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Attention maintains mental extrapolation of target position: Irrelevant distractors eliminate forward displacement after implied motion

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Abstract

Observers' judgments of the final position of a moving target are typically shifted in the direction of implied motion ("representational momentum"). The role of attention is unclear: visual attention may be necessary to maintain or halt target displacement. When attention was captured by irrelevant distractors presented during the retention interval, forward displacement after implied target motion disappeared, suggesting that attention may be necessary to maintain mental extrapolation of target motion. In a further corroborative experiment, the deployment of attention was measured after a sequence of implied motion, and faster responses were observed to stimuli appearing in the direction of motion. Thus, attention may guide the mental extrapolation of target motion. Additionally, eye movements were measured during stimulus presentation and retention interval. The results showed that forward displacement with implied motion does not depend on eye movements. Differences between implied and smooth motion are discussed with respect to recent neurophysiological findings.
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1. Introduction

When observers are asked to localize the final position of a moving target, a systematic tendency to mislocalize the final position in the direction of implied motion has been observed (for an overview, see Hubbard, 1995b). In the present paper, evidence is provided that attention is necessary to generate this error. Previously, links between

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attention and object localization have been neglected. The present paper establishes such links empirically and shows how this approach may integrate apparently unrelated findings such as left–right asymmetries in attentional tracking (Müller & von Mühlenen, 1996), and left–right asymmetries in object localization (Halpern & Kelly, 1993).

In early studies, Freyd and colleagues displayed series of still frames to imply the rotation of a rectangle (e.g. Freyd & Finke, 1984, 1985; Freyd & Johnson, 1987). Observers were presented with three views of a rectangle at different rotations about its center (inducing stimuli). When the orientations of consecutive presentations implied rotation in a consistent manner, participants' memory for the third orientation tended to be shifted in the direction of rotation. That is, the orientation of a fourth probe rectangle had to be rotated slightly further to be judged as being in the same position as the third presentation. The forward shift of the final position of a stimulus undergoing implied motion was explained by postulating that the dynamics of the representational system follow physical laws, such as momentum. The forward displacement was therefore referred to as *representational momentum* (Finke & Freyd, 1985; Finke, Freyd, & Shyi, 1986; Finke & Shyi, 1988; Freyd, 1987).

Here, the term representational momentum is used for the theoretical explanation in terms of internalized physical regularities, whereas the observed mislocalization is referred to as *forward displacement* (FD). The theoretical interpretation in terms of internalized dynamics of the physical world is under debate (Hubbard, 1995b; Kerzel, 2000; Kerzel, Jordan, & Müsseler, 2001), mainly because eye movements may contribute to FD with smooth stimulus motion. To avoid the association of FD and physical principles, the more neutral term *mental extrapolation* is used to refer to the process that underlies the forward localization error (see also Finke & Freyd, 1989). Mental extrapolation may be guided by physical principles, but other factors, such as expectations (e.g. Verfaillie & d'Ydewalle, 1991) may contribute as well. Further, mental extrapolation refers to a rather high-level process that should not be confounded with low-level motion extrapolation. Low-level motion extrapolation was originally thought to compensate for neural transmission delays (Nijhawan, 1994), such that a flashed object would be seen to lag a moving target (but see Krekelberg & Lappe, 2001). In contrast to mental extrapolation, low-level motion extrapolation as proposed by Nijhawan may take place at very early levels of processing, possibly in the retina (Berry, Brivanlou, Jordan, & Meister, 1999).

1.1. Smooth vs. implied motion

The present study is concerned with the localization of objects undergoing implied motion. The distinction between implied and smooth motion is important because there is reason to believe that the two types of motion elicit different eye movement responses and may be processed differently in the cortex (see below). Motion can be implied by showing a target stimulus with large spatial and temporal separations between successive displays. In most studies on representational momentum, the target was presented at the same position for about 250 ms before it was moved to the next position. Successive target presentations were interrupted by blank intervals of about 250 ms. Thus, there was no actual motion of the stimulus; rather, a succession of static images was presented. In contrast, smooth motion on a computer monitor is rendered by avoiding long blank intervals and large distances between successive target presentations. Typically, the target is presented at the same position for only one refresh cycle of the computer monitor (mostly less than 17 ms) before it is moved to the next position. That is, position changes occur at a frequency similar to the refresh rate of the monitor (mostly larger than 60 Hz). Because of the limited temporal resolution of the human visual system, these rapid position changes appear as smooth and continuous, even though the physical stimulus is a rapid series of discrete position changes. As perceived motion is an effective stimulus for the smooth pursuit system (Yasui & Young, 1975), smooth pursuit eye movements may be elicited by smooth stimulus motion, but to a much smaller degree by implied stimulus motion.

In some studies on localization of the final target position, smooth stimulus motion was investigated (e.g. Hubbard & Bharucha, 1988) and FD was confirmed. In contrast to the previous interpretation of FD in terms of representational momentum, a more recent explanation attributed the error to eye movements. When smooth stimulus motion was presented, it was highly likely that observers followed the target with their eyes. After target disappearance, the smooth pursuit eye movements would overshoot the final target position, such that the point of fixation would be shifted in the direction of motion during the retention interval. Persistence of the target's image in the visual system after target offset (Kerzel, 2000), and a bias to localize the target toward the fovea (Kerzel et al., 2001) may contribute to FD after oculomotor overshoot. In support of this hypothesis, it was demonstrated that FD with smooth linear target motion disappeared when observers were instructed not to follow the target with their eyes (Baldo, Kihara, Namba, & Klein, 2002; Kerzel, 2000; Kerzel et al., 2001; Whitney & Cavanagh, 2002; Whitney, Murakami, & Cavanagh, 2000).

An account of FD with implied motion in terms of oculomotor overshoot is rather implausible. Implied motion is unlikely to elicit smooth pursuit eye movements because there are long blank intervals between successive target presentations and no actual motion is involved (Churchland & Lisberger, 2000). Reports of smooth pursuit in the absence of target motion are rare (e.g. Becker & Fuchs, 1985) and may not occur with untrained observers at all (Pola & Wyatt, 1991). However, occurrence of smooth pursuit or other eye movements during the retention interval cannot be ruled out entirely, and for this reason eye movements were measured in one of the present experiments.

1.2. Modification of FD by expectation, context, and direction

FD with implied motion was shown to be affected by a number of factors that were unrelated to physical principles. The displacement of the remembered final target position was reduced when the target disappeared at predictable reversals of target direction (Verfaillie & d'Ydewalle, 1991). Further, changing target identity in the inducing sequence reduced FD. For instance, observers in Kelly and Freyd (1987) were watching a display showing the implied rotation of a target of the same dimension, but with radically changing shapes: a rectangle, an hourglass, and a triangle were presented successively at orientations implying the rotation of the target (Experiment 2 in Kelly & Freyd, 1987). No FD was observed, suggesting that changing target identity disrupts representational momentum. Further, the context surrounding the target modified FD. The remembered orientation of a target rectangle was shifted towards the orientation of a surrounding

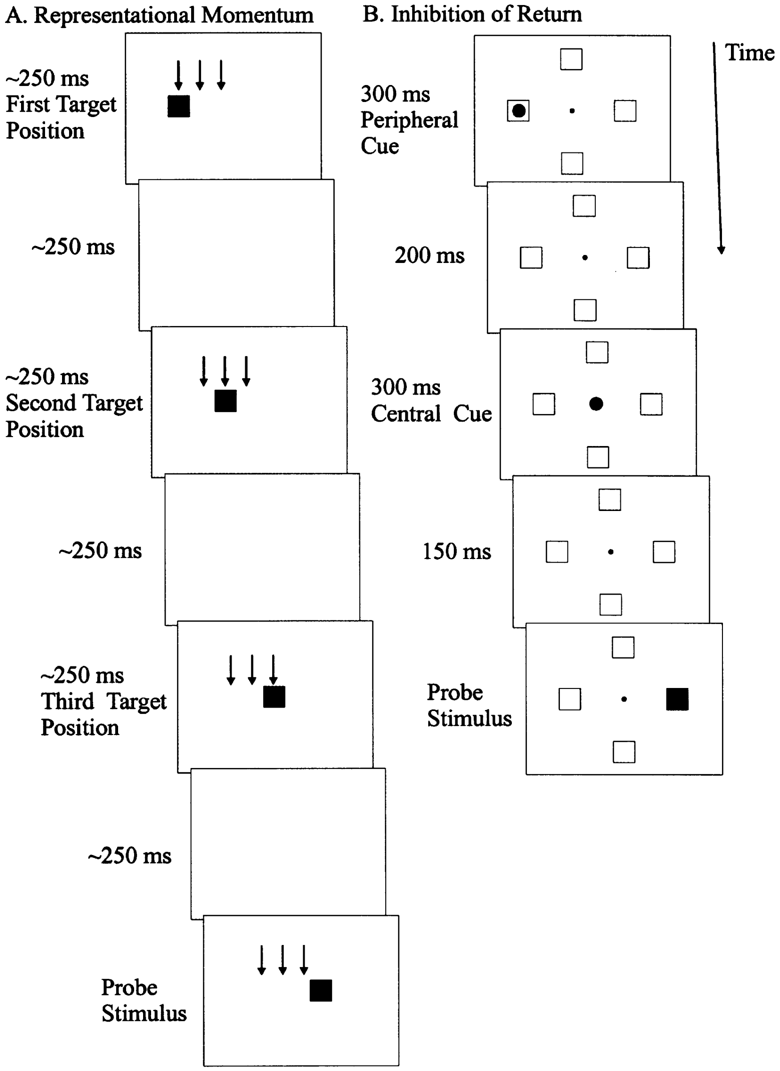

Fig. 1. Stimulus sequences (not drawn to scale) used to study representational momentum (A) and inhibition of return (B). (A) The stimulus sequence approximates studies by Halpern and Kelly (1993) and Reed and Vinson (1996). The arrows serve as placeholders for positions that were occupied by the object. They did not appear in the experimental displays. Three successive views of the object were presented. Then, a probe was shown that was at the same position as the third target view, or shifted either in or opposite the direction of motion. Observers were asked to judge whether the probe stimulus appeared at the same position as the third target presentation. “Same” responses were more likely when the probe stimulus was shifted from the third position of the inducing stimulus in the direction of motion (as shown in the figure). (B) This stimulus sequence was used by Pratt, Spalek, and Bradshaw (1999, Fig. 1). Pratt et al. observed that detection responses to probes appearing at the location opposite to the cued location (as shown in the figure) were fastest, indicating that attention moved past the central cue towards the opposite side. They called this phenomenon “attentional momentum”.

context square (Hubbard, 1993). In addition to the implied rotation used by Freyd and colleagues, researchers have also used implied linear motion to investigate representational momentum (Finke & Freyd, 1985; Finke et al., 1986; Finke & Shyi, 1988; Halpern & Kelly, 1993; Reed & Vinson, 1996). To imply linear motion, successive views of an object being translated by a certain distance were presented (see left panel in Fig. 1). The displacement of the final position was found to be larger with left-to-right than with right-to-left motion (Halpern & Kelly, 1993) and depended to some degree on the identity of the target object (Nagai & Yagi, 2001; Reed & Vinson, 1996).

1.3. Aim of study

In the present contribution, it was investigated whether FD with implied motion was affected by objects presented during the retention interval. Effects of visual distractor presentation may shed light on the role of attention in mental extrapolation of the final target position. In particular, the study aimed at resolving the issue of whether attention was necessary for stopping mental extrapolation or for maintaining mental extrapolation. So far, the reasoning has been that FD is due to an automatic process of mental extrapolation that follows physical regularities and that may be modified by factors such as expectation and context (Finke & Freyd, 1989; Hubbard, 1995b). Although the role of any influences based on internalizations of physical laws is debatable, one may assume that some sort of mental extrapolation of target position occurs if FD is obtained in the absence of eye movements. There is some evidence suggesting that attention contributes to the termination of the mental extrapolation process. In a dual task situation that required subjects to count while simultaneously attending to the localization task, FD was increased compared to the localization task alone (Hayes & Freyd, 2002). Thus, the presumed role of attention was to stop (involuntary) mental extrapolation, because the allocation of attention to another, non-visual task increased the error. It remains unclear, however, what the role of visuo-spatial attention exactly was because attention was divided between a verbal and a visual task, which may involve vastly different processing systems such as spatial working memory and the phonological loop (Baddeley, 1986). Dividing attention between two tasks may decrease observers' ability to monitor performance in the visual task. This may explain why the localization error increased, however, the role of visuo-spatial attention remains unclear. The present study attempts to clarify whether the allocation of visuo-spatial attention increases or decreases FD. On a theoretical level, the present study may clarify whether visual attention is necessary to maintain or halt mental extrapolation. A model of how attention may guide or maintain mental extrapolation is presented in Section 5.

To this end, localization of the final target position was investigated when irrelevant visual information was presented during the retention interval. The distracting stimuli were task-irrelevant, however, they evoked involuntary shifts of attention towards the abrupt onset (e.g. Posner, 1980), in particular because position was task-relevant (Folk, Remington, & Johnston, 1992; Yantis & Jonides, 1990). If the role of visual attention was to halt the process of mental extrapolation, an increase of the forward shift would be expected with distractors appearing during the retention interval. Alternatively, one may reason that the role of visual attention was not to stop mental extrapolation, but rather the opposite, to accompany and guide the mental extrapolation process. Thus, attention may move in the direction of motion towards the expected future target locations. Such a notion is compatible with the aforementioned factors modulating FD (i.e. expectations, context, target identity, direction of motion), because arguably, all of these factors may involve attention: expectations, context, and target identity may induce and modulate shifts of attention, and left–right asymmetries in the attentional span have been reported (McConkie & Rayner, 1976; Pollatsek, Bolozky, Well, & Rayner, 1981). However, more direct evidence for a role of attention is missing. If visual attention was involved in the generation of FD, rather than in its suppression, a reduction of the error would be expected when distractors were presented during the retention interval. To test this prediction, memory of the final target position undergoing implied motion was probed while distractors were presented either along or orthogonal to the axis of target motion.

In Experiment 1, it was confirmed that FD did not depend on eye movements. This is important because research on FD with smooth stimulus motion has demonstrated that displacement was absent when eye movements were suppressed. It would only be justified to talk about mental extrapolation of target position if eye movements did not account for FD. In Experiment 2, distractors were presented during the retention interval and localization of the final target position was measured. In Experiment 3, the distribution of attention in the displays of Experiments 1 and 2 was examined using a reaction time task.

2. Experiment 1

In the first experiment, implied linear motion was presented, and the eye position was recorded. Similar to previous studies on representational momentum with implied motion, a probe stimulus to measure observers' memory was presented after the conclusion of the inducing sequence. Observers were instructed not to follow the target with their eyes, but to look at the center of the screen. Because the stimulus presentation took almost 2 s, and the eyes are constantly moving under natural conditions, the criterion for maintenance of eye fixation was set at 1° which is not terribly strict, but within the range of other studies (e.g. Müsseler & Aschersleben, 1998). Lowering the criterion further produces very high error rates even with very brief fixation intervals (e.g. ~20% errors during a 300 ms interval with a fixation criterion of 0.25°; Stelmach, Campsall, & Herdman, 1997). Thus, subjects were allowed to move their eyes by a maximum of 1° during the target presentation. Eye movements above this criterion were detected online and observers were immediately informed about such errors.

This procedure, of course, does not preclude the occurrence of eye movements smaller than 1°, such as slow anticipatory eye movements that are not noticed by the observer (e.g. Kowler & Steinman, 1979). Because FD with implied motion is typically smaller than 1°, it is possible that eye movements below the 1°-criterion accounted for the mislocalization: if observers tried to remember the final target position in retinal coordinates, and the eye moved unnoticeably during the retention interval into the direction of implied motion, then judgments relative to the stored retinal position of the target would be biased. For instance, if the target was in the fovea before it disappeared, and the eye moved unnoticeably toward the left, an object appearing in the same egocentric (screen-) position as the target would appear displaced toward the right because its retinal position is outside the fovea. To evaluate this hypothesis, the eye position data were stored on disk and later analyzed for small eye movements.

2.1. Method

2.1.1. Participants

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

2.1.2. Apparatus, stimuli and design

The stimuli were created using a Matrox Millenium II graphics card controlled by a personal computer. The display had a resolution of 1280 (H) × 1024 (V) pixels on a 21 inch (diagonal) screen. One pixel measured 1.8 min. The refresh rate was 96 Hz.

The target was a filled black 1° square that was presented three times on a white background at locations separated by 2°. The target was shifted either from left to right or from right to left. Irrespective of direction of motion, the final target location was at the screen center. The target was shown for 260 ms, and successive presentations were separated by a 260 ms blank interval. Then 260 ms after offset of the final view, a probe stimulus that was identical to the target was displayed 0, ±0.2, ±0.4, and ±0.7° relative to the final target position. Positive values indicate that the probes were shifted in the direction of motion, whereas negative values indicate a shift opposite the direction of motion.

2.1.3. Design

Each condition resulting from the factorial combination of direction of motion (left, right) and relative probe position (0, ±0.2, ±0.4, and ±0.8°) was presented in 14 consecutive blocks for a total of 196 trials. In each block, a different random order of conditions was used.

2.1.4. Recording of eye movements

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 digitized at a rate of 250 Hz by a DataTranslation A/D-D/A converter (DT 2821). The observer's head position was stabilized with a bite bar. The apparatus was calibrated before the experiment started and recalibrated after 120 trials. The computer program detected the occurrence and size of saccadic eye movements online.

2.1.5. Procedure

Participants sat in a dimly lit room 50 cm from the screen. Observers were told to fixate the screen center, but no fixation point was presented. As the trial duration was long (7×260 ms $= 1820$ ms), eye movements smaller than 1° were tolerated. Trials with fixation errors were aborted before a response was emitted and repeated in the remainder of the experiment. Observers received at least 15 practice trials drawn randomly from the experimental trials before the experiment started. Observers pressed one of the two mouse

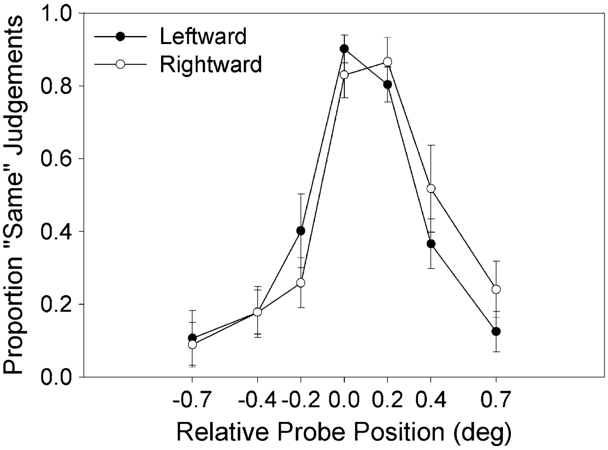

Fig. 2. Mean proportion of "same" judgments in Experiment 1 for each combination of relative probe position and direction of motion. For the relative probe position, positive values indicate that the probe was shifted in the direction of motion, and negative values indicate a shift opposite the direction of motion. The distribution was not symmetric around the true "same" position, but shifted in the direction of motion. This shift was larger for rightward than for leftward motion. Error bars indicate the mean standard error (between-subjects).

keys to indicate "same" or "different". The mapping of mouse button and response was counterbalanced across subjects. Subjects were told that they should not try to respond "same" and "different" equally often if they felt that one response was more likely.

2.2. Results

Eye movement errors occurred on about 15% of all trials. These trials were excluded from further analysis.

2.2.1. Key presses

The proportions of "same" judgments are shown as a function of relative probe position and direction of motion in Fig. 2. The weighted sum of "same" judgments was calculated as a measure of the localization error (displacement). Negative and positive displacement scores indicate mislocalization opposite and in the direction of motion, respectively. This score was calculated from the percentage of times that a participant responded "same" for each probe displacement, weighted by the actual value of the displacement ($-0.8°$ to $+0.8°$).

Displacement in the direction of motion was larger with rightward than with leftward motion (0.36° vs. 0.17°) ($t(7) = 3.20$, $P < 0.025$). Displacement was significantly different from zero with rightward motion ($t(7) = 5$, $P < 0.01$), and marginally different with leftward motion ($t(7) = 2.32$, $P < 0.053$).

2.2.2. Eye movements

Only two observers made small ($<1°$) saccades during the retention interval. These trials were not analyzed any further (0.9%). The mean eye position of four consecutive samples separated by 4 ms (i.e. a 16 ms window) at the beginning and at the end of the retention interval was calculated. The difference between these two values indicates whether the eye changed its position during the retention interval. With rightward implied motion there was a small, nonsignificant trend toward the left (−0.96 minarc, $P > 0.4$). With leftward implied motion there was a similar trend toward the left (1.31 minarc, $P > 0.3$). There was no significant difference between the two conditions (0.35 minarc, $P > 0.7$).

2.3. Discussion

There was significant displacement of the remembered final target position in the direction of motion. The displacement was larger for rightward than for leftward motion which is consistent with a previous report (Halpern & Kelly, 1993). However, the difference between displacement with rightward and leftward motion (0.18°) was smaller than the difference reported by Halpern and Kelly (0.77° in their Experiment 1). No systematic eye movements during the retention interval were observed. This result suggests that the displacement with implied linear motion was not due to eye movements occurring during the retention interval. The data of Experiment 1, in conjunction with the data of previous studies (Kerzel, 2000; Kerzel et al., 2001; Whitney & Cavanagh, 2002; Whitney et al., 2000), suggested that displacement of the final position of a moving target differs between smooth and discontinuous implied target motion: memory of the final position is accurate with eye fixation and smooth motion, whereas a shift in the direction of motion occurs with eye fixation and implied motion.

The reasons for this difference are not entirely clear, however, some recent neurophysiological evidence may shed some light on this issue: it was observed that static pictures implying motion produce activity in cortical areas involved in motion processing (Kourtzi & Kanwisher, 2000; Senior et al., 2000). Therefore, it may be that the ability of implied motion to induce motion processing in the absence of motion (i.e. after stimulus offset in the present case) is larger than that of smooth motion. The reason may be that implied or apparent motion may induce cortical "filling in" of motion information (Shioiri, Cavanagh, Miyamoto, & Yaguchi, 2000), whereas this is not necessary in the case of actual (smooth) motion. The added, endogenous processing of implied motion may continue even after stimulus offset, resulting in "leakage" of motion processing beyond the final target position, whereas the reactive, stimulus-triggered processing of smooth motion may terminate abruptly. Therefore, FD occurs with implied, but not with smooth motion.

3. Experiment 2

Experiment 1 established that there is mental extrapolation of the final position of a moving target in the absence of systematic eye movements. The present experiment examined the potential boundary conditions for FD. If the role of attention was to maintain mental extrapolation, then presentation of distracting elements during the retention interval should decrease the error because attention is involuntarily attracted by the abrupt onset. In contrast, if the role of attention was to terminate mental extrapolation, as suggested by experiments using between-modality divided attention (Hayes & Freyd,

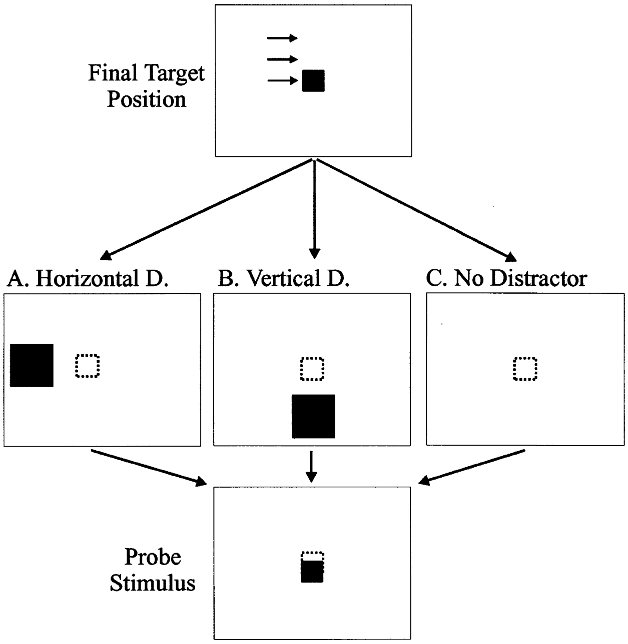

Fig. 3. Distractor conditions presented in Experiment 2 (not drawn to scale). The distractor appeared at 7.15° or 9.1° from the center of the screen. Either a distractor appeared orthogonal to the direction of target motion (A), or along the direction of target motion (B), or no distractor was presented at all (C). With orthogonal distractor placement the distractor appeared either left or right of the screen center; with distractor placement along the direction of motion, it appeared either above or below the screen center. After the distractor had disappeared, the probe stimulus was presented. The final target position is indicated by an unfilled rectangle.

2002), an increase of FD would be predicted. To test these conflicting views, a distractor was presented at some distance from the target. Both the position and the size of the distractor were clearly distinguishable from the target, such that the distractor presentation would not be perceived as a change of target trajectory or target identity. Such changes have been shown to decrease FD (Freyd & Finke, 1984; Kelly & Freyd, 1987). To avoid saccades to the distractor, its presentation time was below the minimal response latency of most saccades (smaller than 200 ms; Fischer & Weber, 1993). Further, vertical target motion was used to avoid the strong asymmetries between leftward and rightward motion that may even reverse FD (Halpern & Kelly, 1993). There have been reports of asymmetries for vertical implied motion, too, but these effects were much smaller (e.g. Reed & Vinson, 1996). Note that with smooth motion, this pattern is reversed: typically, asymmetries between leftward and rightward motion are much smaller than asymmetries between upward and downward motion (Hubbard, 1990; Hubbard & Bharucha, 1988).

3.1. Method

3.1.1. Participants

Thirty-four students at the Ludwig-Maximilians University of Munich were paid for

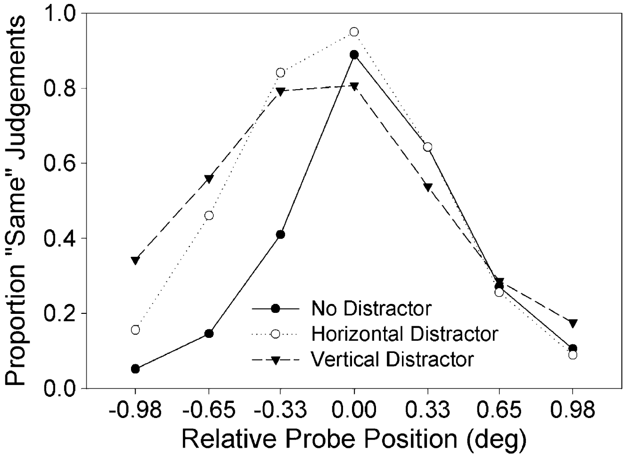

Fig. 4. Mean proportion of "same" judgments in Experiment 2 for each combination of relative probe position and distractor condition. For the relative probe position, positive values indicate that the probe was shifted in the direction of motion, and negative values indicate a shift opposite the direction of motion. Whereas the distribution of "same" responses was shifted in the direction of motion without a distractor, a backward shift occurred when distractors were presented. For clarity, error bars were omitted.

their participation. All reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment.

3.1.2. Stimuli, apparatus, and procedure

The stimuli, apparatus, and procedure were the same as in Experiment 1 with the following exceptions. Eye fixation was not monitored. The separation between successive target presentations was 1.8°. The target was shown for 302 ms, and successive presentations were separated by a 156 ms blank interval. The probe stimulus appeared 260 ms after offset of the third target presentation. The slightly changed presentation time did not change the visual impression conveyed by the display, as the interval between target onsets was approximately the same (~500 ms). The target moved vertically and disappeared randomly at the screen center, or 1.63° above or below the screen center. Immediately after the third target presentation, a 2° filled black square was presented at 7.15° or 9.1° (center-to-center) from the screen center for 156 ms. The distractor was easily discriminated from the target as the area it covered was four times as large, and it was presented far from the last target position. The probe stimulus appeared 260 ms after target disappearance (i.e. 104 ms after distractor disappearance) and was offset from the final target position by 0°, ±0.33°, ±0.65°, and ±0.98°.

3.1.3. Design

Each condition resulting from the factorial combination of direction of target motion (up, down), final target position (center, ±1.63°), relative distractor position (left–right or above–below, if applicable), distractor distance (7.15°, 9.1°), and probe position (0°,

±0.33°, ±0.65°, and ±0.98°) was presented once in two consecutive blocks for a total of 336 trials. In each block, a different random order of conditions was used.

The axis of the relative distractor position was manipulated between participants (see Fig. 3). In the horizontal distractor (HD) group ($n = 10$), it was always shifted horizontally, such that the distractor appeared orthogonal to the direction of motion on the left or right of the screen center. In the vertical distractor (VD) group ($n = 12$), the distractor was always vertically shifted such that it appeared in or opposite the direction of motion above or below the screen center. In the no distractor group (D −) ($n = 12$), the distractor was invisible (white). Cell sizes in the D − , HD, and VD groups differed slightly.

3.2. Results

The proportions of "same" judgments are shown for each group as a function of probe displacement in Fig. 4.

3.2.1. Effects of distractor presentation

Participants in VD showed negative displacement of −0.43° that was significantly different from zero ($t(11) = -4.77$, $P < 0.0006$), as did those in HD (−0.26°) ($t(9) = -3.5$, $P < 0.0064$). Displacement scores did not differ between VD and HD. Participants in D − showed a positive shift (0.21°) that was significantly different from zero ($t(11) = 2.46$, $P < 0.0317$). The difference between VD and D − was significant ($t(22) = -5.15$, $P < 0.0001$), as was the difference between HD and D − ($t(20) = 4.08$, $P < 0.0006$).

3.2.2. Effects of distractor position

In the VD group, the displacement was more negative when distractors appeared in the direction of motion than when distractors appeared opposite the direction of motion (−0.61° vs. −0.24°) ($t(11) = 2.46$, $P < 0.0316$). In the HD group, there were no differences as a function of distractor position (left or right, $P > 0.7$).

3.2.3. Effects of direction of motion

Negative displacement was nonsignificantly larger with upward than with downward motion in the VD group (−0.53° vs. −0.32°) ($t = -1.67$, $P < 0.1228$). No difference was visible in the HD group (−0.28° vs. −0.25°) ($t(9) = -0.18$, $P > 0.8$). In the D − group, upward motion produced marginally less memory displacement (0.13° vs. 0.29°) ($t(11) = -1.97$, $P < 0.0739$).

3.3. Discussion

When distracting visual information was presented, the usual FD was reversed. With distractors appearing along the direction of motion, or orthogonal to the direction of motion, displacement was consistently negative. Without distracting information, we replicated the standard FD (positive displacement) and some indication of an up–down asymmetry that is not as strong as that observed with smooth target motion (e.g. Hubbard, 1995a). The reversal of FD with the addition of a distractor contradicts the view that visual attention was necessary for stopping mental extrapolation of implied target motion. If visual attention was necessary for stopping mental extrapolation, the mental extrapolation process would decelerate at a slower rate with reduced visual attention at the final target position, thereby increasing the error. However, the opposite pattern was observed. When attention was diverted from the target location by presentation of a distractor, the error was eliminated and in fact reversed. This finding suggests that visual attention is involved in generating the error, rather than stopping it.

Further, inspection of Fig. 4 shows that the shape of the distribution of "same" responses was much broader in conditions with a distractor. The broadening of the curves indicates that observers were less sensitive to the difference between target and probe positions when distracting information was presented. Such a reduction of sensitivity shows that the distractors were indeed processed and focal attention was attracted away from the final target position. Generally, attention increases visual resolution and therefore visual sensitivity (Handy, Kingstone, & Mangun, 1996; Yeshurun & Carrasco, 1998).

The reversal of the localization error is consistent with the notion of memory averaging (Freyd & Johnson, 1987; Hubbard & Ruppel, 2000): the target's final position may have been averaged with its previous positions resulting in a backward shift. Freyd and Johnson (1987) reported that displacement in the direction of motion increased at short retention intervals, and decreased at long retention intervals (>250 ms). They suggested that the time course of displacement was due to two conflicting processes: a forward bias (representational momentum) that dominates briefly after target disappearance and memory averaging that dominates at later intervals. The present results are consistent with the idea that processing distracting irrelevant information eliminates the forward bias, but leaves memory averaging intact.

In the present experiment, eye movements were not monitored. Therefore, observers may have directed their eyes at the distractor position. The distractor was presented for only 156 ms, such that observers were not able to bring the distractor into foveal view before it disappeared. However, observers may have made an eye movement to the distractor position after it disappeared. Two arguments make this possibility unlikely. First, observers were asked to make judgments about a probe appearing around the final target position, not around the distractor position. If the eyes were directed at the distractor position, the final target position would be in the retinal periphery. Due to the acuity drop in the retinal periphery, judgments would be much more difficult. It seems unlikely that observers would opt for a more difficult strategy. Second, it has been shown that peripheral objects are localized toward the fovea (e.g. Kerzel, 2002c; Sheth & Shimojo, 2001). Thus, if observers had been looking at the distractor position when judging the final target position, judgments should have been biased toward the distractor.

However, the opposite pattern was observed: in the group with vertical distractors, backward displacement was stronger with distractors in the direction of motion than with distractors opposite the direction of motion, indicating that the target was in fact localized away from the distractor. These findings extend previous work (Kerzel, 2002c; Suzuki & Cavanagh, 1997): when stationary targets had to be localized, a bias away from another stationary object was observed (but see Hubbard & Ruppel, 2000). Perhaps observers overestimated the distance between distractor and target which shifted memory for the target away from the distractor (Kerzel, 2002c). Further, the present study shows that memory averaging and repulsion from the distractor are additive: the target was mislocalized opposite the direction of motion (memory averaging) and this bias increased when a distractor appeared in the direction of motion and decreased when a distractor appeared opposite the direction of motion (distractor repulsion).

4. Experiment 3

If it was the case that visual attention guided mental extrapolation into the direction of motion after target offset, then such a shift of attention should be evident in reaction time measures. That is, shorter latencies would be expected for responses to stimuli appearing at locations not occupied by the target during a trial (i.e. in the direction of motion) compared to locations previously occupied by the target (i.e. opposite the direction of motion). To test this hypothesis, the distribution of attention was measured by a task that required speeded manual responses to the shape of a probe stimulus. The probe stimulus appeared after the target disappeared and was offset from the final target position either in or opposite the direction of motion.

This procedure is akin to that used in studies on inhibition of return (IOR). In a typical experiment on IOR, the target may appear at one of two locations to the left and right of a central fixation dot. One of these locations is cued by the onset of a stimulus, such as a filled rectangle. In the standard paradigm, attention is summoned back to the center by presenting a second central fixation cue some time after the peripheral cue was shown (Abrams & Dobkin, 1994; Posner & Cohen, 1984; Pratt & Abrams, 1995, 1999). After a variable interval longer than 300 ms, the target appears in one of the two locations, and participants press a key as soon as they detect it. Detection latencies were found to be longer in the cued than in the uncued location. To answer the question of where attention would be directed after being drawn from a peripheral to a central cue, Pratt, Spalek, and Bradshaw (1999) probed multiple locations around the central position (see Fig. 1B). It was observed that responses at locations opposite the cued location were fastest. Pratt et al. suggested that the movement of the attentional focus overshoots on its way from the peripheral to the central location (see also Bennett & Pratt, 2001). In other words, attentional tracking of the cue appears to go beyond the final position, enhancing performance at locations in the direction of motion, and leaving the previously visited locations inhibited. Further, a pronounced asymmetry in attentional tracking was observed (Müller & von Mühlenen, 1996). Responses to changes in an object moving from left to right were detected faster than changes in objects moving from right to left, even when the object moving from right to left had been cued.

The similarities between the findings on IOR and the localization data from Experiment 1 are obvious: there was an asymmetry between leftward and rightward motion, and generally, there was a bias in the direction of motion.

4.1. Method

4.1.1. Participants

Thirty-six students fulfilling the same criteria as in Experiment 1 participated. All participants were right-handed.

4.1.2. Apparatus and stimuli

The same apparatus and stimuli as in Experiment 2 were used with the following exceptions. After three target presentations that implied either vertical or horizontal motion, the target disappeared at the screen center. Then, a probe stimulus was presented. The symbols " + " or "x" were used as probes. Each probe measured 1.3° and was presented for 63 ms. One of the two probe stimuli appeared 260 ms after target offset either in the direction of motion at 3.6° (center-to-center) from the final target position, or opposite to the direction of motion at 3.6° (center-to-center) from the final target position (i.e. the position of the first target presentation). When the target moved horizontally, a probe in the direction of motion would be to the right of the screen center with rightward motion, and to the left with leftward motion. When the target moved vertically, a probe in the direction of motion would be above the screen center with upward motion, and below with downward motion.

4.1.3. Design

Each condition resulting from the factorial combination of direction of motion (left–right or up–down), relative probe positions (in or opposite to the direction of motion), and probe type (" + ", "x") was presented once in 45 consecutive blocks for a total of 360 trials. In each block, a different random order of conditions was used. A group of 24 observers saw horizontal motion, and 12 observers saw vertical motion.

4.1.4. Procedure

Half of the participants were instructed to press a left key as soon as they identified a " + " probe, and a right key as soon as they identified an "x" probe. The other participants received the opposite probe–key mapping. The next trial was started 1500 ms after a response was obtained. Participants had the opportunity to rest by keeping the response key depressed. Trials with latencies shorter than 100 ms were considered anticipations, and trials with latencies longer than 800 ms were considered late. When a choice error occurred or a response was anticipated or late, visual feedback about the type of error and an auditory signal, a 500 Hz square-wave tone lasting 100 ms, were presented. These erroneous trials were repeated at a random position in the remainder of the block until a correct response was obtained.

4.2. Results

Reaction time and error rates were subjected to separate two-way ANOVAs (direction of motion × relative probe position).

4.2.1. Horizontal motion

Anticipations and late trials (0.8% of all trials) were not analyzed any further. Responses were faster when the probe appeared in the direction of motion (429 vs. 434 ms) ($F(1,23) = 6.88$, $MSE = 88.9$, $P < 0.025$). Direction of motion and relative probe position interacted ($F(1,23) = 4.79$, $MSE = 76.18$, $P < 0.05$). With rightward motion, responses were faster to probes in the direction of motion (427 vs. 436 ms) ($t(23) = 3.4$, $P < 0.005$), but not with leftward motion (431 vs. 432 ms) ($t(23) = 0.44$, $P > 0.6$). A second two-way ANOVA on percentage of errors (PEs) did not reveal any significant effects. Overall, 4.2% choice errors were made.

4.2.2. Vertical motion

Anticipations and late trials (1.3% of all trials) were not analyzed any further. Responses were faster when the probe appeared in the direction of motion (456 vs. 465 ms) ($F(1,11) = 9.46$, $MSE = 91.2$, $P < 0.025$). The interaction of direction of motion and relative probe position was far from significant ($F < 1$). A second two-way ANOVA on PEs revealed a significant effect of relative probe position ($F(1,11) = 5.27$, $MSE = 0.0005$, $P < 0.05$). Fewer errors were made when the probe appeared in the direction of motion (3.98% vs. 4.63%). The interaction of relative probe position and direction of motion reached significance ($F(1,11) = 8.58$, $MSE = 0.0024$, $P < 0.025$). With downward motion, error percentages were about the same for probes in and opposite the direction of motion (3.7% vs. 3.6%). With upward motion, more errors were made when probes appeared opposite the direction of motion (5.6% vs. 2.4%).

4.3. Discussion

The results provide evidence for attention shifts with implied motion and an asymmetry between left-to-right and right-to-left motion. About 250 ms after offset of the final view of the target, attention was shifted in the direction of motion with rightward motion, but not with leftward motion. The results replicate asymmetries in attentional tracking reported by Müller and von Mühlenen (1996). The size of the effect was small (9 ms), however, reliable IOR effects in the order of 10 ms (and smaller) have been reported before (Abrams & Dobkin, 1994; Müller & von Mühlenen, 1996; Pratt & Abrams, 1995, 1999). Also, the results parallel findings of asymmetric FD with implied horizontal motion (Halpern & Kelly, 1993), but do not provide strong evidence for asymmetries between upward and downward motion. In the error rates, there was an asymmetry between upward and downward motion, but this asymmetry was not observed in the reaction times.

It would be interesting to measure attention closer to the target's final position to see where the focus of attention was after target offset. IOR has been exclusively studied in the retinal periphery (typically at eccentricities of 5° or more), and there are no studies examining effects of eccentricity (except for one study on IOR in infants that compared IOR at 10° and 30° by Harman, Posner, Rothbart, & Thomas-Thrapp, 1994). Therefore, the suspicion arises that IOR does not occur in foveal or parafoveal vision, or that it is masked by other processes in this retinal area. Further experiments in our lab that are not reported here showed that within about 1° of the target's final position (i.e. within 1° of retinal eccentricity), no reaction time difference between forward and backward locations could be observed. Effects of eccentricity on IOR warrant further research. Here, it may suffice to show that attention does indeed move into the direction of motion after target offset to corroborate the findings from Experiment 2. Another issue that remains unresolved is whether potential future locations were facilitated, or whether past positions were inhibited. Research on IOR does not provide a clear answer, as IOR has been attributed to both facilitation of uncued (Pratt et al., 1999) and inhibition of cued locations (Posner & Cohen, 1984).

5. General discussion

In the present series of experiments, displacement of the final position of a target undergoing implied linear motion was investigated. Three main findings were obtained. First, Experiment 1 showed that the mislocalization of the final target position in the direction of implied motion occurred in the absence of eye movements. Thus, it seemed justified to assume that target position was extrapolated beyond the final target position in the visual system. This is important because in previous studies using smooth motion, FD was obtained only when the eyes followed the target, but not when the eyes were motionless. Second, Experiment 2 showed that FD was absent when distracting irrelevant stimuli were presented during the retention interval. This finding suggests that the role of visual attention in FD is not to halt the mental extrapolation process, but to maintain it. When distractors diverted attention from the target, a reduction of FD occurred. Experiment 3 showed that attention was shifted in the direction of motion after stimulus offset. A left–right asymmetry similar to that observed in memory displacement was confirmed.

Overall, the present study shows that visual spatial attention is necessary to mentally extrapolate the target position after implied motion. Contrary to previous theorizing (Finke & Freyd, 1989; Finke & Shyi, 1988; Freyd, 1987), mental extrapolation may not be a fully automatic process.

5.1. How attention maintains extrapolation: the spreading activation model

A possible way for attention and mental extrapolation to interact is in terms of spreading activation (Hubbard, 1995b; Müsseler, Stork, & Kerzel, 2002): different areas of visual space may receive varying degrees of activation. Stimulated and attended areas typically have a high degree of activation. Thus, as a target moves through space, it traces a path of activation that is perceived as motion. In the case of implied motion, one may assume that the visual system interpolates activation between the stimulated locations to yield the impression of motion. Once a particular area of space is activated, the activation may spread from this particular location. Because memory of previous target locations may suggest to the visual system that the target will continue to move in a particular direction, areas in front of the target would receive more activation (i.e. would be attended more) than areas behind the target, or alternatively, areas behind the target would be inhibited. Once the target stops, activation will initially spread in the direction of motion, and the perceived position would correspond to this shifted center of activation. Thus, activation spreading in the direction of motion could result in a forward localization error.

The data are consistent with the hypothesis that the spreading of activation is stronger with implied motion, as higher-level processes (i.e. expectations, past experiences) are used to fill in the target's path. This notion is fully compatible with the distinction between short-range and long-range motion (Braddick, 1980). It was assumed that the perception of apparent motion is a high-level phenomenon that is separate from the operation of low-level motion detectors that detect small stimulus displacements (i.e. short-range motion, but see Cavanagh & Mather, 1989). As implied and smooth motion may be considered examples of long- and short-range motion, respectively, high-level processing should be dominant with implied motion. Therefore, the mental extrapolation process may have a slower decay function with implied motion than with smooth motion such that FD would be larger with implied than with smooth motion. Smooth motion elicits “reactive” motion signals in the brain that may decay rapidly such that no FD occurs (provided that the eyes are motionless). In sum, the model implements mental extrapolation with implied motion as a shift of the center of activation after target offset. Similar ideas have been developed to explain the flash–lag effect (see below), and some neurophysiological evidence supports such a model (Berry et al., 1999; Erlhagen & Schöner, 2002).

5.2. Reinterpretation of previous results

There are a number of studies on “representational momentum” that may be reinterpreted in light of the present results. Reduction of FD at predictable reversals of target direction (Verfaillie & d’Ydewalle, 1991) may have occurred because observers directed their attention toward the anticipated positions at the reversal points (i.e. opposite the current direction of motion). Also, a context surrounding the target may attract attention, such that the remembered orientation of a target rectangle would be shifted towards the context (Hubbard, 1993). Further, changing the target identity during implied motion (Kelly & Freyd, 1987) may have made “filling in” and subsequent attentional overshoot impossible, resulting in a reduction of FD. Larger FD with left-to-right than with right-to-left motion (Halpern & Kelly, 1993) may result from a larger attentional span (McConkie & Rayner, 1976; Pollatsek et al., 1981) and better attentional tracking (Müller & von Mühlenen, 1996) toward the right. Finally, effects of target identity may be explained by subtle changes of attentional deployment (Nagai & Yagi, 2001; Reed & Vinson, 1996). For instance, Reed and Vinson (1996) reported larger FD with a rocket than with a steeple. Maybe subjects automatically attend to the potential path of a rocket such that FD increases.

5.3. Exogenous shifts of attention

The major claim of the present study was that visual attention maintains mental extrapolation of target position. It was suggested that attention moves beyond the final position and distorts memory of the final target position. Importantly, the shift of attention after implied motion occurred as a result of previous target presentations, not because another object suddenly appeared and captured attention. It was suggested that these two situations involve different attentional mechanisms (e.g. Müller & Rabbitt, 1989; Umilta, Riggio, Dascola, & Rizzolatti, 1991). Experiment 2 showed that exogenous (i.e. externally triggered) shifts of attention during the retention interval eliminate FD, presumably because the suddenly appearing distractors attracted attention and suppressed the forward shift of attention induced by implied motion. Further, Experiment 2 showed that targets were localized away from the distractors: distractors in the direction of motion increased memory averaging whereas distractors opposite the direction of motion decreased memory averaging. This indicates that the judged target position was repelled from a second, irrelevant object. Very similar effects have been reported for stationary targets (Kerzel, 2002c; Suzuki & Cavanagh, 1997).

Thus, one may conclude that exogenous shifts of attention triggered by distractors produce repulsion from the focus of attention, whereas shifts of attention resulting from implied motion produce attraction. However, such a distinction is contradicted by another study that investigated effects of briefly flashed distractors on the localization of the final position of a smoothly moving target (Kerzel, 2002a). In this study, observers were asked to track a target moving on a horizontal trajectory with their eyes. Some time before or after the target disappeared, a distractor was briefly flashed above or below the target. When the distractor was flashed at target disappearance or slightly later, judgments of the final target position were displaced toward the position of the distractor. These results show that position judgments may be biased in the direction of an exogenous shift of attention.

Related studies found that FD of the final target position was larger when the target moved toward a large stationary object than when it moved away from it (Hubbard & Ruppel, 1999) and that small stationary targets were localized towards a large stationary object (Hubbard & Ruppel, 2000). These results are consistent with the idea that object localization is biased toward an exogenous shift of attention because a large stationary object may attract observers' attention. However, the results from the studies of Hubbard and Ruppel (1999, 2000) are ambiguous: it may have been that observers looked at the large stationary object and not at the target because the large object was visible throughout target presentation and eye movements were not monitored. If this was the case, a localization bias toward the point of fixation (foveal bias, see Kerzel, 2002c; Sheth & Shimojo, 2001) may explain these results.

Thus, some studies report localization toward an exogenous shift of attention whereas others report the opposite. To reconcile these apparently contradictory findings, two different effects of a distracting object may be distinguished. First, suddenly appearing objects may attract attention and bias target localization toward the shift of attention (Kerzel, 2002a). Second, irrelevant objects may be used as a reference for target localization (Kerzel, 2002c). That is, the distance between target and distractor may be used to localize the target. Position judgments based on distance estimates are referred to as exocentric localization. It has been suggested that the target–distractor distance may be overestimated which results in target localization away from the distractor (Kerzel, 2002c). Further research is needed to clarify when a distractor is used as a reference mark for exocentric localization and when it only captures attention. One obvious difference between the above-mentioned studies was the relative duration of target and distractor presentation. In the study reporting a bias toward the exogenous shift of attention (Kerzel, 2002a), the target was visible for a rather long time (more than 500 ms) compared to the briefly flashed distractor (10 ms). This may have discouraged observers from using the distractor as a reference object. In contrast, the difference between the distractor and target presentation times was not as pronounced in studies reporting distractor repulsion (e.g. 156 vs. 302 ms in the present study).

5.4. Related phenomena

The present study is not the only one claiming that attention contributes to the perception of object position. Attention has been invoked as an explanation of the flash–lag effect in which a moving object is seen to lead a flashed, physically aligned object (Baldo et al., 2002; Baldo & Klein, 1995). Presumably, a shift of attention from the moving to the stationary object is necessary to consciously process the flash. As the shift takes some time and the moving object continues to move, spatial misalignment results (for a conflicting view, see Khurana & Nijhawan, 1995; Khurana, Watanabe, & Nijhawan, 2000). Attention has also been invoked to explain the Fröhlich illusion (Kirschfeld & Kammer, 1999; Müsseler & Aschersleben, 1998). When observers are asked to determine the first position of a moving target, judgments deviate from the actual starting position in the direction of motion (Fröhlich, 1923). One account suggests that it takes time for attention to reach the moving stimulus. Because attention is necessary for conscious processing, the initial positions do not reach awareness as the stimulus moves while the shift of attention is underway (Müsseler & Aschersleben, 1998). In support of an attentional involvement, it has been found that the Fröhlich illusion is reduced when attention is summoned to the first position by a cue preceding motion onset (Kerzel & Müsseler, 2002; Müsseler & Aschersleben, 1998; Whitney & Cavanagh, 2000).

Accounts of the Fröhlich illusion and the flash–lag phenomenon mostly incorporated attention to explain differential temporal delays or the differential accuracy of visual processing. In the present case, none of these attributes of attention seem to be involved: with attention being fully allocated to the task, and visual attention being focused on the target location, FD occurred. However, when attention was withdrawn from the target location, FD disappeared. Therefore, one may argue that FD occurred due to the full allocation of visual attention whereas previous studies suggested that localization errors occurred due to the lack of focal attention. A reason for this discrepancy may be that visual attention sustained the endogenous generation of motion signals in V5 with implied motion (Kourtzi & Kanwisher, 2000; Senior et al., 2000). Additionally, attention may be necessary to determine the direction of the mental extrapolation process on the basis of previous experience. It has been shown that FD is affected by knowledge about the future path of the target (Hubbard, 1994; Kerzel, 2002b; Verfaillie & d'Ydewalle, 1991). For instance, FD with implied rotation only occurs if observers have knowledge about the direction of motion or the final target position (Kerzel, 2002b). The brain may need attention to make use of stimulus-related memories for motion mental extrapolation. Therefore, the cortical processing of an irrelevant object attracting visual attention may interrupt the motion signals in V5 generated on the basis of such experiences.

In sum, the present results establish that there is FD with implied motion that may not be attributed to eye movements, and that the mental extrapolation process producing FD may be disrupted by new objects appearing in the visual scene. If mental extrapolation was an automatic process that did not require attention, it would be hard to explain why processing irrelevant stimuli disrupted extrapolation. Rather, attention may be necessary for maintaining the mental extrapolation process. The visual system may actively extrapolate future target positions by activation spreading into the direction of motion.

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