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Eye movements and visible persistence explain the mislocalization of the final position of a moving target

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Abstract

When observers are asked to localize the final position of a moving target, the judged position is usually displaced from the actual position in the direction of motion. The short-term time course of the displacement was investigated to test theories that attribute the localization error to spatial and temporal properties of human perception or to representational momentum. It was found that briefly after target offset, the judged position is already displaced in the direction of motion. It is argued that the shift results from eye movements after target offset that move the target's persisting image in the direction of motion. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

When observers are asked to judge the final position of a moving target, the remembered position of the moving target is shifted in the direction of motion (for an overview, see Hubbard, 1995a). Memory-related accounts hold that this forward shift is attributable to higher-level, cognitive processes. It is assumed that the position of a moving object is mentally extrapolated while visible. Analogous to the physical momentum of real-world objects, the mental extrapolation process continues for some time after the moving stimulus vanished, resulting in a forward shift of the remembered position. The inability to stop the mental extrapolation process is referred to as representational momentum (e.g. Hubbard, 1995a; Freyd, 1987). Functionally, mental extrapolation was supposed to help predict the future position of a moving object and allow for better regulation of bodily movements (e.g. Hubbard, 1995a; Freyd & Johnson, 1987).

Hubbard extended the notion of representational momentum by demonstrating that mental representations of the final position of a moving target may be influenced by physical principles other than momentum such as gravity (Hubbard & Bharucha, 1988; Hubbard, 1990), friction, mass (Hubbard, 1995b), weight (Hubbard, 1997) and context (Hubbard, 1993). Hubbard presented displays showing smooth linear motion and asked observers to position a mouse cursor on the final position of the target (e.g., Hubbard, 1990, 1995b; Hubbard & Bharucha, 1988). Importantly, observers in Hubbard's experiments were not given any instructions concerning eye movements. Thus, it appears most likely that observers tracked the linearly moving target with their eyes. In a typical experiment, the target moved at moderate velocity (e.g. 4.2–17.7°/s in Hubbard, 1990; 5.4–34.8°/s in Hubbard & Bharucha, 1988) across a part of the screen (an average distance of approximately 10°). Velocity and duration of the stimulus motion were mostly adequate for smooth pursuit eye movements (see Robinson, 1965; Meyer, Lasker, & Robinson, 1985).

1.1. Time course with pursuit and fixation

One of the goals of the present study was to explore the time course of the localization error with smooth linear motion and different types of eye movement. In a related study, Freyd and Johnson (1987) tracked the

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time course of representational momentum with rotational motion. They showed that the judged final orientation of a rotating rectangle deviated in the direction of rotation, and that the deviation increased for 200–300 ms after stimulus offset. Subsequently, the forward shift decreased, and in some conditions, a shift of the remembered position opposite to the direction of rotation was observed. The reversal of the forward shift was attributed to memory averaging of the target's previous positions. It is important to note that the localization error and its characteristic time course were assumed to arise at a post-perceptual processing stage. Perceptual variables related to eye movements were not supposed to affect the localization error. In fact, a number of studies attempted to rule out the possibility that low-level, sensory factors account for memory displacement (e.g. Finke & Freyd, 1985; Hubbard & Bharucha, 1988, see Hubbard, 1995a, for an overview).

However, there is evidence supporting the view that eye movements affect localization of the final target position. First, Mitrani and Dimitrov (1978) established that after the disappearance of a target tracked by the observer, the eyes drift in the direction of motion with the same velocity as the target for 300–500 ms. The continuing eye movement is referred to as overtracking. Then, the eye decelerates and comes to a rest. The target velocities of 9.2 and 19.4°/s used by Mitrani and Dimitrov are very similar to those used by Hubbard (e.g. Hubbard & Bharucha, 1988). Second, Mitrani, Dimitrov, Yakimoff, and Mateeff (1979) found that overtracking, as well as size of the localization error depended on where the target disappeared. For a target vanishing at a random point on a trajectory of a fixed length, overtracking and mislocalization decreased as the target approached the end of the trajectory, suggesting that eye movements and mislocalization are closely linked.

Therefore, it may be hypothesized that localization will differ as a function of eye movement. In contrast, if displacement of the final position arises at a post-perceptual stage, no differences should emerge. To test these conflicting predictions, the time course of the displacement was examined with fixation and pursuit eye movements.

1.2. Spatial and temporal properties of human vision that may affect localization

A second goal of the present study was to test explanations of the localization error with pursuit and smooth motion that refer to temporal or spatial properties of the human visual system. An explanation in terms of a spatial distortion is related to a foveal bias observed with stationary stimuli. If a stimulus is briefly presented in the periphery, it is localized toward the fovea (e.g. Osaka, 1977; O'Regan, 1984; Müsseler, Van der Heijden, Mahmud, Deubel, & Ertsey, 1999; Van der Heijden, Van der Geest, De Leeuw, Krikke, & Müsseler, 1999). This foveal bias was measured to be about 10% of the target's eccentricity (Van der Heijden et al., 1999). If a smoothly moving target vanishes at a random point along its trajectory as in Hubbard's experiments (see Hubbard 1995a), observers are very likely to overtrack its final position (Mitrani & Dimitrov, 1978), such that the final point of fixation is displaced in the direction of motion. Given that localization of peripheral stimuli is toward the fovea, a forward shift would result. The forward shift would be expected to be 10% of the overtracking response.

A second explanation relates the displacement to temporal properties of the visual system. Early research by Hazelhoff and Wiersma (1924), already showed that temporal aspects of human vision result in localization errors. In Hazelhoff and Wiersma's experiments, subjects were instructed to track a target moving on a straight trajectory with their eyes. At some point during the pursuit of the stimulus, a second test stimulus was briefly flashed and observers' task was to localize its position. It was found that judgements of the position of the test stimulus were shifted in the direction of motion (see also Mitrani and Dimitrov, 1982). Hazelhoff and Wiersma argued that the ratio between the mislocation and the velocity of tracking is a measure of the time it takes to register a visual stimulus, the 'perception time' for visual stimuli. Conversely, the time it takes to register the stationary, flashed stimulus introduces an error in its localization.

Lately, a related phenomenon has received much interest. When a stationary stimulus is briefly flashed in physical alignment with a moving stimulus that is not tracked by the observer, observers report the flash to lag behind the moving stimulus (flash lag effect, e.g. MacKay, 1958; Nijhawan, 1994). First, it was thought that the visual system extrapolates future positions of a moving target to compensate for visual latency (Nijhawan, 1994). Quite similar to the argument made by Freyd and Johnson (1987) about the function of mental extrapolation, Nijhawan (1994) claimed that bodily actions such as catching require accurate timing and motion extrapolation may help achieve the required temporal precision. Lately, however, it has been shown that the flash lag effect may be better accounted for by latency differences between stationary and moving stimuli (Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney & Murakami, 1998). Moving stimuli have a shorter visual latency, presumably in order to suppress motion smear (Burr, 1980; di Lollo & Hogben, 1985), such that a stationary stimulus has to be presented at a position along the future trajectory of a moving stimulus to appear aligned with the moving stimulus.

A similar argument that emphasizes temporal properties of the visual system may be made against mental extrapolation. As the mislocalization of the last position of a moving stimulus concern the offset of a stimulus, not the onset of a stimulus as in Hazelhoff and Wiersma (1924) or Nijhawan (1994), a temporal explanation of the displacement does not involve visual latency, but rather *visible persistence*, that is, the time the visual response lasts after stimulus offset (for an overview, see Coltheart, 1980). It may be argued that the perception of a smoothly moving target as used by Hubbard (e.g. Hubbard & Bharucha, 1988) persists for some time such that eye movements in the direction of motion occurring after stimulus offset (overtracking) result in the perception of a target displaced in the direction of motion. It should be noted that observers will therefore perceive the target to be displaced during this period, such that continuation of mental extrapolation, or other memory-related phenomena do not apply.

The account in terms of temporal properties (visible persistence) is contrasted with an account in terms of spatial properties (foveal bias). The two accounts differ with respect to the predicted time course of the shift. The spatial distortion resulting from the foveal bias predicts that the displacement will progress at 10% of the overtracking response because the foveal bias is 10% of a target's eccentricity. In contrast, if observers continue to perceive the moving target in the first phase of the overtracking response, then the velocity of the displacement will closely match the velocity of the pursuit eye movement.

To test the conflicting predictions of memory-related and perceptual accounts, the following experiments were run. In Experiment 1, the judged final location of the stimulus was determined at various intervals after stimulus offset when observers tracked the target. Experiments 2 and 3 examined the visible persistence of the target; and Experiments 4 and 5 contrasted fixation and pursuit eye movements.

2. Experiment 1

The aim of the first Experiment was to measure the time course of the perceived final position of a smoothly moving target that was tracked by the observer. It was expected that the displacement in the direction of motion increased with time. At some point, the shift is expected to reach an asymptotic level or reverse (Freyd & Johnson, 1987). To measure the subjective position of the physically final target position at various intervals after target offset, probe stimuli were presented that were displaced in or opposite the direction of motion. Probe stimuli appeared simultaneous with the last presentation of the target or some time after target offset. Observers were asked to indicate whether they saw the probe stimulus to the left or to the right of the target stimulus as long as the target was subjectively visible, or whether the probe appeared to the left or right of the position where the target had disappeared. Left-right judgements were used to estimate the subjective vanishing point (VP) of the target. Due to visible persistence, the subjective VP may correspond to the position of a subjectively visible target briefly after target offset, whereas later, it corresponds to a remembered position. Although the absolute position of subjective disappearance may be somewhat distorted due to the Hazelhoff–Wiersma illusion (see above), the time course of the displacement, that is, differences between time intervals, may be accurately tracked by this method. To avoid masking, the probe stimuli were presented slightly above the target stimulus. To determine whether observers complied with the instruction to follow the target with their eyes, a group of observers without eye movement control was compared to a group in which eye movements were (coarsely) monitored.

2.1. Method

2.1.1. Participants

Thirty two students at the Ludwig-Maximilians University of Munich participated for pay. All reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment. Eight students were randomly assigned to each of the four experimental conditions.

2.1.2. Apparatus and stimuli

The stimuli were created using an ATI or a Matrox Millenium graphics card with refresh rates of 86 and 96 Hz, respectively. The display had a resolution of 1280 (H) $\times$ 1024 (V) pixels on a 21 in. (diagonal) screen. Stimuli were presented on a square display window centered on the screen. The display window completely filled the screen vertically but only partially horizontally. The window had an approximate size of 32° $\times$ 32° (1024 $\times$ 1024 pixel) and was white, the remaining parts of the screen were rendered black.

The target was a black disk with a diameter of 0.5°. Black on white stimulus displays were used for compatibility with the methods of Hubbard (e.g. Hubbard & Bharucha, 1988). The target entered at one edge of the display window and moved toward the opposite side. It disappeared randomly at one of five possible VPs that were 2.5° apart and centered around the midpoint of the display window. The target position was updated on each screen refresh, yielding the impression of smooth motion.

The probe stimulus was identical to the target stimulus and was presented 0.7° (center-to-center) above the target stimulus for one screen refresh (i.e. 10.4 or 11.6 ms). The stimulus-onset asynchrony (SOA) between the last presentation of the target and the onset of the probe was varied by presenting the probe stimulus in the same screen refresh cycle as the last stimulus presentation (i.e. an SOA of 0 ms), or in one of the following refresh cycles, resulting in SOAs of approximately 11 ms for the following cycle, 22 ms for the second refresh cycle after final target presentation, etc. The probe stimuli were displaced by a minimum of $\pm 0.2°$ from the VP of the target. Probe displacement from the VP was increased in steps of $\pm 0.39°$. Positive and negative numbers indicate displacement in the direction of motion and opposite to the direction of motion, respectively.

In Condition II, the horizontal position of the left eye was monitored with a head-mounted, infrared, light-reflecting eyetracker (Skalar Medical B.V., IRIS Model 6500). The analog signal was bandpass, demodulated, and low-pass filtered (DC 100 Hz, 3 dB) and then digitized at a rate of 1 kHz by a DataTranslation A/D–D/A converter (DT 2821). Eye movements were recorded from 200 ms before target disappearance until 50 ms after target disappearance.

2.1.3. Procedure

Participants sat in a dimly lit room 50 cm from the screen. Head movements were restricted by a chin-forehead rest, and viewing was binocular. Observers received about 80 practice trials and were instructed to pursue the target with their eyes. Physically, the probe stimulus and the target were simultaneously visible only with a 0 ms SOA. However, pilot studies had shown that for some time after physical target offset, observers perceived target and probe stimulus to be simultaneously visible. Thus, observers were asked to indicate the relative probe position with respect to the persisting target image while the target was visible, and with respect to the target's final position after the target had subjectively vanished. Observers pressed a left or right key to indicate that the probe stimulus was to the left or right of the physically final target position (i.e. the persisting target or its remembered position), respectively. Once a response had been obtained, the next trial was initiated after an inter-trial interval of 0.75 s. During this time, subjects were free to look at any point on the display. No feedback was provided.

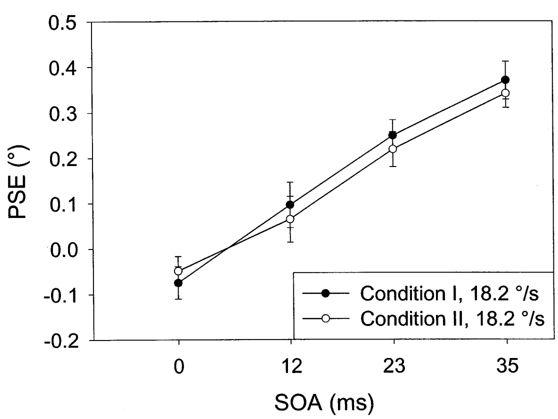

Fig. 1. Mean points of subjective equality (PSE) and (between subject) standard error as a function of stimulus onset asynchrony (SOA). Condition I and II from Experiment 1 are shown. Negative numbers indicate that the PSE was shifted opposite to the direction of motion, whereas positive numbers indicate a shift in the direction of motion.

2.1.4. Design

2.1.4.1. Condition I. The SOA between the last presentation of the target and the onset of the probe varied among 0, 12, 23, and 35 ms. The probe stimuli were displaced by ± 1.37, ± 0.98, ± 0.59, and $\pm 0.2°$ from the VP of the target. A total of 320 trials was administered (4 SOA $\times$ 8 probe positions $\times$ 2 directions of motion $\times$ 5 VPs). The target moved at 18.2°/s.

2.1.4.2. Condition II. The same trials as in Condition I were run with the following exception. The position of the pupil was registered by the eyetracker. No calibration was performed as the only purpose was to determine in which direction the eye had moved (left or right). When the eye did not move in the direction of motion during the last 200 ms before target offset, it was assumed that the subject did not follow the target. In this case, an error message appeared and the trial was repeated at a random position in the remainder of the experiment. This was rarely the case (less than 1% of all trials). Further, it was determined whether the eye had moved in the direction of motion 50 ms after target offset.

2.1.4.3. Condition III. SOAs of 0, 35, 70, and 139 ms were used. The probe stimuli were displaced by ± 1.76, ± 1.37, ± 0.98, ± 0.59, and $\pm 0.2°$ from the VP of the target. A total of 400 trials (4 SOAs $\times$ 10 probe positions $\times$ 2 directions of motion $\times$ 5 VPs) was administered. The target moved at 18.2°/s.

2.1.4.4. Condition IV. SOAs of 62, 125, 250, and 499 ms were used. The probe stimuli were displaced by -0.98, -0.59, -0.2, 0, $+0.2$, $+0.59$, $+0.98$, $+1.37$, $+1.76$, $+2.15$, and $+2.54°$ from the VP of the target. A total of 400 trials (4 SOAs $\times$ 10 probe positions $\times$ 2 directions of motion $\times$ 5 VPs) was administered. Target velocity was 18.75°/s.

2.2. Results

To estimate the point where observers perceived the target to vanish, the 50% points of subjective equality (PSE) were computed by a PROBIT analysis (Finney, 1971; Lieberman, 1983) for every participant and SOA

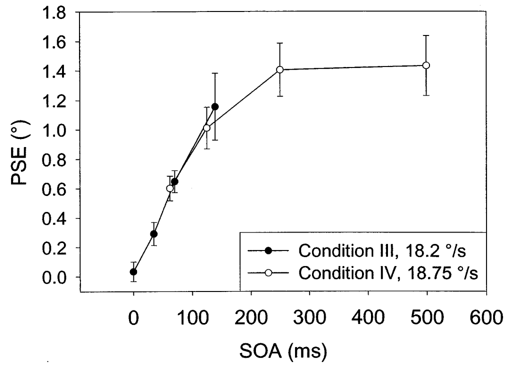

Fig. 2. Mean points of subjective equality (PSE) and (between subject) standard error as a function of stimulus onset asynchrony (SOA). Condition III and IV from Experiment 1 are shown. Negative numbers indicate that the PSE was shifted opposite to the direction of motion, whereas positive numbers indicate a shift in the direction of motion.

Table 1
Mean points of subjective equality in degrees as a function of vanishing point (VP) in Experiment 1[a]

Condition	VP				
	−5°	2.5°	0°	2.5°	5°
I	0.27°	0.21°	0.16°	0.09°	0.11°
	(0.05)	(0.02)	(0.03)	(0.07)	(0.04)
II	0.26°	0.19°	0.12°	0.09°	0.08°
	(0.03)	(0.04)	(0.05)	(0.036)	(0.04)
III	1.02°	0.87°	0.72°	0.68°	0.6°
	(0.15)	(0.07)	(0.1)	(0.08)	(0.11)
IV	1.45°	1.03°	0.65°	0.34°	0.17°
	(0.25)	(0.14)	(0.13)	(0.16)	(0.15)

[a] The (between subjects) standard error of the mean is given in brackets. Negative VPs indicate that the target disappeared before crossing the screen center, positive VPs indicate that it disappeared after crossing it.

condition (see Figs. 1 and 2). To this end, the data were collapsed across VP and direction of motion, leaving ten data points for each combination of SOA and probe condition. Also, PSEs were calculated for every participant and VP, collapsed across SOA and direction of motion, leaving eight data points for each combination of VP and probe position (see Table 1). PSE values indicate where observers perceived the physical target offset with respect to the actual VP. Negative PSEs indicate a displacement opposite to the direction of motion whereas positive PSEs indicate displacement in the direction of motion.

2.2.1. Condition I

A one-way repeated-measures ANOVA confirmed that PSEs increased with SOA from 0 to 35 ms, $F(3, 21) = 30.31$, $P < 0.0001$. T-tests ($P < 0.05$) showed all differences between successive SOAs to be significantly different from zero. A regression of SOA (in s) on PSE explained 70% of the variance with the regression equation being $\text{PSE} = 12.82°/\text{s} \times \text{SOA} - 0.06°$. A second ANOVA on PSEs as a function of VP showed that PSEs decreased towards the end of the trajectory, $F(4, 28) = 3.54$, $P < 0.0186$.

2.2.2. Condition II

A mixed-factor ANOVA with SOA as a within-subject and eye-movement monitoring as a between-subject factor was conducted on the data from Conditions I and II. There was a main effect of SOA, $F(3, 42) = 51.38$, $P < 0.0001$, but no effect of eye-movement monitoring and no interaction (Fs < 1). By t-test ($P < 0.05$), PSEs at successive SOAs were significantly different. A regression of SOA on PSE on the combined data from Condition I and II explained 68% of the variance with the regression equation being $\text{PSE} = 11.57°/\text{s} \times \text{SOA} - 0.06°$. A second ANOVA on PSEs as a function of VP on the combined data showed that PSEs decreased towards the end of the trajectory, $F(4, 28) = 7.98$, $P < 0.0001$. Analysis of the eye movement data showed that in 99% of all trials the eye had moved in the direction of motion 50 ms after stimulus offset.

2.2.3. Condition III

A one-way repeated-measures ANOVA confirmed a shift of PSE with SOAs from 0 to 135 ms, $F(3, 21) = 24.74$, $P < 0.0001$. By t-test ($P < 0.05$), PSEs at successive SOAs were significantly different. A regression of SOA on PSE explained 65% of the variance with the regression equation being $\text{SOA} = 12.06°/\text{s} \times \text{SOA} - 0.18°$. A second ANOVA on PSEs as a function of VP showed that PSEs decreased towards the end of the trajectory, $F(4, 28) = 4.12$, $P < 0.0095$.

2.2.4. Condition IV

A one-way repeated-measures ANOVA confirmed a shift of PSE with SOAs from 62 to 499 ms, $F(3, 21) = 13.65$, $P < 0.0001$. By t-test ($P < 0.05$), PSEs at successive SOAs were significantly different up to the 250 ms SOA. A regression of SOA on PSE explained 27% of the variance with the regression equation being $\text{PSE} = 1.68°/\text{s} \times \text{SOA} + 0.72°$. Inspection of the data showed that the function relating PSE and SOA was not linear. A second ANOVA on PSEs as a function of VP showed that PSEs decreased towards the end of the trajectory, $F(4, 28) = 15.98$, $P < 0.0001$.

2.3. Discussion

The results clearly show that the judged final position of a moving target that is tracked by the observers shifts in the direction of motion with time. As the regression equations show, the PSE moved at a velocity of about 12°/s in the direction of motion for 130 ms after target offset. Then, the displacement reached an asymptote at about 250 ms.

Two things should be noted. First, unlike in Freyd and Johnson (1987), the shift of PSE did not decrease after 200–300 ms. Quite clearly, the judged VP reached an asymptote around this time. The longest SOA (499 ms) does not differ from an SOA of 250 ms. Second, the velocity of the shifting PSE was lower than the actual target velocity of 18.2°/s (20.3°/s), even shortly after target offset. This is consistent with the results of Freyd and Johnson who reported the velocity of the memory shift to be in the same range, but somewhat lower than the actual rotation (19 vs. 32°/s).

Further, PSEs were found to be lower toward the end of the trajectory. Mitrani et al. (1979) already noted that overtracking and localization error decreased toward the end of the trajectory. If the assumption is correct that eye movements contribute to the localization error, then anticipatory eye movements may account for this finding. Observers anticipate predictable changes in target direction by decreasing the velocity of pursuit eye movements (Dodge, Travis, & Fox, 1930; Kowler, 1989; Boman & Hotson, 1992). Thus, observers may have reduced the velocity of the tracking movement toward the end of the trajectory. Consistent with this finding, the PSEs decreased toward the end of the trajectory. Because the data were collapsed across VP to determine the PSEs as a function of SOA, the velocity of the shift with SOA may be underestimated. An attempt at eliminating this confound was made in Experiment 5.

Condition II showed that observers complied with the instruction to track the target. Observers rarely failed to move the eyes in the direction of target motion. Because no effect of eye movement control was observed, it may be assumed that observers tracked the target even if not controlled by the experimenter. In fact, Experiments 4 and 5 show that if observers had not complied with this instruction, the shift of PSE would be absent. Also, the results of Mitrani and Dimitrov (1978) were replicated. It was found that observers' eyes were shifted in the direction of motion briefly after target offset, indicating overtracking.

Thus, briefly after target offset, observers' eyes were shifted beyond the point that was fixated when the target vanished. From the foveal bias with stationary targets, it is predicted that localization of the target's final position will be in the direction of motion. A constant bias toward the fovea predicts a shift of PSE with SOA similar in size to the bias observed with stationary stimuli (10%; Van der Heijden et al., 1999). Thus, the velocity of the shifting PSE is expected to be about 10% of the overtracking response. As the velocity of the overtracking response was determined to be about the same as the target velocity (Mitrani & Dimitrov, 1978), or maybe even lower due to anticipatory slowing towards the end of the trajectory, one would predict the velocity of the shifting PSE to be about 1.8°/s (2.3°/s) or slower. However, 130 ms after stimulus offset, the velocity of the shift was about six times as fast (approximately 12°/s). Thus, localization performance with stationary stimuli provides but a poor fit for localization performance observed with moving stimuli.

Therefore, spatial characteristics of human vision appear insufficient to account for the observed pattern of displacement, and an examination of the temporal characteristics is warranted. In particular, it may be the case that the target's image persisted for some time such that observers perceived the target to be displaced in the direction of motion briefly after target offset. If this was the case, then the velocity of the PSE-shift should be quite similar to the velocity of the tracking movement. The ratio of actual and expected shift may be considered an index of the fit of the conflicting predictions. In Conditions I–III, the ratio was $12/18.2 = 0.66$ for the temporal versus $12/1.8 = 6.67$ for the spatial account. Thus, the temporal account provides a much better explanation of the observed velocity of the shift than the foveal bias.

To further test the temporal account, two experiments were run. In Experiment 2, observers were asked to discriminate successive and simultaneous presentation of target and probe stimulus. In Experiment 3, observers had to judge the onset and offset of a moving visual stimulus relative to an acoustic probe. By means of this procedure, visible persistence was estimated.

3. Experiment 2

The purpose of the present experiment was to test whether observers perceived target and probe stimulus to be successively presented when a target-probe SOA of 23 ms was used. In Condition I of Experiment 1, this SOA had been shown to yield a significant shift of PSE in the direction of motion. Memory-related accounts would argue that a mental extrapolation process continued after target offset, resulting in a localization error. As mental extrapolation is supposed to operate in memory, one may argue that perceptual processes dealing with the stimulus should have ceased when the displacement first occurs. Otherwise, it would be hard to maintain that the shift is a product of memory-related processes. Therefore, observers are expected to notice simultaneous and successive presentations. In contrast, if the sluggishness of the visual system, that is, visible persistence, contributed to the effect, then it may be expected that observers are unable to discriminate between successive and simultaneous presentation of target and probe.

3.1. Method

3.1.1. Participants

Eight observers from Experiment 1, Condition I, participated for pay.

3.1.2. Apparatus and stimuli

Apparatus and stimuli were the same as in Experiment 1. The target moved at 18.2°/s.

3.1.3. Design

The SOA between the last presentation of the target and the onset of the probe varied between 0 and 23 ms. Otherwise, the same design as in Experiment 1, Condition I, was used. The probe stimuli were displaced by ± 1.37, ± 0.98, ± 0.59, and $\pm 0.2°$ from the actual VP or the subjective VP (PSE) of the target. The subjective VPs were determined in Experiment 1 for each observer and SOA condition. The type of assumed VP (actual or subjective) was blocked and the order of presentation was balanced across subjects. A total of 320 trials was administered (2 types of VP × 2 SOAs × 8 probe positions × 2 directions of motion × 5 VPs).

3.1.4. Procedure

The procedure was as in Experiment 1 with the following exceptions. Observers had to judge whether the presentation of target and probe stimulus was simultaneous by selecting either 'simultaneous' or 'not simultaneous' as response category. No feedback was provided. Observers participated in Experiment 1 and 2 within 1 week.

3.2. Results

Mean proportion of correct responses (PCR) were computed for each type of VP. Also, the data were treated as a yes-no detection task, and d'-values were computed. The percentage of 'simultaneous' judgements varied between 47 and 64% with a mean of 54%. T-test showed that overall, observers were unable to reliably discriminate between SOAs of 0 and 23 ms with both actual (0.48 PCR), $t(7) = -0.47$, $P > 0.64$, and subjective VP (0.48 PCR), $t(7) = -0.84$, $P > 0.43$. D'-values were not significantly different from zero for actual (-0.08), $t(7) = -0.44$, $P > 0.67$, and subjective VP (-0.12), $t(7) = 0.8$, $p(7) > 0.45$.

3.3. Discussion

Clearly, observers were unable to reliably discriminate between simultaneous and asynchronous presentation of target and probe stimuli. This inability was present with probe stimuli centered around the subjective and the objective VP. This result is unexpected from the viewpoint of memory-related accounts. If the shift of PSE observed 23 ms after stimulus offset was due to memory-related processes, then observers should be able to tell when the sensory input ceases. The inability to discriminate between simultaneous and successive presentation, however, supports the view that the sensory activity related to the target stimulus was still present when the probe stimulus was presented. This result suggests that the target's visible persistence was at least 23 ms.

4. Experiment 3

In order to determine the exact visible persistence of the target stimulus, temporal order judgements were used (e.g. Bowen, 1981; Rutschmann & Link, 1964; see Coltheart, 1980, for an overview). An acoustic probe stimulus was presented around the time of the physical onset or offset of the visual stimulus. Observers' task was to indicate whether the acoustic probe stimulus was presented before or after the visual offset. The real-time delay from offset of visual stimulus to onset of probe stimulus that is judged as simultaneous serves as an estimate of the relative offset time of the visual stimulus. In order to determine the visible persistence, the difference between relative onset and offset times may be used (e.g. Bowen, 1981). This measure factors out differences in the visual and acoustic response latencies (these should be evident in the relative onset times) and estimates the absolute duration of the visual response, that is, visible persistence.

4.1. Method

4.1.1. Participants

Ten students at the Ludwig-Maximilians University of Munich were paid for their participation. All reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment.

4.1.2. Apparatus, stimuli, and procedure

The same apparatus, stimuli, and procedure were used as in Experiment 1 with the following exceptions. No visual probe stimuli were presented. The target moved at 20.3°/s. As acoustic probe stimulus, a 3 ms click, presented via headphones, was used. The acoustic probe stimulus was presented around the onset or offset of the visual stimulus. To determine the relative offset time, the same display parameters were used as in Experiment 1. In the onset condition, the target appeared at the center of the screen and moved to the right or left until it vanished in the black frame. Observers had to indicate whether the acoustic probe stimulus was presented before or after the onset/offset of the visual target by pressing one of two keys. The inter-trial interval varied randomly between 1050 and

1650 ms. Thereby, the time at which the response was emitted could not be used as a cue to target onset.

4.1.3. Design

The stimulus-onset asynchrony (SOA) between the first or last presentation of the target and the onset of the acoustic probe varied among ± 312, ± 208, ± 104, and ± 42 ms. Positive numbers indicate that the tone was presented after onset/offset of the visual stimulus, negative numbers indicate that the tone preceded the onset/offset. In the offset condition, eight levels of SOA were fully crossed with five possible VPs, and two possible directions of initial motion. Each combination was presented three times for a total of 240 trials. In the onset condition, the eight levels of SOA were combined with two possible directions of motion. Each condition was presented 15 times for a total of 240 trials. Onset and offset condition were blocked and the order of presentation balanced across subjects.

4.2. Results

For onset and offset condition, the point of subjective simultaneity was determined by means of a PROBIT analysis. To this end, the data were collapsed across VP, direction of motion and repetition, leaving 30 data points for each level of SOA in both the onset and the offset condition. In order for visual onset and acoustic probe to be perceived as simultaneous, the acoustic stimulus had to be presented at an SOA of -8 ms, which was not significantly different from zero, $t(9) = -0.56$, $P > 0.58$. Visual offset and acoustic probe were perceived as simultaneous with an SOA of 51 ms, which was significantly different from zero, $t(9) = 4.26$, $P < 0.0025$. The difference between relative onset and offset time (59 ms) was different from zero, $t(9) = 4.26$, $P < 0.0021$.

4.3. Discussion

The acoustic probe had to be presented at about the same time as the visual onset to be perceived as simultaneous, which is in agreement with previous studies (e.g., Aschersleben & Müsseler, 1999). To achieve subjective simultaneity with the visual offset, however, the acoustic probe had to be delayed by 51 ms. Thus, the visual response to the target stimulus persisted for 59 ms. The implications of this result are far-reaching. It has to be concluded that during the first 59 ms after physical target offset, observers still perceived the target. Because observers were overtracking the final position of the target, they actually saw the target's persisting image displaced from the true VP in the direction of motion. Therefore, the observed displacement during this time interval may be a product of memory, but not the high-level, cognitive memory referred to by Hubbard (1995a), but rather a form of low-level afteractivity in the visual system (e.g. Coltheart, 1980).

5. Experiment 4

So far, it was established that the subjective VP of targets tracked by the eyes shifts in the direction of motion briefly after stimulus offset. Part of the shift occurs during a time interval in which the visual response to the target has not ceased. Thus, a form of visual short-term memory results in the perception of a target that moves in the direction of motion, although the physical target has disappeared. Experiments 4 and 5 were designed to compare the time course of displacement with fixation and pursuit eye movements.

First, such a comparison allows for a direct test of the hypothesis that eye movements occurring after stimulus offset carry the persisting image of the target in the direction of motion. If this is indeed the case, then no shift should be observed in the absence of pursuit eye movements.

Second, comparing fixation with pursuit clarifies whether differences in instruction concerning eye movements affect the time course. Whereas Freyd (e.g. Freyd & Finke, 1984) instructed observers to maintain fixation, Hubbard (e.g. Hubbard & Bharucha, 1988) did not give any specific instruction so that one may assume that observers in his experiments tracked the target. In Experiment 1, it was demonstrated that the time course with pursuit and smooth, linear motion differs from that reported by Freyd and Johnson (1987) who presented rotational motion. Thus, one may ask whether the time course with linear motion will more closely resemble Freyd and Johnson's findings when fixation is maintained, which they claimed their observers did. This prediction, of course, is at odds with what is expected from a perceptual explanation of the effect.

5.1. Method

5.1.1. Participants

Eight students at the Ludwig-Maximilians University of Munich were paid for their participation. All reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment.

5.1.2. Apparatus, stimuli, and procedure

The same apparatus, stimuli, and procedure were used as in Experiment 1 with the exception that a fixation dot (0.03°) was visible 2° below the screen center. The target moved at 20.3°/s.

Eye movements were displayed on a LCD display and monitored by the experimenter. Again, no exact calibration was performed such that eye movement control was rather crude. This was done because it had proven difficult for untrained observer to maintain fixation within one degree of visual angle for the presentation times used. With exact eye movement control, observers were preoccupied with suppression of eye movements, eye blinks, and head movements, and performed poorly on the primary task. As a lack of eye movement control would work against the hypothesis that different types of eye movements contribute to the localization error (observers spontaneously tracked the target, see Experiment 1), exact eye movement control was abandoned in favor of more informal monitoring. When the experimenter detected an eye movement error (eye motion in the fixation condition and no eye movement in the pursuit condition), an error message informed the observer about the error and the trial was repeated at a random position in the remainder of the block. This was the case for 2% of the trials with pursuit eye movements and 5% of the trials with fixation.

5.1.3. Design

The SOA between the last presentation of the target and the onset of the probe varied between 0, 21, 42, and 62 ms. The probe stimuli were displaced by ± 1.37, ± 0.98, ± 0.59, and $\pm 0.2°$ from the VP of the target. The target stimulus moved at a velocity of 20.3°/s and disappeared randomly within 5° of the screen center. Observers participated in three sessions. In each session, they were instructed to either follow the target with their eyes or to maintain fixation. Eye movement condition was blocked, and the order balanced across subjects. During each of the three session, a total of 384 trials was administered (2 eye movement conditions × 4 SOAs × 8 probe positions × 2 directions of motion × 3 replications) for a total of 1152 trials.

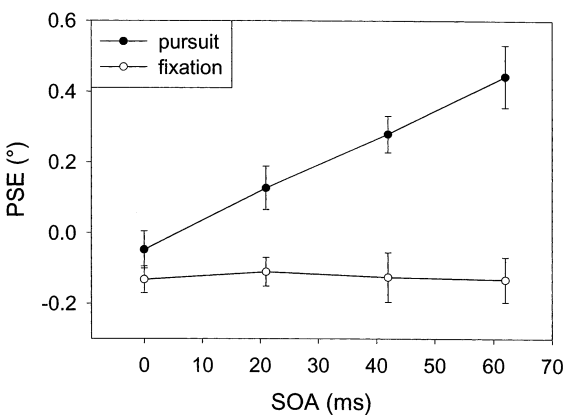

Fig. 3. Mean points of subjective equality (PSE) and (between subject) standard error as a function of stimulus onset asynchrony (SOA) and eye movement condition from Experiment 4 are shown. Negative numbers indicate that the PSE was shifted opposite to the direction of motion, whereas positive numbers indicate a shift in the direction of motion.

5.2. Results

PSEs were computed by a PROBIT analysis for every participant, eye movement, and SOA condition (see Fig. 3). To this end, the data were collapsed across VP and direction of motion, leaving 18 data points for each combination of eye movement condition, SOA and probe condition. In order to assess the influence of trajectory, trials were divided according to whether the target had disappeared before crossing the center screen, or after passing it. In the fixation condition, this division corresponds to a distinction of motion towards the fovea or away from the fovea. Then, PSEs were calculated for every participant, eye movement condition and VP.

A two-way repeated-measures ANOVA (SOA × eye movement) confirmed that PSEs increased with SOA from 0 to 62 ms, $F(3, 21) = 17.06$, $P < 0.0001$. PSEs were smaller with fixation than with pursuit (−0.12 vs. 0.2°), $F(1, 7) = 44.3$, $P < 0.0003$. Importantly, the interaction between SOA and eye movement condition reached significance, $F(3, 21) = 16.77$, $P < 0.0001$. Separate ANOVAs for each eye movement condition confirmed a significant influence of SOA on PSE in the pursuit condition, $F(3, 21) = 33.35$, $P < 0.0001$, but not in the fixation condition, $F(3, 21) = 0.08$, $P > 0.96$.

In the pursuit condition, a regression of SOA (in s) on PSE explained 53% of the variance with the regression equation being $\text{PSE} = 7.81°/\text{s} \times \text{SOA} - 0.04°$. In the fixation condition, the regression explained 2×10^{-4}% of the variance with the regression equation being $\text{PSE} = -0.08°/\text{s} \times \text{SOA} - 0.12°$.

A second two-way ANOVA (VP × eye movement) on PSEs showed that PSEs for targets vanishing in the first part of the trajectory were larger than those for targets vanishing in the later part (0.16 vs. −0.07°), $F(1, 7) = 52.95$, $P < 0.0002$, and PSEs with pursuit were larger than with fixation (0.21 vs. −0.12°), $F(1, 7) = 44.25$, $P < 0.0003$.

5.3. Discussion

In the pursuit condition, the standard forward shift, although somewhat less pronounced, was observed. In contrast, PSE values did not vary with SOA when observers maintained fixation. This finding supports the view that the localization error is accounted for by eye movements that shift the target's persisting image in the direction of motion. In contrast, the results are at odds with the notion that high-level memory functions are responsible for the displacement. If this was the case, no difference should be observed between fixation and pursuit, because representational momentum is thought to occur at a post-perceptual stage. Also, the present results are at odds with the findings of Freyd and Johnson (1987) who reported memory displacement with fixation. Two possible explanations for this discrepancy will be discussed in Section 7.

Further, PSEs were found to decrease in the later part of the trajectory both during pursuit and fixation. Although the direction of the effect was the same in both conditions, the reasons for the decrease may differ for the two eye movement conditions. In the pursuit condition, the reduction of PSE with trajectory length from Experiment 1 was replicated. The reduction was attributed to anticipatory slowing of the eyes towards the end of the trajectory. In the fixation condition, the PSE was shifted in the direction of motion for targets disappearing when moving toward the point of fixation, and opposite the direction of motion for targets moving away from the fovea. Thus, the effect of VP in the fixation condition may be a result of the foveal bias that is also observed with stationary stimuli (e.g. Van der Heijden et al., 1999).

6. Experiment 5

The purpose of the present Experiment was to replicate Experiment 4 with a slightly different methodology. In Experiment 4, the velocity of the forward shift in the pursuit condition was decreased compared to Experiment 1 (7.8 vs. approximately 12°/s with target velocities of 20.3 and 18.2°/s, respectively). The reason for the reduction may have been response strategies. In Experiment 4, observers were instructed to perform different types of eye movements, and it appears likely that they noticed different percepts as a function of eye movement. Therefore, they may have tried to compensate for the ‘wrong’ perceptions in the pursuit condition. To eliminate this confound, laboratory observers were used instead of untrained observers. Further, in order to reduce the influence of anticipatory slowing towards the end of the trajectory, observers were instructed to closely monitor their own eye movements, in particular towards the end of the trajectory. If they felt they had slowed down, they were to discard the run. The method of adjustment was used.

6.1. Method

6.1.1. Participants

The author and two laboratory observers who did not know the purpose of the study participated in the Experiment.

6.1.2. Apparatus, stimuli, procedure and design

The same apparatus and procedure were used as in Experiment 1 with the following exceptions. The target moved at 20.3°/s and vanished randomly within 3° of the screen center. A fixation dot was presented 2° below the screen center. The dot was visible with pursuit and fixation. In Condition I, SOAs of 0, 21, 42, and 62 ms were combined with two directions of motion. In Condition II, SOAs of 104, 198, 302, and 395 ms were used. At the beginning of each run, the probe stimulus appeared randomly within 1° of the actual VP of the target. The task of the observer was to adjust the position of the probe via key-presses until it appeared aligned with the last position of the target. All observers completed Condition I before Condition II. Observers MT and SM completed both conditions within 2 weeks, DK ran Condition II two months after Condition I. Nine repetitions of each condition were collected. The data were collapsed across direction of motion for 18 repetitions per SOA and eye movement condition.

6.2. Results and discussion

PSEs as estimated by the adjustment procedure are depicted for each observer, SOA, and eye movement condition in Fig. 4. Regression equations for the short and long SOAs as a function of eye movement and observer are presented in Table 2.

With pursuit eye movement and short SOAs (0–62 ms), the PSE shifted in the direction of motion at about 16°/s for all three observers which is somewhat below the target velocity of 20.3°/s. Thus, the relatively slow shift of the PSE in Experiment 4 (7.8°/s) may have been due to response strategies of untrained observers. With fixation and short SOAs, the increase was largely absent and even slightly reversed for observers DK and SM.

With pursuit and long SOAs, the velocity of the shifting PSE was small (DK and MT) or slightly reversed (SM). Only the PSE velocity of MT in the pursuit/long SOAs condition (1.12°/s) was in the range of what a foveal bias would predict (2.3°/s, i.e. 10% of the target velocity). With long SOAs and fixation, all observers showed a small shift of PSE of about 0.3°/s which may be accounted for by a drift of the eyes in the direction of motion after target offset. In sum, a substantial forward shift was only observed in the pursuit condition with small SOAs. All other conditions yielded only small and even negative shifts. Again, this result is unexpected from the point of view of memory-related theories.

Further, the confidence limits for the estimated PSEs increased with SOA. This is expected if one assumes that memory for the spatial location somehow decays. Strikingly, observers’ judgements become highly variable after 62 ms in the pursuit condition. A similar observation can also be made in Conditions III and IV of Experiment 1. Given the high variation, it may be doubted that observers had a stable representation of the final target position with pursuit after about 60 ms. The relatively small variability up to an SOA of 62 ms,

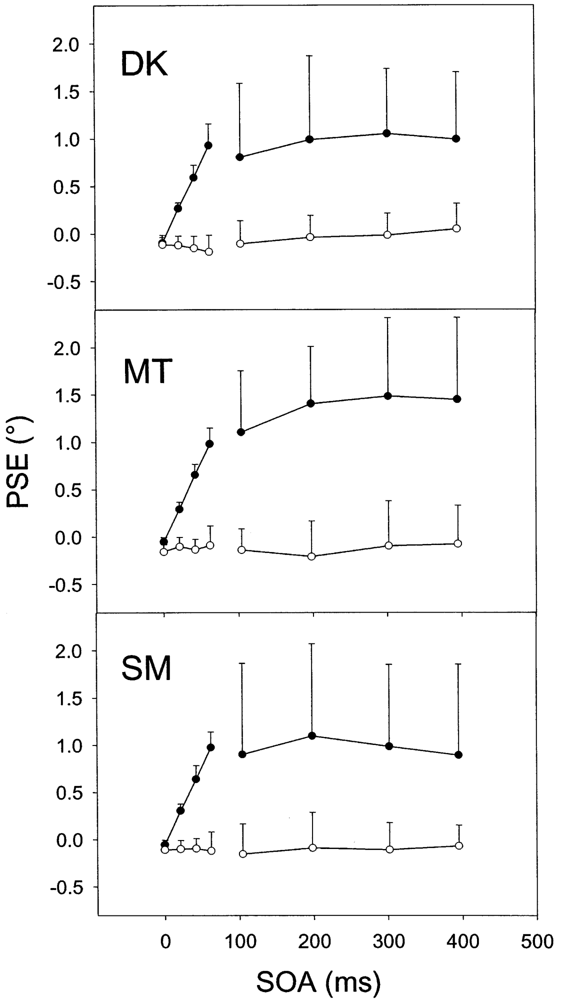

Fig. 4. Mean points of subjective equality (PSE) and 95%-confidence limits as a function of stimulus onset asynchrony (SOA) and eye movement condition in Experiment 5. Data from three observers (DK, MT, SM) are shown. Negative numbers indicate that the PSE was shifted opposite to the direction of motion, whereas positive numbers indicate a shift into the direction of motion.

however, supports the view that during this time, observers still experienced a visual response related to the target which was used to judge the final location.

A possible explanation of the increase in variability after 62 ms in the pursuit condition may be greater task difficulty. After the visual response to the target ceased, observers' pursuit eye movements continued for some time. Thus, the final retinal position of the target (ideally foveal) could not be used for the comparison with the probe. Rather, only the egocentric position of the target was available. In contrast, the fixation condition allowed for a comparison of final target and probe position in retinal coordinates. This suggests that the transformation of retinal into egocentric coordinates during overtracking was difficult and produced highly variable judgements. Further, this result suggests that untrained observers who showed a shift of PSE up to 250 ms (see Experiment 1) may have compared the final retinal target position with the probe stimulus. In other words, they may have compared their shifting point of fixation during overtracking with the probe stimulus. Trained laboratory observers were more accurate, but the high variability witnessed to the difficulty of the task.

7. General discussion

In the present series of experiments, the short-term time course of localization of the final position of a moving target was examined. The basic finding that was elaborated on is the mislocalization of the final position of a moving target in the direction of motion. Previously, the displacement has been accounted for by mental extrapolation (e.g. Hubbard, 1995a), a post-perceptual, cognitive process. In the present paper, evidence was provided for the alternative hypothesis that the displacement results from eye movements that move the persisting image of the target in the direction of

Table 2
Results of linear regressions of stimulus onset asynchrony (SOA) between target offset and probe onset on the point of subject equivalence (PSE) in Experiment 5

		Condition I (SOA 0−62 ms)		Condition II (SOA 104–395 ms)	
Observer		Pursuit	Fixation	Pursuit	Fixation
DK	Coefficient (°/s)	16.35	−1.24	0.33	0.49
	Intercept (°)	−0.09	−0.11	0.89	−0.15
	r^2	0.96	0.18	0.03	0.16
MT	Coefficient (°/s)	16.56	0.78	1.13	0.31
	Intercept (°)	−0.05	−0.15	1.08	−0.21
	r^2	0.97	0.07	0.09	0.03
SM	Coefficient (°/s)	16.48	−0.15	−0.14	0.24
	Intercept (°)	−0.05	−0.1	1.01	−0.16
	r^2	0.97	2.8×10^{-3}	10×10^{-3}	0.03

motion. Experiment 1 showed that the judged location shifted in the direction of motion for about 250 ms. After SOAs as short as 11 ms, a significant forward shift was confirmed. Experiment 2 showed that observers were unable to discriminate between simultaneous and successive (SOA of 23 ms) presentation. Visible persistence was measured to be 59 ms in Experiment 3. Experiments 4 and 5 showed that the displacement was eliminated when observers maintained fixation. Experiment 5 showed that there was only a very small increase in displacement after 62 ms, and that judgements became highly variable with pursuit eye movements after 62 ms.

In the present experiments, it was demonstrated that the characteristic time course of representational momentum (Freyd & Johnson, 1987) does not obtain with linear target motion. In Experiment 1, no decrease or reversal of the forward shift was observed after 200–300 ms with tracking movements. Experiments 4 and 5 showed that with fixation, no forward shift occurs at all. These results are at odds with Freyd and Johnson's report of an increasing forward shift. Freyd and Johnson used stimuli that implied the rotation of a rectangle about its center. Three consecutive pictures of a rectangle at different orientations were shown. Each picture was presented for about 250 ms and successive presentations were separated by blank intervals of about 250 ms. Between presentations, the degree of rotation was increased by 17°. A theoretical and a methodological argument may account for the discrepancies between the present results and Freyd and Johnson's. First, it may be the case that memory displacement applies to only a limited class of motion, that is, implied motion. This may explain the failure to obtain the characteristic time course with smooth, linear motion. However, such an explanation would be inconsistent with that of Hubbard (1995a) claim that displacement observed with linear motion is due to mental extrapolation. Also, it would be inconsistent with the claim that representational momentum, and related distortions of visual memory (representational gravity, friction, etc.) are general properties of human memory that have evolved phylogenetically from the interaction with the physical environment. The kind of implied motion employed by Freyd and colleagues is rather artificial compared to the more natural, smooth motion of Hubbard. Thus, if prior experience with the physical environment was the cause of the mislocalization, then the effect should be more pronounced with smooth motion. This is inconsistent with the present results.

Second, it may have been the case that observers in Freyd and Johnson (1987) tracked parts of the complex stimulus despite the instruction to maintain fixation. Although the motion of the rectangle was rotational, the trajectory of single elements (e.g. the corners) was almost linear for the degree of rotation that was presented (the rectangle was rotated twice by 17° for a total rotation of 34°). As Experiment 1 showed, naive, untrained observer have a strong tendency to track a moving stimulus. Even if they tried to abide by the instruction not to track the stimulus, involuntary shifts in fixation may have occurred. However, as eye movements were not registered, these ideas are only speculations. Even more so given that very little is known about the exact stimulus characteristics used by Freyd. For instance, Freyd and Johnson (1987) do not report the color or the dimensions of the rectangle they presented, such that it is impossible to determine the effect sizes in degrees of visual angle (only angles of rotation are given). In sum, the reasons for the discrepancy with the results of Freyd and Johnson remain obscure and warrant further research. However, the present results are hard to reconcile with the claims of Hubbard (1995a).

Another issue that needs further clarification is why the velocity of the shifting PSE was consistently below the target velocity. If observers tracked the target accurately, and if the overtracking response continued at about the same speed as the tracking response, then one would expect the shift of PSE to be about the same as the target velocity. In Experiment 5, the PSE-shift velocity was 16°/s with a target moving at 20.3°/s, that is, a ratio of 0.78, which is in reasonable agreement with this prediction. However, one may wonder how the difference between PSE-shift velocity and target velocity relates to characteristics of pursuit eye movements, such as catch-up saccades occurring during pursuit, pursuit gain, etc. (e.g. Engel, Anderson, & Soechting, 1999). Further research that examines the relation between the quality of smooth pursuit and displacement will help to clarify these issues.

The interpretation of the localization error provided in the present paper does not refer to higher-level cognitive processes. However, this is not to say that higher-level processes do not affect mislocalization. Any higher-level process that affects pursuit behavior will also affect localization of the last position. Experiments 1 and 4 showed that the localization error was reduced when the target vanished toward the end of the trajectory, presumably, because anticipatory slowing of the eye movement occurred. Thus, expectancies about the future position of a moving object do play a role in the localization error, albeit a very indirect one. Only inasmuch as knowledge about the future path of a moving target is anticipated by predictive eye movements (Dodge et al., 1930; Kowler, 1989; Boman & Hotson, 1992) do higher level processes come into play.

The major result of the present experiments is that the localization error observed when observers are asked to judge the final position of a moving target does not result from mental extrapolation. The visible persistence of the target after its physical offset, and the absence of displacement with fixation challenge such an interpretation. The present results suggest that visible persistence combined with eye movements may account for the displacement.

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