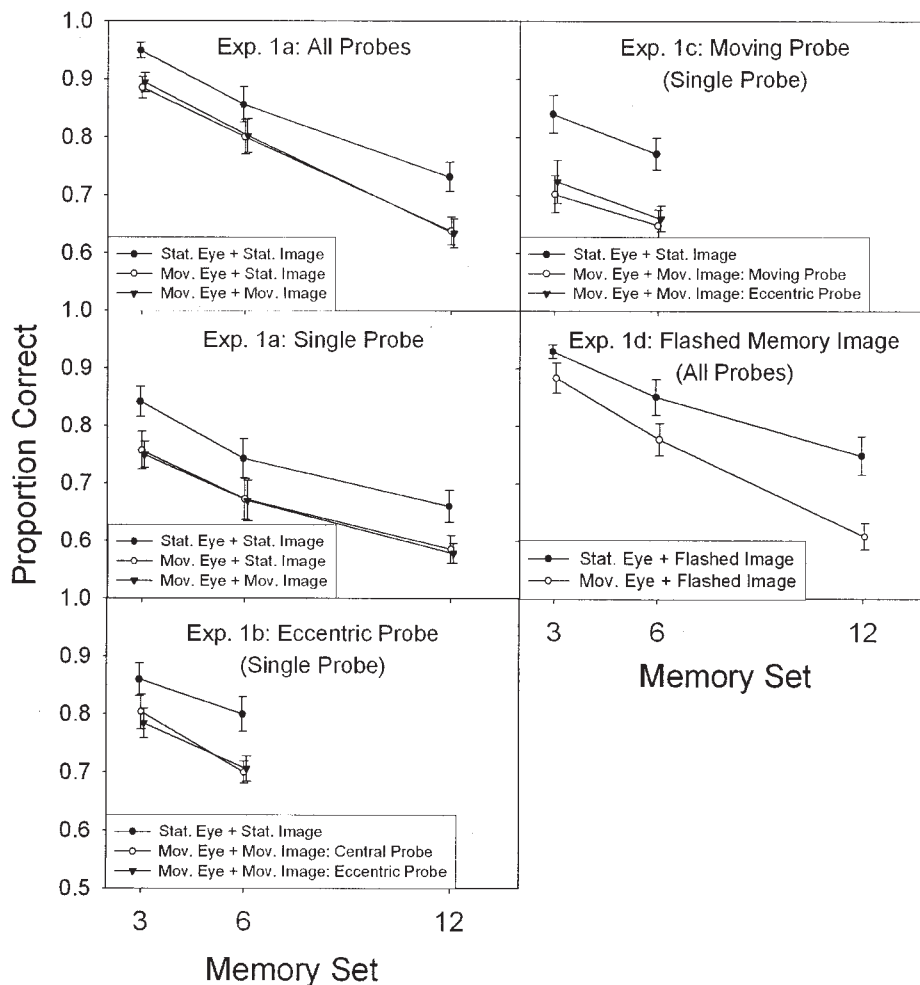


Figure 3. Results of Experiment 1. Mean proportions correct and between-subjects standard errors (error bars) are shown as a function of memory set size and movement condition. In Experiment 1b, the probe image was shown in an eccentric position such that no saccade back to the center was necessary. In Experiment 1c, the probe image was shown during smooth pursuit. In Experiment 1d, the memory image was only briefly flashed. Exp. = experiment; Stat. = stationary; Mov. = moving.

sensitive acceleration criterion of $3,250 \text{ deg/s}^2$, which 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 smooth pursuit. A high gain indicates good smooth pursuit performance and is typically accompanied by few catch-up saccades. Mean pursuit gains for all experiments are shown in Appendix A. The mean gain was always above 0.90. It was slightly higher when the image moved with the eye (~ 0.99) than during trials without an image (~ 0.97). When observers made smooth pursuit eye movements through the static image, pursuit gain dropped to ~ 0.94 . The dependence of smooth pursuit gain on the presence of a background is consistent with the literature on this topic (Collewijn & Tamminga, 1984).

Also, we calculated how much the fixation cross moved on the retina while the memory image was presented (see Appendix A). When the memory image was also moving, motion of the fixation cross on the retina and motion of the memory image on the retina were equivalent. In this analysis, we included saccadic episodes. However, doing so did not change the results significantly. Two indexes were calculated. First, we averaged the absolute eye velocity between two successive eye samples (4-ms separation) during pursuit and fixation. In the conditions with smooth pursuit, we subtracted the instantaneous target velocity before averaging. Thus, this index estimated pure retinal motion of the target. As can be seen in Appendix A, the jitter of the target on the retina was 2–3 times higher during smooth pursuit eye movements (3–4 deg/s vs. 7–11 deg/s). Second, we calculated the variability of the eye position relative to the target after the average lead or lag of the eye was subtracted. As can be seen in Appendix A, the standard deviation of the eye position was 2–4 times larger during smooth pursuit than during fixation ($0.02\text{--}0.09 \text{ deg}^2$ vs. $0.16\text{--}0.33 \text{ deg}^2$). Note that the latter index is more strongly affected by the occurrence of saccades: If the position of the eye relative to the target changes due to a saccade, the deviation will be calculated relative to the mean position, which is in between the two fixation points. Thus, a high variability may result even if the eye is still for most of the time. Further, we calculated the average lag or lead during smooth pursuit (not reported for each experiment). In all experiments, the eye lagged behind the target by less than 0.2 deg.

Further, we determined the proportion of trials on which a saccade occurred during the presentation of the memory image and the average number, duration, and size of those saccades (see Appendix B). For this analysis, the output of the EyeLink II eye movement parser was used. It classified episodes with acceleration larger than $4,000 \text{ deg/s}^2$ and a velocity larger than 22 deg/s as saccades. It is clear from Appendix B that saccades smaller than 1 deg were rather frequent during smooth pursuit (30%–50% of the trials).

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 ($<1 \text{ deg}$) and short ($\sim 20 \text{ ms}$) relative to the presentation time of the memory image (400 ms). Previous research has demonstrated that saccadic suppression does not occur for small saccades ($<2 \text{ deg}$; see Ross et al., 2001).

Discussion

There were three main results. First, the experiment showed that VSTM for position is not dysfunctional during smooth pursuit. Quite to the contrary, performance during smooth pursuit was well above chance. Second, there was no difference between the two smooth pursuit conditions, which makes it unlikely that VSTM for position during smooth pursuit is strictly spatiotopic or retinotopic. Rather, it did not matter whether the items moved with the eye or were stationary. In agreement with research on transsaccadic memory, VSTM for position during smooth pursuit may be relatively abstract. Consistent with this conclusion, we were able to replicate Jiang et al.'s (2000) finding that elimination of relative-position information impairs VSTM for position. When all squares were present in the probe image, performance was better than it was with a single probe. This was the case with fixation and with smooth pursuit. Therefore, VSTM for position during smooth pursuit follows some of the same principles as VSTM for position with fixation. Third, performance was best with eye fixation and retinal plus spatial overlap of the memory and probe items. VSTM capacity was 4.2 items in the fixation condition and dropped by 1 item in the smooth pursuit conditions (3.1 items).¹ This result is particularly striking because in the moving-eye/moving-image condition, the retinal input was on average about the same as in the stationary-eye/stationary-image condition: Smooth pursuit gain in this condition was close to unity (0.99). Therefore, the memory image was approximately stabilized on the retina. However, the instantaneous retinal jitter (see Appendix A) was stronger with pursuit, and Experiment 1d clarifies whether this difference may explain the performance drop.

The impairment of VSTM for position during smooth pursuit compared with fixation is consistent with the ideas presented in the introduction: First, it may be that both egocentric and retinotopic object position is coded in VSTM, such that motion in one or the other reference frame (as in the pursuit conditions) impaired performance relative to the fixation condition. Second, it may be that smooth pursuit used visuospatial or central resources that were not available for the VSTM task. Experiments 2 and 3 tested these two assumptions.

Further, it may be important to point out that the performance drop due to smooth pursuit did not interact with the number of items in the probe image (Eye Movement \times Single Probe vs. All Probes; $p = .78$). This is important because it might be argued that the perception of position was distorted during smooth pursuit eye movements, resulting in a performance drop relative to that in the fixation condition. However, such an account would predict a larger difference between the single-probe and all-probes conditions with smooth pursuit compared with fixation. In the single-probe condition, the viewer-centered (spatiotopic) position is more important because the context of the other items is removed during

¹ To determine the number of items that would have to be stored to yield 80% correct responses, we used the following method (Irwin & Zelinsky, 2002): We corrected for guessing by applying the formula $p = (x - g)/(1 - g)$, where x is the raw proportion correct, g is the guessing probability (always 0.5), and p is the corrected proportion correct (Busey & Loftus, 1994). We then multiplied p by the number of objects in the display to estimate the number of objects remembered (Sperling, 1960).

recall. Viewer-centered localization during an eye movement (not so much during fixation) requires the integration of retinal and extraretinal signals, which may be erroneous under some circumstances (see Schlag & Schlag-Rey, 2002, for an overview). In contrast, the all-probes condition allows for distance-based localization of single elements relative to others and does not require information about eye position. Therefore, one might expect particularly bad performance in the single-probe condition with pursuit.

However, conditions that produce eye-movement-related mislocalization vary vastly from the conditions used here. First, target-presentation times have typically been brief (flashes of less than 100 ms) in previous studies concerned with object localization during smooth pursuit. Therefore, latency differences between extraretinal and retinal signal may have led to errors (e.g., Brenner, Smeets, & van den Berg, 2001; Kerzel, 2000; Mateeff, Yakimoff, & Dimitrov, 1981; Mitrani & Mateeff, 1981). Second, targets have been presented in isolation or even in complete darkness so as to separate viewer-centered (spatiotopic) from eye-centered (retinotopic) localization (e.g., Brenner et al., 2001; Kerzel & Gegenfurtner, 2003). In contrast, stimuli in the present study were presented for a rather long time (400 ms), and the experimental room was fully lit such that contextual cues (including the fixation cross) were abundant even when only a single item was presented. This may explain why performance in the single-probe condition was no worse with smooth pursuit than with fixation.

Before it can be concluded that VSTM capacity for position is reduced during smooth pursuit, alternative explanations in terms of saccadic eye movements (Experiment 1b), recall context (Experiment 1c), and retinal jitter due to imperfect pursuit (Experiment 1d) need to be ruled out (see Figure 1). To this end, in the following experiments we systematically varied the position, motion, and presentation time of the probe image.

Experiment 1b: Eccentric Probe-Image Position

In our experimental protocol, observers had to make a saccade back to screen center before comparing memory and probe images. It may be that this saccade produced the performance decrement. To prevent the saccade from the final, eccentric trajectory position to screen center, in Experiment 1b we showed the probe image at the end of the trajectory. Further, we made the velocity of the trajectory sinusoidal so as to smooth the increase from zero velocity and the decrease to zero velocity. This allowed for a smooth transition from smooth pursuit to fixation and, thereby, eliminated saccades (e.g., Collewijn & Tamminga, 1984).

Method

Participants. General characteristics of the participants were as specified in Experiment 1a.

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 conditions were run. One variant of the moving-eye/moving-image condition was similar to that in 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 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 8.0 deg to the opposite side and stopped at 8.0 deg on the other side of screen center. The fixation cross remained there until a response was given. To prevent saccades, we smoothed onset and offset of the trajectory in the moving-image/moving-eye conditions. The velocity profile was sinusoidal, with an amplitude of 8.0 deg and a temporal frequency of 0.38 Hz (i.e., one half cycle took 1,300 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 and 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, and mean proportion correct is shown in Figure 3. A two-way (Memory Set Size \times Movement Condition), repeated measures ANOVA confirmed that performance decreased with increasing set size (.76 and .70 for 3 and 6 squares, respectively), $F(1, 11) = 16.79$, $MSE = 2.651E-02$, $p < .005$. The proportion correct was higher in the stationary condition (.81) than in the moving-image/moving-eye condition with probes at the center (.68) or the moving-image/moving-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 ($p > .70$). *T* tests confirmed that the difference between fixation and smooth pursuit conditions was significant ($ps < .005$), whereas there was no difference between smooth pursuit conditions ($p = .603$).

Discussion

Removing the large “back” saccade from the experimental protocol did not change the results. VSTM capacity for position dropped from 2.8 items with fixation to 1.7 items with pursuit. 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, whereas it was different in the smooth pursuit conditions: The memory image was shown during smooth pursuit, whereas the probe image was presented during fixation. In contrast, both memory and probe images were shown during fixation in the stationary condition. The performance decrement in the smooth pursuit conditions may therefore have resulted from the mismatch of cues present at encoding and retrieval. To test this account, in Experiment 1c we presented the probe image during smooth pursuit. That is, observers pursued the target on its way from one side of the screen to the other, and the memory image was shown during this initial part of the trajectory. 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

Participants. General characteristics of the participants were as specified in Experiment 1a.

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 1.0 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 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 and 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, and mean proportion correct is shown in Figure 3. A two-way (Memory Set Size \times Movement Condition), repeated measures ANOVA showed that performance decreased with increasing memory set size (.82 and .74 for 3 and 6 squares, respectively), $F(1, 11) = 45.50$, $MSE = 1.857E-02$, $p < .001$. The proportion of correct responses was higher in the stationary condition (.83) than in the moving-eye/moving-image condition with a static probe image (.75) or with a moving probe image (.74), $F(2, 22) = 7.58$, $MSE = 5.688E-02$, $p < .005$. The interaction was far from significant ($p > .70$). T tests confirmed that the difference between fixation and smooth pursuit conditions was significant ($ps < .025$), whereas there was no difference between smooth pursuit conditions ($p = .664$).

Discussion

The results obtained mirror those in Experiments 1a and 1b. With fixation, VSTM capacity for position was larger with fixation (3.0 items) than it was with smooth pursuit (2.2 items). 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 smooth pursuit eye movements is high, the variability in eye velocity will cause the retinal image to move on

the retina (see Appendix A). Because the visual system compensates for eye movements to some degree such that the visual world appears approximately stationary during smooth pursuit, one may argue that this jitter is not likely to affect memory performance.² However, to further rule out the possibility that the higher retinal velocity with smooth pursuit caused the performance drop, in Experiment 1d we briefly flashed the memory image either during pursuit or during fixation. The memory image was presented for one refresh cycle, yielding 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. Further, the all-probes condition was run such that the position of the eye relative to the display should not matter, because judgments could be based exclusively on in-trial relations (i.e., the pattern).

Method

Participants. General characteristics of the participants were as specified in Experiment 1a.

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 1a were not visible with this presentation duration. Therefore, we used dark gray squares of 2 cd/m². Only the condition with all squares in the probe image was run (all-probes condition).

The moving-eye 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 and 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. 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. A two-way (Memory Set Size \times Movement Condition), repeated measures ANOVA showed that performance decreased with increasing memory set size (.91, .81, and .70 for 3, 6, and 12 squares, respectively), $F(2, 20) = 99.39$, $MSE = 1.988E-02$, $p < .001$. The proportion of correct responses was higher in the stationary condition (.84) than in the moving eye condition (.76), $F(1, 10) = 15.70$, $MSE = 5.224E-02$, $p < .003$. The interaction was far from significant ($p > .30$).

Discussion

The results obtained mirror those in Experiments 1a–1c: VSTM capacity for position dropped by about 1.0 item, from 4.8 during fixation to 3.6 during smooth pursuit. Therefore, differences in the

² The velocity of the eye is slightly underestimated during smooth pursuit, such that a stationary background is perceived to move slightly opposite to the direction of motion (Filehne illusion; Mack & Herman, 1973). However, the world is not perceived to jump with every jerky eye movement during pursuit such that compensation does occur.

retinal velocity of the memory image between fixation and pursuit may not explain the difference in performance 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 smooth pursuit 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/stationary-image and moving-eye/moving-image conditions were run. If smooth pursuit entails focusing of attention on the pursuit target that impairs processing of the peripheral image, this performance drop should be eliminated with foveal presentation of the memory image. As outlined in the introduction, there are reasons to believe that visuospatial attention during smooth pursuit is tied to the target. If, however, the change in the spatial position was the exclusive cause of the performance decrement in Experiment 1, the difference between smooth pursuit and fixation conditions should persist with the miniature image. Similarly, if central performance limitations were responsible for the performance drop with smooth pursuit, the difference between smooth pursuit and fixation should persist.

Method

Participants. General characteristics of the participants were as specified in Experiment 1a.

Materials, procedure, and design. All aspects of the method were identical to that of Experiment 1a, with the following exceptions. A black 1.0×1.0 -deg square with a 0.4×0.4 -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 10×10 grid (0.75×0.75 deg) centered on the square. Each cell consisted of 1 target pixel and 0.5-pixel padding. The minimum separation between 2 target pixels was 1 pixel. Only the condition with all elements in the probe image was run (all-probes condition). 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 pursued 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 (plus 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, and mean proportion correct is shown in Figure 4. A two-way (Memory Set Size \times Movement Condition), repeated measures ANOVA showed that the proportion of correct responses decreased with increasing set size (.95, .85, and .70 for 3, 6, and 12 squares, respectively), $F(2, 22) = 77.10$, $MSE = 4.384E-02$, $p < .001$. There was no significant difference between stationary-eye/stationary-image condition (.85) and the moving-eye/moving-image condition (.82), $F(1, 11) = 2.01$, $MSE = 3.603E-02$, $p = .184$. The interaction was far from significant ($p > .50$).

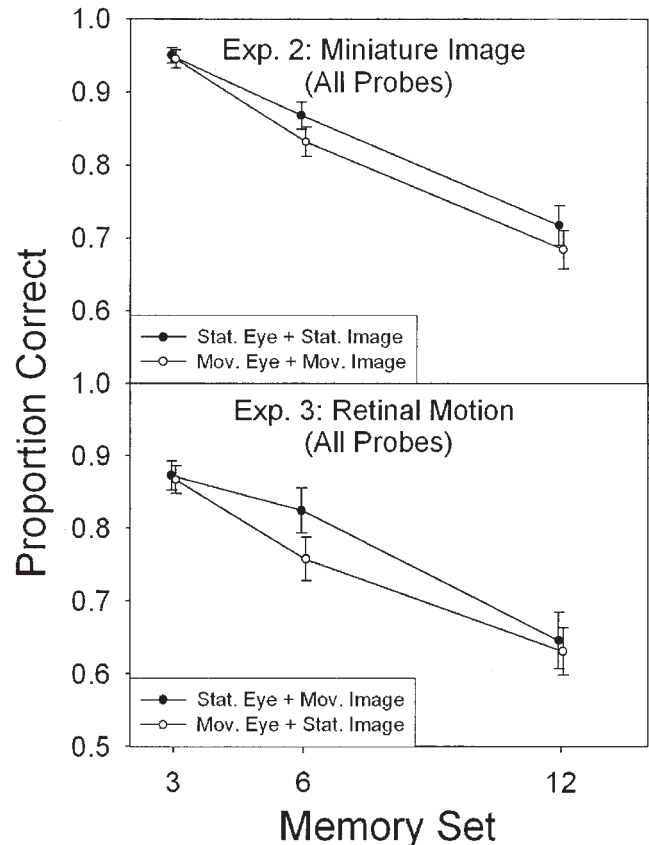


Figure 4. Results of Experiments 2 and 3. Mean proportions correct and between-subjects standard errors (error bars) are shown as a function of memory set size and movement condition. In Experiment 2, the image was presented in the fovea. In Experiment 3, the image moved in the condition with stationary eyes. Exp. = experiment; Stat. = stationary; Mov. = moving.

Discussion

With miniature images on the pursuit target, the highly reliable performance drop between fixation and smooth pursuit conditions from Experiment 1 was strongly reduced and no longer significant. VSTM capacity for position was 4.9 items with fixation and 4.5 items with pursuit, which is less than half of the difference observed in Experiment 1. This favors an account in terms of attentional focusing: During smooth pursuit, attention may “zoom in” on the pursuit target, which may have impaired processing of the peripheral image in Experiment 1. In contrast, the foveal image in Experiment 2 was contained in the attentional focus. Thus, smooth pursuit had less detrimental effect on VSTM for position.

An alternative explanation of the results states that the better acuity in the fovea improved performance during pursuit. This alternative explanation has two problems: First, the items were presented in the fovea with fixation and with pursuit. Therefore, both conditions should have benefited equally from the higher retinal acuity. Second, the ratio of element spacing and positional jitter of the eye was much smaller in the present experiment than in previous experiments ($1.7/0.16 = 10.6$ in Experiment 1a; $0.03/$

0.13 = 0.23 in Experiment 2). Previous studies have shown that perception suffers when fine details (high spatial frequencies) are presented during smooth pursuit (Long & Homolka, 1992; Murphy, 1978). The reason is that fine details are smeared when they are moved across the retina. On the basis of these perceptual factors, performance would be expected to be worse with a small image on the retina. However, performance was actually better in this case. This provides support for the attentional account.

With respect to the remaining mechanisms that may impair VSTM for position during smooth pursuit, the following answer may be given on the basis of the present results: Because the changes in spatial position in the present experiment were the same as 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 position were important for the encoding and retrieval of position information in VSTM, performance should have dropped with smooth pursuit 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 smooth pursuit and fixation conditions with the miniature image.

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 for position. This conclusion would be in line with the importance of relative position in VSTM. Indeed, Irwin (1991) found no detrimental effects of displacement of target arrays on VSTM. To see whether this conclusion is justified for continuous position changes, in Experiment 3 we compared two conditions that had approximately 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 for position is governed by relative position alone, performance in the condition with a moving image and stationary eyes should be superior to that in the smooth pursuit condition because it replicates the stationary-eye condition from Experiment 1. However, if spatial and retinal stability is important for VSTM, performance in the condition with stationary eyes should drop to the level of the smooth pursuit condition, because motion of the image induces changes in both the retinal and spatial reference frames.

Method

Participants. General characteristics of the participants were as specified in Experiment 1a.

Materials, procedure, and design. The materials and procedure were the same as in Experiment 1a, with the following exceptions. 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/moving-eye condition in Experiment 1a. That is, the probe image moved for 200 ms before it passed screen center and continued to move for another 200 ms. The retention interval was 500 ms. The all-probes condition was run.

The stationary-image/moving-eye condition and moving-image/stationary-eye conditions 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 and 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, and mean proportion correct is shown in Figure 4. A two-way (Memory Set Size \times Movement Condition), repeated measures ANOVA showed that performance decreased with increasing memory set size (.87, .79, and .64 for 3, 6, and 12 squares, respectively), $F(2, 22) = 125.05$, $MSE = 1.591E-02$, $p < .001$. The proportions of correct responses were not significantly different with stationary eyes and moving image (.78) than they were with moving eyes and stationary image (.75), $F(1, 11) = 1.51$, $MSE = 7.536E-02$, $p = .245$. The interaction was not significant, $F(2, 22) = 1.60$, $MSE = 2.880E-02$, $p = .225$.

Discussion

The advantage of the fixation condition was lost when the memory image moved. VSTM capacity for position was slightly, but not significantly, larger with eye fixation (3.5 vs. 3.9 items). Thus, retinal and spatial stability do contribute to VSTM for position. It is interesting to note that conditions with approximately equal retinal input do not always yield similar results: In Experiment 1, the retinal projections in the stationary-eye/stationary-image condition were approximately equivalent to those in the moving-eye/moving-image condition. 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 can 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 only 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 instability in two reference frames (spatial and retinal), and only relative position was stable. 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, VSTM during smooth pursuit was explored. We observed that the focusing of visuospatial attention and positional stability contribute to VSTM for position. Up to this point, the retention interval was ~ 1.0 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 the memory and the probe image is perceived as apparent motion between two image elements. Note that the contribution of sensory memory is rather indirect: Sensory memory preserves the position

of the items that are not moving. This allows for a single item that is changing position to be perceived as moving or “jumping” (average amplitude of 10.3 deg) to some other location in a pattern of stationary items. Without position persistence of the stationary items, the position change would be ambiguous, and no motion of a single element could be perceived. Previous studies on transsaccadic memory have shown that apparent motion is eliminated if a saccade intervenes between memory and probe images (Irwin, 1991). The question is whether the sensory store will 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 will 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 will still be perceived in this case.

Method

Participants. General characteristics of the participants were as specified in Experiment 1a.

Materials, procedure, and design. All aspects of the method were identical to that of Experiment 1a, with the following exceptions (see Figure 5). The stationary-eye/stationary-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 the same amount of time 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. The distance covered by the target was 0.9 or 1.0 deg. In the moving-image/moving-eye condition, the memory image was presented while the target was in one half of the screen, and the probe image was shown in the other half (always centered around the pursuit target) after the target had passed the midpoint of the screen. 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 smooth pursuit and produced a saccade. The downside of this 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 were in foveal view during presentation of the memory image (the first part of the trajectory), but they were in the far periphery during presentation of the probe image (the second part of the trajectory). Only the all-probes condition was run.

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 and 20 blank trials). The order of blocks varied according to a

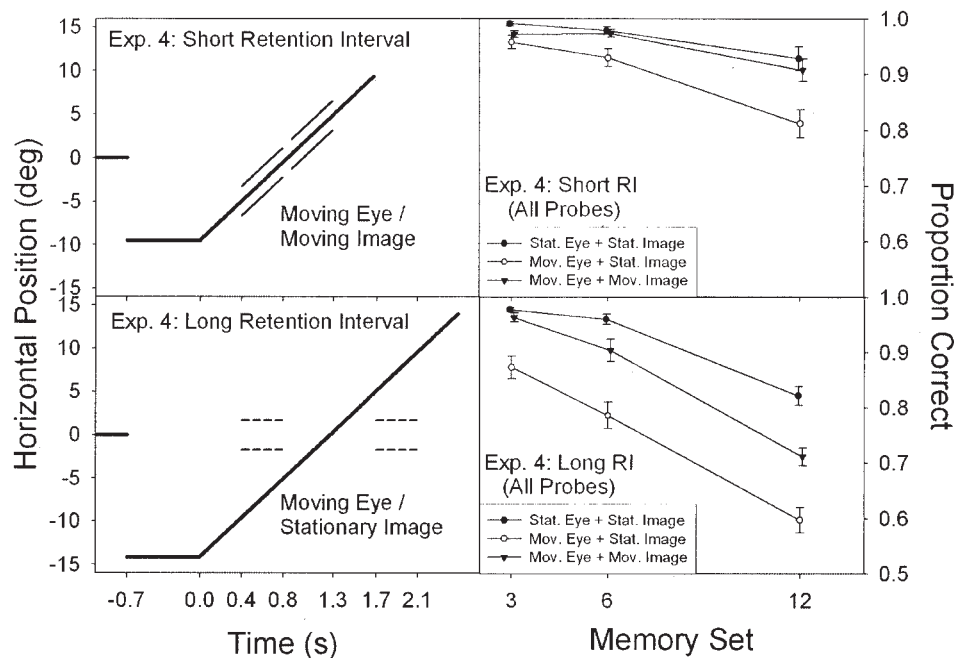


Figure 5. Space-time plots of eye and image movement in Experiment 4 are shown on the left. The set of dashed lines on the left side of each graph represents the memory image, which contains the to-be-remembered items. The set of dashed lines on the right side of each graph represents the probe image, which contains the critical probe item. Results of Experiment 4 (mean proportions correct and between-subjects standard errors [error bars]) as a function of memory set size, movement condition, and retention interval [RI] are shown on the right. In contrast to Experiment 1, the mean gaze angle varied between memory and probe images when the eyes moved and the image was stationary. Exp. = experiment; deg = degrees; Stat. = stationary; Mov. = moving.

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, and mean proportions correct are shown in Figures 5 and 6. A three-way (Retention Interval \times Memory Set Size \times Movement Condition), repeated measures ANOVA showed that proportion correct decreased as memory set size increased (.96, .92, and .80 for 3, 6, and 12 squares, respectively), $F(2, 22) = 126.33$, $MSE = 4.507E-02$, $p < .001$. The proportion of correct responses was higher with the short (.94) than with the long retention interval (.84), $F(1, 11) = 158.22$, $MSE = 3.761E-02$, $p < .001$. The main effect of movement condition, $F(2, 22) = 84.24$, $MSE = 3.532E-02$, $p < .001$, showed that proportion correct was highest with stationary image and eyes (.94) and dropped when both eyes and image moved (.91). Performance was worst with stationary image and moving eyes (.82). The Retention Interval \times Memory Set Size interaction, $F(2, 22) = 12.91$, $MSE = 2.815E-02$, $p < .001$, indicated that the performance drop with increasing memory set size was larger with the long retention interval than with the short retention interval. The Retention Interval \times Movement Condition interaction, $F(2, 22) = 8.01$, $MSE = 2.469E-02$, $p < .01$, showed that performance differed more strongly between the three movement conditions with the long than with the short retention interval. However, separate t tests confirmed that the differences between the three eye-movement conditions were significant for both retention intervals (see Table 2). Finally, the three-way Retention Interval \times Memory Set Size \times Movement Condition interaction was significant, $F(4, 44) = 3.00$, $MSE = 2.366E-02$, $p < .05$. At first sight, this interaction appears to have been due to a larger performance drop with the short retention interval and stationary image/moving eyes. However, two separate two-way (Memory Set Size \times Move-

Table 2
Pairwise Comparisons (t Tests) of Mean Performance in the Movement Conditions of Experiment 4 as a Function of Retention Interval

Movement condition	Stationary eye/stationary image	Moving eye/stationary image	Moving eye/moving image
Stationary eye/stationary image		6.63%**	1.49%*
Moving eye/stationary image	16.81%**		5.14%**
Moving eye/moving image	5.99%**	10.82%**	

Note. Bolded values represent differences in proportion correct for the short retention interval (80 ms). Nonbolded values represent differences in proportion correct for the long retention interval (900 ms). The t tests were run on arcsine-transformed proportions correct.
* $p < .0125$. ** $p < .001$.

ment Condition) ANOVAs 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: $F[4, 44] = 1.54$, $MSE = 2.674E-02$, $p = .206$).

Discussion

We replicated the finding of Experiment 1 that performance was best when the eyes and the image were stationary. In contrast to Experiment 1, however, performance was worse with smooth pursuit and a stationary image compared with smooth pursuit and a moving image. The most likely explanation is that it was more difficult to match memory and probe images when they 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, whereas the probe image was viewed after the pursuit target had moved to the other half. In Experiment 1, the mean viewing angle was the same for probe and memory images. Similar to transsaccadic memory (Irwin, 1992; Irwin & Zelinsky, 2002), it may be that objects that were close to the fovea/focus of attention (i.e., pursuit/saccadic target) were preferentially maintained in VSTM. Because different items were presented close to the fixation target during memory-image and probe-image presentations, it may have been more difficult to match the contents of VSTM against the probe image.

Memory performance was superior (6.2 vs. 4.8 items retained) with the short retention interval, and the effect of memory set size was strongly reduced. This result indicates that apparent motion was available as a cue in all three conditions, even with smooth pursuit. It may be that the displacement of an element in the memory and probe images (average amplitude of 10.3 deg) during the retention interval of 80 ms was detected by long-range motion processing, whereas the motion of the items induced by the eye movement was processed by a 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. However, short-range motion of an

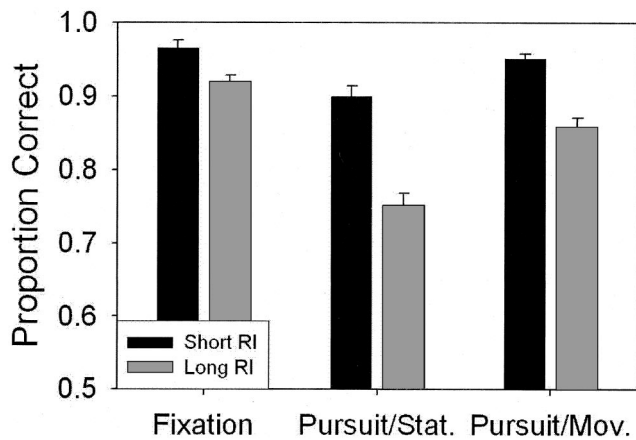


Figure 6. Results of Experiment 4. Mean proportions correct and between-subjects standard errors (error bars) are shown as a function of retention interval (RI; short [80 ms], long [900 ms]) and movement condition (fixation and stationary [Stat.] image, pursuit and stationary image, pursuit and moving [Mov.] image). The all-probes condition was run.

image may mask long-range motion at least partially: As shown in Table 2, performance with smooth pursuit and a stationary image was worse than it was with smooth pursuit and a moving image. Further, the fact that performance in the condition with moving eyes and a moving image was about the same as with fixation and a stationary image suggests that sensory memory during smooth pursuit is retinotopic (consistent with Sun & Irwin, 1987): When the retinal input during smooth pursuit and fixation was about the same, apparent motion cues were equally available during smooth pursuit and fixation, and about the same accuracy was achieved.

Experiment 5: Color

So far, we have demonstrated that VSTM for object position is impaired during smooth pursuit when the position 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, we argued that attention was tied to the target during smooth pursuit. This is plausible because during smooth pursuit, the visual system has to monitor the positional error between fovea and target so as 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 smooth pursuit 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; Müller, Reimann, & Krummenacher, 2003). Thus, the question is whether the performance drop during smooth pursuit generalizes to other dimensions. Therefore, in Experiment 5 we probed observers' memory for color during smooth pursuit.

Method

Participants. General characteristics of the participants were as specified in Experiment 1a.

Materials, procedure, and design. All aspects of the method were identical to that of 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. Commission Internationale de l'Eclairage (CIE) x -, y -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 CIE coordinates of (0.321, 0.336). All stimuli had a luminance of 32 cd/m². Memory and probe images 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. Note that, prior to this experiment, observers had to decide whether the critical probe changed position. Memory set size was fixed to eight items, and the number of items was identical for memory and probe images. The all-probes condition was run.

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 on 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. A one-way, repeated measures ANOVA showed that there was no significant difference between performance in the stationary condition (.65 correct), the moving-eye/stationary-image condition (.67), and the moving-eye/moving-image condition (.67), $F(2, 22) = 0.68$, $MSE = 7.738E-03$, $p = .517$.

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 the memory image was stationary with no eye movement (2.6 items retained). Thus, performance decrements due to smooth pursuit depend on which dimension is considered. If the position of peripheral objects has to be remembered, performance drops when smooth pursuit is executed. Experiment 2 suggests that this drop results from the narrowing of attention to the target. However, focusing of attention may be restricted to information about an object's position. The reason may be that position is important for the control of smooth pursuit: The distance between the fovea and the target has to be monitored to allow for accurate pursuit. Therefore, it is difficult to attend to spatial relations or distances among peripheral objects. However, attention to color may not be affected by smooth pursuit, because it is not response relevant.

Further, overall performance was somewhat lower than it was in a comparable condition run by Jiang et al. (2000): Proportion correct was $\sim .67$ in the present experiment, whereas it was $\sim .90$ in the previous study. This may be due to the usage of isoluminant color stimuli. In Jiang et al., the color stimuli were created by permutation of the three phosphors (red, green, blue), which typically results in changes of color and brightness. Because brightness cues were absent in the present task, the task was harder. To check whether the additional cue would alter the results, we tested 4 observers with combined color-and-luminance stimuli and found performance to be better ($\sim .77$ correct). 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 image 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 strongly alter the average retinal speed (instantaneous speed did increase, however) but changed the rate of spatial displacement. The question was whether performance

would decrease or remain stable with increased speed. If it remained stable, the process impairing VSTM for position during smooth pursuit would be discrete in the sense that it only mattered that smooth pursuit was executed, not how fast this occurred. In contrast, a decrease of performance with smooth pursuit would suggest that the process impairing smooth pursuit is affected by the smooth pursuit task demands. One may assume that increasing smooth pursuit 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 extent. Similarly, it may be that a faster moving pursuit target requires more visuospatial attention around the fovea. And finally, it may be that central processing is more strongly challenged by faster target motion.

Method

Participants. General characteristics of the participants were as specified in Experiment 1a.

Materials, procedure, and design. All aspects of the method were identical to that of 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. 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 single-probe condition was run.

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 on half of the trials. The order of blocks was balanced across observers. Each observer worked through two repetitions of each movement condition for a total of 288 trials.

Results

Data treatment was as in Experiment 1a. A two-way (Velocity \times Movement Condition), repeated measures ANOVA confirmed that proportion correct decreased as velocity increased (.72, .70, and .65 for 3.7, 11.3, and 22.6 deg/s, respectively), $F(2, 22) = 5.97$, $MSE = 2.604E-02$, $p < .01$. T tests showed that the slowest velocity did not differ from the medium velocity ($p > .30$), whereas the fastest velocity differed significantly from the other two, $t_s(11) > 2.8$, $p_s < .02$. None of the other main effects or interactions reached significance ($p_s > .30$).

Discussion

Performance dropped from about 2.5 items with the slow and medium velocities to 1.8 items with the fastest velocity. Thus, VSTM for position during smooth pursuit is affected by target velocity, but the relationship is not linear. Again, it is surprising that the condition in which the image was approximately stabilized on the retina did not produce superior performance compared with 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 con-

dition, such that the increasing retinal velocity did not impair VSTM any more than did increased spatial velocity.

General Discussion

We investigated VSTM for position and color during continuous eye and object motion. Although there is a large body of research on abrupt changes in eye (saccades) or object position, studies on continuous changes are rare. There were two questions that we tried to answer. First, we wanted to know whether VSTM for position during smooth pursuit was retinotopic or spatiotopic. To this end, we compared conditions with either spatial or (approximate) retinal stability and found no difference between the two. Thus, VSTM for position during smooth pursuit is neither strictly spatiotopic nor strictly retinotopic but, rather, is abstract in nature. Second, we asked whether VSTM capacity for position or color would be impaired by the concomitant execution of smooth pursuit. Overall, we observed that VSTM capacity during smooth pursuit was reduced by about one item. However, observers' performance was still well above chance.

When VSTM for object position was probed in Experiment 1, we found that the execution of smooth pursuit produced performance decrements compared with a condition without eye or object motion. This was surprising because in one smooth pursuit condition, the memory image moved with the target such that the retinal input was about the same as it was with stationary eyes. Experiment 2 showed that the performance decrement with smooth pursuit was absent when the memory image was shown in the fovea. This suggests that attention is tied to the target during smooth pursuit, which may impair processing of peripheral targets. 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 smooth pursuit (Experiment 3). Experiment 4 examined ultrashort-term (sensory) memory during smooth pursuit. Sensory memory preserves object position for stationary objects and allows for the perception of apparent motion of an item that changes position. Usage of this cue was possible in the fixation and smooth pursuit conditions. Experiment 5 showed that the performance drop with smooth pursuit does not hold for color. VSTM for color was unaffected by the execution of smooth pursuit, suggesting that the focusing of attention was restricted to position. In Experiment 6, we varied the velocity of smooth pursuit and found that performance decreased with increasing velocity. This suggests that increasing the difficulty of the eye movement task adversely affected VSTM for position.

In sum, the present study shows that VSTM during smooth pursuit represents items in a relatively abstract format and that the impairment of VSTM during smooth pursuit compared with fixation may not be the same for all attributes: Although memory for peripheral positions is impaired, this is not the case for foveal positions or color. Our experiments have demonstrated that the most likely cause of this impairment is a narrowing of the attentional focus to the pursuit target. Our argument is that focusing of attention around the fovea is necessary because of the task demands during smooth pursuit. Observers have to monitor differences between the target and the fovea and adjust the parameters of eye movement so as to accurately follow the target. Therefore,

the current study provides evidence for the close relationship of 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 and attention (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 deg) in a number of distractor items (e.g., green blocks at 135 deg, orange blocks at 45 or 135 deg). Observers were instructed to look at the target, and accuracy and latency of the first saccade was measured. The important manipulation was the manual task that accompanied 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, not its orientation, was response relevant. In contrast, both position and orientation were response relevant for grasping movements, because the wrist had to be rotated for successful grasping. Observers selected objects with a wrong orientation less frequently when they were asked to grasp the object compared with when they were asked to point 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 it did with pointing. Thus, task-specific requirements enhanced attention to the response-relevant dimension.

In contrast, in the present study, attending to position during smooth pursuit did not enhance performance along this dimension; 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 smooth pursuit, 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; Müller 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).

Further, VSTM during short-term memory may be compared to VSTM across saccades (transsaccadic 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 a target array overlapped and a condition in which observers executed a saccade (spatial but not retinal overlap). This comparison is similar to the present comparison between stationary eyes and stationary image and moving eyes and stationary image. Compared with the performance difference in Irwin (1991), the difference in performance that we observed was rather small (on the order of 6%–12% correct responses). Second, Irwin noted that there was no advantage of short retention intervals over long retention intervals for transsaccadic memory (retention intervals from 40–5,000 ms). In contrast, the present study shows that there was a clear advantage of short over long intervals when

smooth pursuit intervened. This shows that the sensory store was intact even with strong retinal motion (i.e., the condition with moving eyes and stationary image). However, the relation between pursuit-induced continuous motion ($0.08 \text{ s} * 11.3 \text{ deg/s} = 0.9 \text{ deg}$) and long-distance item motion (average of 10.3 deg) was very different in Irwin's study. In Irwin (1991), observers were asked to make a saccade of 3.0 deg, and the array containing the to-be-remembered items was only $2.4 \times 2.4 \text{ deg}$. Thus, the amplitude ratio of continuous and apparent motion may have favored the detection of apparent motion in the present study. Further research is needed to clarify if and when apparent motion is masked by pursuit-induced short-range motion.

In sum, there are differences between VSTM across saccades and VSTM during smooth pursuit. However, we believe that these differences may reflect different task demands and that they 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 (see Experiment 1).

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Appendix A

Smooth Pursuit Gain, Instantaneous Eye Velocity (After Target Velocity Was Subtracted), and Standard Deviation of Eye Position Relative to the Target Position for Each Experiment and Experimental Condition

Experiment and condition	Pursuit gain	Instantaneous velocity (deg/s)	SD of eye position (deg ²)
1a (all probes)			
Fixation		3.09 ± 30.25	0.06 ± 0.51
Stationary image	0.91 ± 1.98	7.89 ± 32.45	0.23 ± 2.71
Moving image	0.99 ± 1.20	7.38 ± 31.42	0.17 ± 2.09
Blank	0.97 ± 1.28	7.31 ± 33.04	0.16 ± 1.73
1a (single probe)			
Fixation		3.51 ± 16.79	0.06 ± 0.67
Stationary image	0.93 ± 2.68	8.52 ± 30.34	0.24 ± 4.05
Moving image	0.99 ± 1.46	7.99 ± 23.58	0.17 ± 2.33
Blank	0.97 ± 1.47	8.05 ± 24.76	0.18 ± 2.21
1b			
Fixation		3.79 ± 16.55	0.08 ± 0.95
Central probe	0.96 ± 1.20	11.01 ± 28.00	0.33 ± 3.80
Eccentric probe	0.95 ± 1.04	10.96 ± 21.01	0.33 ± 3.89
Blank	0.93 ± 1.92	10.92 ± 26.82	0.32 ± 4.22
1c			
Fixation		3.79 ± 21.83	0.07 ± 0.87
Moving probe	0.94 ± 1.56	10.51 ± 37.01	0.25 ± 2.49
Eccentric probe	0.94 ± 1.46	10.56 ± 32.64	0.25 ± 1.70
Blank	0.94 ± 1.34	10.61 ± 37.05	0.24 ± 2.13
1d			
Fixation		2.87 ± 23.52	0.02 ± 0.10
Flashed image	0.98 ± 1.13	7.08 ± 46.34	0.07 ± 0.64
Blank	0.98 ± 1.16	7.05 ± 38.21	0.06 ± 0.47
2			
Fixation		3.32 ± 25.21	0.07 ± 0.44
Moving image	1.00 ± 0.80	7.39 ± 28.94	0.13 ± 0.69
Blank	0.99 ± 0.83	7.51 ± 31.16	0.13 ± 0.91
3			
Fixation		3.71 ± 14.73	0.09 ± 0.82
Stationary image	0.94 ± 2.54	8.30 ± 14.33	0.22 ± 2.80
Blank	0.97 ± 2.08	7.98 ± 14.56	0.18 ± 2.55
4			
Fixation		2.99 ± 17.15	0.05 ± 0.27
Stationary image	0.94 ± 2.13	7.98 ± 34.25	0.22 ± 3.28
Moving image	0.99 ± 1.10	7.35 ± 22.71	0.16 ± 1.65
Blank	0.98 ± 1.38	7.58 ± 27.72	0.17 ± 1.94
5			
Fixation		3.01 ± 9.89	0.06 ± 0.45
Stationary image	0.94 ± 2.59	8.25 ± 17.91	0.22 ± 1.34
Moving image	0.99 ± 1.72	7.56 ± 14.70	0.16 ± 1.12
Blank	0.97 ± 1.88	7.89 ± 15.02	0.18 ± 1.37
6			
4 deg/s			
Stationary image	0.99 ± 2.24	4.66 ± 17.67	0.12 ± 1.01
Moving image	0.97 ± 1.49	4.71 ± 22.40	0.11 ± 0.86
Blank	0.97 ± 2.57	4.56 ± 16.97	0.10 ± 0.73
11 deg/s			
Stationary image	0.98 ± 1.42	8.28 ± 22.50	0.20 ± 1.54
Moving image	0.99 ± 1.35	7.99 ± 21.59	0.16 ± 1.17
Blank	0.99 ± 1.30	8.09 ± 17.87	0.16 ± 1.13
23 deg/s			
Stationary image	0.95 ± 1.14	12.25 ± 31.65	0.29 ± 2.45
Moving image	0.98 ± 1.40	11.77 ± 30.59	0.25 ± 1.71
Blank	0.97 ± 1.42	11.43 ± 36.31	0.23 ± 2.45

Note. Means and between-subjects standard errors are given in the $M \pm SE * 10^{-2}$ format. The indexes were computed for an interval of 400 ms (except for Experiment 1d, for which 50 ms before and 50 ms after the flash were used). deg = degrees.

Appendix B

Mean Proportions of Trials on Which a Saccade Occurred During Presentation of the Memory Image, With Mean Numbers of Saccades, Mean Saccade Durations, and Mean Saccade Amplitudes for Trials on Which a Saccade Occurred

Experiment and condition	Proportion of trials	Number of saccades	Saccade duration (ms)	Saccade amplitude (deg)
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
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
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
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
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
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
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
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
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

Note. Means and between-subject standard errors are given in the $M \pm SE * 10^{-2}$ format. In fixation conditions, up to 3 participants did not make any saccades at all. deg = degrees.

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