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Perceived shifts of flashed stimuli by visible and invisible object motion

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Abstract. Perceived positions of flashed stimuli can be altered by motion signals in the visual field—position capture (Whitney and Cavanagh, 2000 *Nature Neuroscience* **3** 954 – 959). We examined whether position capture of flashed stimuli depends on the spatial relationship between moving and flashed stimuli, and whether the phenomenal permanence of a moving object behind an occluding surface (tunnel effect; Michotte 1950 *Acta Psychologica* **7** 293 – 322) can produce position capture. Observers saw two objects (circles) moving vertically in opposite directions, one in each visual hemifield. Two horizontal bars were simultaneously flashed at horizontally collinear positions with the fixation point at various timings. When the movement of the object was fully visible, the flashed bar appeared shifted in the motion direction of the circle. But this position-capture effect occurred only when the bar was presented *ahead of* or *on* the moving circle. Even when the motion trajectory was covered by an opaque surface and the bar was flashed after complete occlusion of the circle, the position-capture effect was still observed, though the positional asymmetry was less clear. These results show that movements of both visible and 'hidden' objects can modulate the perception of positions of flashed stimuli and suggest that a high-level representation of 'objects in motion' plays an important role in the position-capture effect.

1 Introduction

Relative localization of visual objects appears simple at the outset. All the information that is needed is already on the retina, and, in principle, the visual system could use it. However, recent research has indicated that the visual system does not simply rely on positional signals in the retina but integrates information from other sources (for review, see Schlag and Schlag-Rey 2002). For example, relative localization is influenced by eye direction and movements (Cai et al 1997; Deubel et al 1996; Matin 1972; Ross et al 1997) and vestibular and/or proprioceptive input (Schlag et al 2000).

In addition to motor afferent/efferent, visual motion is a prominent modulator of relative localization (De Valois and De Valois 1991; Fröhlich 1923; Matin et al 1976; Nijhawan 1994; Nishida and Johnston 1999; Ramachandran and Anstis 1990; Snowden 1998; Watanabe et al 2001, 2002; Whitney 2002; Whitney and Cavanagh 2000). The relative position of a visual stimulus can be biased in the direction of motion signals contained within a stimulus (De Valois and De Valois 1991; Ramachandran and Anstis 1990). Moreover, when a brief flash is to be localized, the position of a flashed target is 'captured' by motion signals that originate even in substantially distant regions of the visual field (position capture—Whitney and Cavanagh 2000). Thus, transient positional signals of stationary stimuli seem to automatically get integrated with motion signals in the visual field.

One of the aims of the present study was to examine whether the position-capture effect depends on the spatial relationship between moving and flashed stimuli. We were particularly interested in how the position of a flash is perceived in the spaces ahead of and behind a moving object. This is because the behavioral relevance of these locations may be different. The space ahead of a moving object is, by definition, the place where the object will arrive in the near future. In contrast, the space behind the moving object is the place where observers have already seen the object. Therefore, it may be advantageous to process the space ahead of a moving object differently from (eg more quickly and/or more accurately than) the space behind it. Presumably reflecting this, when observers track a moving object with their eyes, reaction times to suddenly appearing stimuli ahead of the tracking target are shorter than those to stimuli behind it (van Donkelaar 1999; Tanaka et al 1998). Additionally, during a smooth-pursuit eye movement, flashes ahead of the eye are mislocalized in the direction of pursuit but flashes behind the eye are not (van Beers et al 2001; Matsumiya and Uchikawa 2000; Mitrani and Dimitrov 1982). However, no researchers so far have compared localization errors for stimuli ahead of and behind a moving object without eye movement. In the present study, we asked whether such asymmetry in mislocalization can be found in flashed stimuli with moving objects.

The other aim of the present study was to investigate effects of occlusion on position capture. Moving objects may often be occluded by other objects in the visual field and they may be invisible for a while. Occlusion disrupts the continuity of the retinal image of objects in both space and time. But the object does not seem to immediately cease to exist. Instead, it is perceived to exist through space and time while it is hidden behind other objects. The perception of continuity of hidden visual objects, or phenomenal permanence (Burke 1952; Michotte 1950, 1963, 1991; Yantis 1995), has led several researchers to propose that the retinal image is first parsed into surfaces or pre-objects (Gibson 1966, 1979; He and Nakayama 1992, 1994; Marr 1982; Nakayama and Shimojo 1992), which in turn may be integrated into visual objects by some individuation processes (Chun and Cavanagh 1997; Kahneman and Treisman 1984; Kahneman et al 1992; Kanwisher 1987; Pylyshyn 1989; Pylyshyn and Storm 1988; Scholl and Pylyshyn 1999; Scholl et al 2001; Wolfe and Bennett 1997; Yantis 1995; Yantis and Johnson 1990; Yantis and Jones 1991). Our question was: Can motion of an invisible but phenomenally existing (ie 'hidden') object produce a position-capture effect? An answer to this question will be informative as to the level of visual processing at which motion and position signals are integrated.

In order to address the questions mentioned above, we presented a flash ahead of and behind a moving object while observers performed visual localization of the flash; and, in some conditions, we covered the motion trajectory of the object such that the object appeared to move behind an occluding surface.

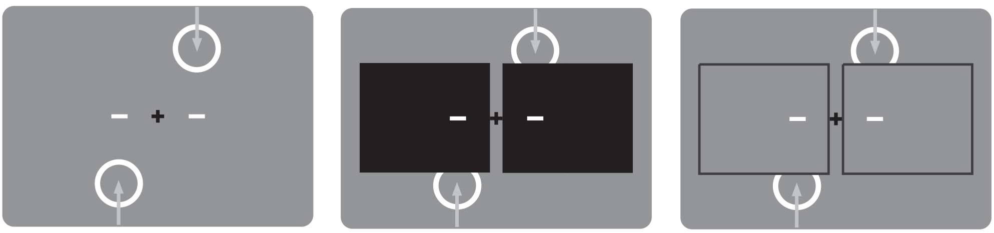
2 Experiment 1: Perceived shifts of flashed stimuli by visible and invisible object motion

2.1 *Methods*

2.1.1 *Observers.* Four observers, including authors KW and TRS, participated. Except for the authors, they were all naïve as to the purpose of the experiment. All observers had normal or corrected-to-normal vision.

2.1.2 *Stimuli.* Visual stimuli were presented on a color monitor operating at 85 Hz in a dark room. The computer screen subtended 42 deg horizontally and 32 deg vertically. Throughout a session, a black fixation cross (0.03 cd m^{-2}, 0.46 deg) was displayed on a gray background (20.3 cd m^{-2}) at the center of the screen. Three occlusion conditions were tested:

(i) *Full-view condition.* Two white circles (59.7 cd m^{-2}; 3.3 deg size, 0.21 deg line thickness) appeared 5.85 deg above and below and 2.95 deg or 7.95 deg to the left and right of the fixation cross (center-to-center distance). The circles moved vertically at 14.2 deg s^{-1} toward the opposite sides of the screen (figure 1a), and disappeared after traveling 11.7 deg (in 70 frames = $\sim$824 ms). The two circles always appeared at an equidistance and moved in opposite directions. The direction of motion was randomized. Two white horizontal bars (83.2 cd m^{-2}; 0.13 deg $\times$ 0.8 deg) were flashed for one frame ($\sim$11.8 ms) on a horizontal plane with the fixation.(1) The eccentricity of the flashes was the same as the horizontal eccentricity of the circles (ie 2.95 or 7.95 deg). Therefore, the bar was flashed always on the straight trajectory of motion. The bars were flashed 0, 6, 12, 18, and 24 frames before or after (ie 0, $\sim$70, $\sim$141, $\sim$212, and $\sim$282 ms before or after) the moment the centers of the circles were aligned with the horizontal plane with the fixation. These relative timings correspond to the relative positions between the circle and flash; the bar was flashed 0, 1, 2, 3, and 4 deg ahead of or behind the center of the moving circle.



(a) (b) (c)

Figure 1. Stimuli and occlusion conditions. (a) No occluding surface was presented in the full-view condition. (b) In the explicit-occlusion condition, two black rectangles allowed observers to see the motion trajectory of the circle only for the initial and last portions. (c) In the implicit-occlusion condition, the rectangles had the same luminance value as the background. Observers had a clear impression that the circles disappeared behind the occluding surface, traveled invisibly, and reappeared at the other ends. In the figure, the rectangles are depicted with black lines for illustrative purpose but they were invisible in the experiment. The sizes of the visual stimuli in the figure are roughly proportional to those used in the experiments.

(ii) *Explicit-occlusion condition.* The motion trajectories of the circles were occluded by two black rectangles (0.03 cd m^{-2}, 8.4 deg $\times$ 10 deg). The circles gradually disappeared behind the black rectangles and they were completely occluded 20 frames ($\sim$235 ms) after their onset. Then, they re-emerged at the other ends of the rectangles 20 frames before their offset (figure 1b). The black rectangles were horizontally separated by 0.9 deg. Otherwise, the stimulus was identical to that in the full-view condition.
(iii) *Implicit-occlusion condition.* The stimulus was identical to that in the explicit-occlusion condition except that the occluding surface had the same luminance level as the background. The circles underwent gradual deletion and accretion along the contours at the invisible occluding boundaries as in the explicit-occlusion condition (figure 1c).

2.1.3 *Procedure.* The observer viewed the stimulus display binocularly from a distance of 75 cm while fixating at the black cross. After viewing the stimulus sequence, two continuously visible bars were presented at the same locations where the bars had been flashed (ie on a horizontal plane with the fixation). By using a computer mouse, the observer adjusted the vertical position of each bar to indicate where the bars had been flashed relative to the fixation cross (relative localization). The order of

(1) We presented the two circles moving in opposite directions in order to control the eye-movement artifact. Also, the two bars were used to make the judgment of the perceptual (vernier) offset easier.

adjustment (left or right first) was randomized. For each combination of conditions [occlusion (3) $\times$ eccentricity (2) $\times$ flash timing/position (9) $=$ 54 conditions], 16 trials were repeated randomly. Since each trial consisted of two adjustments, there were 32 measurements for each condition, from which mean positional shifts of the flash were calculated for each observer. The experiment was divided into 4 sessions, resulting in 216 trials per session.

2.2 *Results and discussion*

Averaged results from the authors and the naïve observers followed the same pattern, so we have averaged the data from all the observers for presentation in figure 2. A three-way ANOVA with repeated measures indicated that the position-capture effect was greater when the bar was flashed more peripherally ($F_{1,3} = 47.6$, $p < 0.001$), that occlusion reduced the position-capture effect ($F_{2,6} = 11.5$, $p < 0.001$), and that the

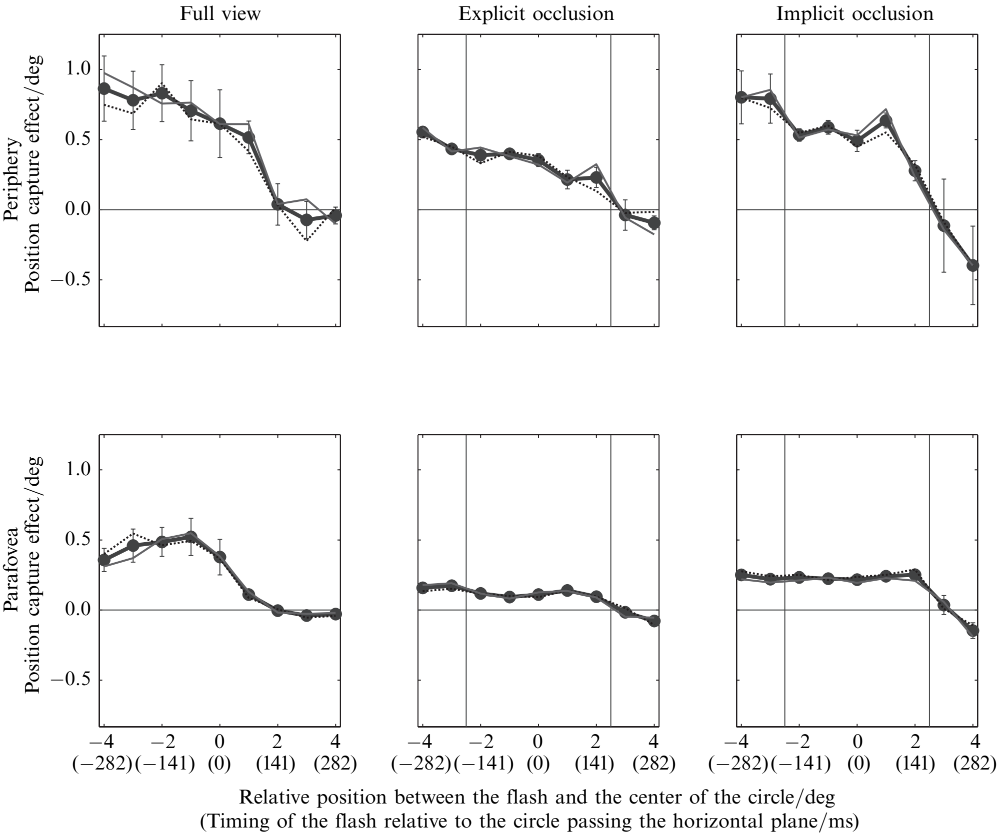


Figure 2. The results of experiment 1. Solid, thin lines represent the averaged data from the authors; broken lines represent averaged data from the naïve observers. As both data followed the same pattern, the data from all observers were averaged (thick lines with disk symbols; vertical bars denote ± 1 SE). The ordinate shows the magnitude of the positional shift. A larger positive value means a larger magnitude of positional shift in the direction of motion of the circle. The abscissa shows the relative position between the center of the circle and the flash on the horizontal plane with the fixation (deg) and the timing of the flash relative to the moment (or implied moment) when the center of the circle passed the flash location on the horizontal plane with the fixation (ms). At a negative value, the center of the circle was approaching the location of the flash. It may help understanding the figure to imagine the circle moving upward as time goes from left to right and the flash occurring on the abscissa; the data point would be the perceived position of the flash. The area between the vertical lines at -2.55 deg and $+2.55$ deg positions in the occlusion conditions represents the region within which no part of the moving circle was visible (complete occlusion).

perceived shift of the flash depended on the relative timing/position between the circle and flash ($F_{8,24} = 25.0$, $p < 0.001$). Significant interaction was also found between eccentricity and position ($F_{8,24} = 4.7$, $p < 0.001$). The other interactions did not reach a significant level (eccentricity–occlusion: $F_{2,6} = 0.23$, $p = 0.80$; occlusion–position: $F_{16,48} = 2.19$, $p = 0.07$; three-factor interaction: $F_{16,48} = 0.49$, $p = 0.95$). All observers asserted that they naturally localized the bars with respect to the fixation cross and the perceptual misalignments were about the same for the two bars, but in opposite directions.(2)

In general, the position capture was stronger in the peripheral visual field than in the parafovea. Owing to the spatial density of the mosaic of photoreceptors (in parafoveal retina) or ganglion cells (in peripheral retina), positional signals become less accurate as the retinal eccentricity increases (De Valois and De Valois 1988). The enhanced position capture in the peripheral visual field may indicate that the visual system relies on contextual cues when retinal position signals are not reliable.

The perceived shift of the flash position was significantly affected by the relative timing/position between the circle and flash in the full-view condition. The position capture effect tended to be stronger in the initial phase of the movement of the circle. Depicting the spatial relationship between the flash and circle (figure 3) suggests that the position capture occurred when the bar was presented *ahead of* or *on* the moving circle, but not when the bar was presented *behind* the circle. This hypothesis was further tested in the subsequent experiment.

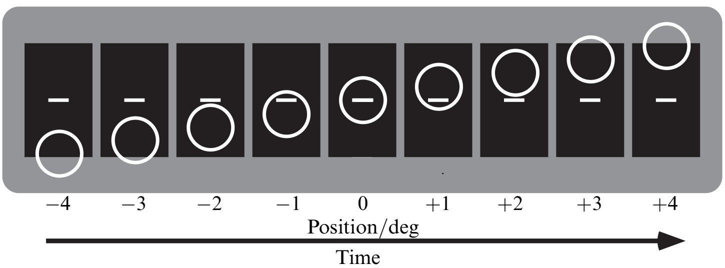


Figure 3. Relative positions between the circle and bar in experiment 1. The numbers show the relative positions between the bar and the center of the circle (deg) and time flows from the left to the right. Black rectangles are drawn to indicate the area of the occluding surface. In the experiment, the circle was not visible in the region of the black rectangle in the two occlusion conditions.

As expected, in the explicit-occlusion condition, the observers reported a clear impression that the circle disappeared behind the occluding surface, traveled invisibly in the interval, and reappeared at the other end. This was also the case in the implicit-occlusion condition, probably because the motion cue of accretion and deletion was effective enough to lead to the phenomenal permanence of the moving circle (Gibson 1979; Gibson et al 1969; Michotte 1950). Intriguingly, even when the rectangles completely occluded the moving circles at the moment the bars were flashed, the position capture was still present, although the magnitude of the effect was somewhat reduced.(3) This implies that implicit motion of a hidden, hence invisible, object can modulate the perceptual position of flashed stimuli. However, in contrast to the full-view condition, the position capture effect in the occlusion conditions does not seem to depend on the distance between the flashed bar and the implied location where the circle would arrive

(2) In an additional experiment, we observed that physical displacements of the flashed bars in opposite directions can null the perceptual misalignments. This observation confirmed that the perceptual misalignment is not specific to the method of adjustment.

(3) Additionally, the explicit (black) occlusion attenuated the position-capture effect more than the implicit (gray) occlusion (Fisher PLSD test, $p < 0.05$). This is probably because the black surface added a reference frame for visual localization.

by assuming it moved with constant velocity. Rather, the effect persisted until a part of the circle reappeared at the occluding boundaries (figure 3; see also figure 2). This could be because, in the amodal completion of a movement, there is a phenomenal dilatation of the time required for completion (Burke 1952). In other words, the speed of an invisible object may be underestimated and its position lags behind the location assumed with constant velocity.

3 Experiment 2: Position capture depends on the spatial relationship between the flash and moving object

The results of experiment 1 suggest that the perceived position of a flash in the full-view condition depends on the spatial relationship between the flash and a moving object. The results also suggest that the position-capture effect in the occlusion conditions persists until a part of the moving object reappears at the occluding boundaries. However, it is possible that a temporal, rather than spatial, factor (eg relative timing between the flash presentation and the onset of the movement of the circle) is important in the full-view condition. Moreover, the position-capture effect in the occlusion conditions might simply continue for a certain period of time and it might accidentally be equal to the interval from the motion onset to the reappearance of the circle from the edges of the rectangle (50 frames $= \sim 588$ ms in experiment 1). In experiment 2, we tested these possibilities by reducing the speed of the circle while keeping the other conditions identical to those in experiment 1. If the spatial relationship at the time of the flash presentation is the primary factor in the perceived shift in the present display, results plotted as a function of relative position would follow the same pattern as those in experiment 1.

3.1 *Method*

The observers, stimuli, and procedure were identical to those in experiment 1, except that the circle displacement per frame was reduced to half of that in experiment 1, resulting in the speed of 7.1 deg s^{-1}.

3.2 *Results and discussion*

The results of experiment 2 are presented in figure 4, with the results of experiment 1 for comparison. The results of both experiments nearly overlie each other when they are plotted as a function of relative position between the flashed bar and the center (and the implied center) of the moving circle (thick lines with symbols versus thin solid lines). Obviously, when the results are plotted as a function of relative timing, they differ significantly (thick lines with symbols versus thin broken lines). As in experiment 1, in the full-view condition of experiment 2, the position-capture effect was present when the bar was flashed ahead of or on the moving circle, but it was not when the bar was flashed behind the circle ($F_{8,24} = 39.4$, $p < 0.001$). Furthermore, the position-capture effect in the occlusion conditions endured until the circle reappeared at the edge of the occluding surface. The position capture effect was larger with the greater eccentricity ($F_{1,3} = 37.8$, $p < 0.001$) and without occlusion ($F_{2,6} = 11.4$, $p < 0.001$). There were significant interactions between eccentricity and position ($F_{8,24} = 8.4$, $p < 0.001$) and between occlusion and position ($F_{16,48} = 2.5$, $p < 0.005$). Neither interaction between eccentricity and occlusion ($F_{2,6} = 1.12$, $p = 0.33$) nor three-factor interaction ($F_{16,48} = 0.63$, $p = 0.86$) was significant.

The results of experiment 2, combined with those of experiment 1, have shown the following: (i) The perceived position of a flash is dependent on the spatial relationship between a moving object and the flash at the moment of the flash onset when the moving object is visible. (ii) When the moving object is invisible but it appears to move behind an occluding surface, the position-capture effect was present all along but terminated at the time when the object reappeared at the occluding boundaries. These results are consistent with the idea that, in the present experimental paradigm of position

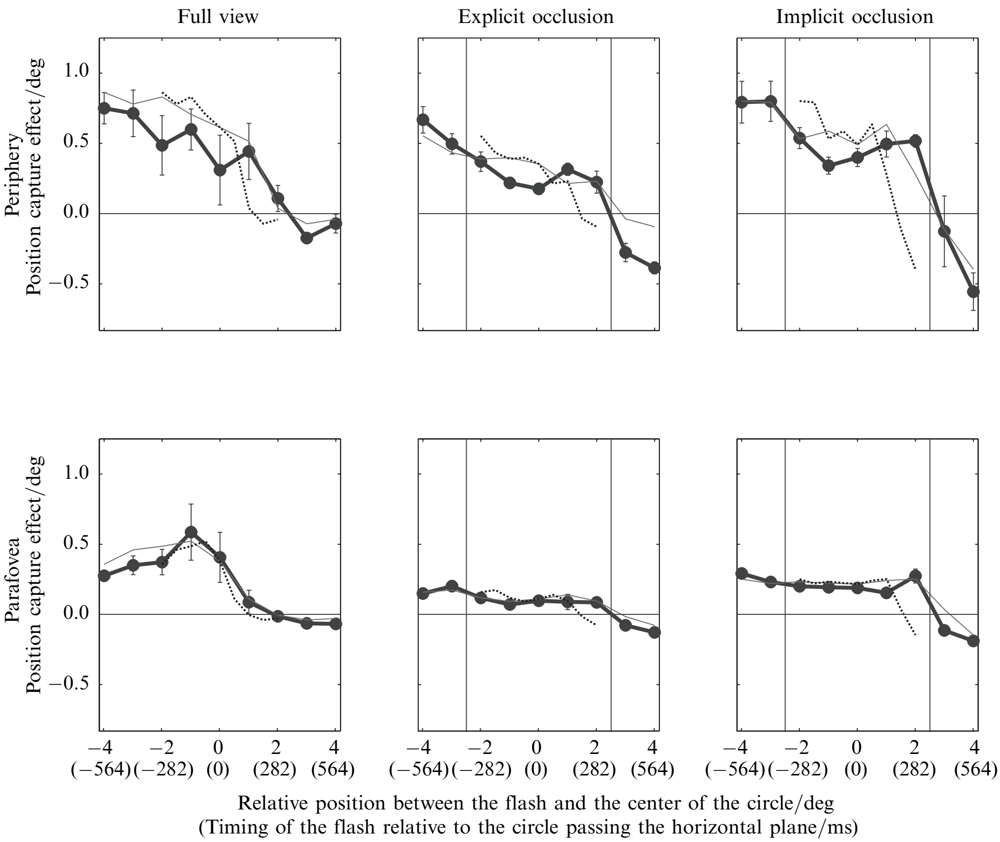


Figure 4. The results of experiment 2 (half speed; thick lines with disks). Data are plotted together with those from experiment 1 (thin lines, as a function of relative position; thin broken lines, as a function of relative timing).

capture, the spatial, rather than temporal, relationship is the crucial factor for both visible and invisible object motion.

The dependence on the spatial factor seems in conflict with the results of Durant and Johnston (2002). By varying the speed of the motion stimulus, they showed that relative timing between the moving object and flash mattered in position capture, not spatial relationship. There are several differences in visual display between their study and ours. First, they used a rotating bar as motion stimulus, whereas we used translating objects. Second, the moving stimulus (and the expected trajectory of the moving stimulus) did not overlap with the flash in their study. This is also the case in the original demonstration of position capture (Whitney and Cavanagh 2000). Third, the eccentricity of the flash in their experiments was smaller than that used in the present study. Finally, our study is the first to introduce the occlusion conditions, intermixed with the full-view condition, in a position-capture experiment. These differences in visual stimuli are mainly due to the difference in research motivation. Position capture has been investigated in the context of interaction between motion and position signals at rather early levels of visual processes (Durant and Johnston 2002; Whitney and Cavanagh 2000). On the other hand, our motivation was to investigate the spatial asymmetry between the spaces ahead of and behind a moving object and the effect of occlusion, both of which were expected to involve relatively high-level representations of moving objects. Accordingly, we made the visual display to encourage observers to anticipate and attentively track the trajectory of the object motion. Our tentative hypothesis for the discrepancy between their results and ours is that the task/attentional demand may affect position capture. However, how exactly these differences in visual stimuli influence position capture warrants further empirical investigations.

4 Experiment 3: Attentional repulsion does not account for position capture by visible and invisible moving objects

One may suspect that the perceived shift of the flash in the occlusion conditions might be caused by a factor other than the phenomenal existence of object motion behind the occluding surface. One possibility was the attentional repulsion effect; when attention is focused at a specific location in the visual field, flashed stimuli appear displaced away from the focus of attention (Suzuki and Cavanagh 1997). Our visual stimulus involved the abrupt onset of the circle in the peripheral visual field, which was likely to attract attention (Hillstrom and Yantis 1994; Jonides and Yantis 1988; Shimojo et al 1996; Watanabe and Shimojo 1998; Yantis and Jonides 1990). In experiment 3, instead of presenting the smoothly moving circles, we flashed the circles at the locations that corresponded to the start and end positions of the motion trajectory of previous experiments (figure 5), so that there were no smooth motion signals in the full-view condition and no accretion/deletion motion cue in the occlusion conditions. If attentional repulsion was the sole cause of the perceived shift of the flash position, we should obtain the same results as in experiment 1.

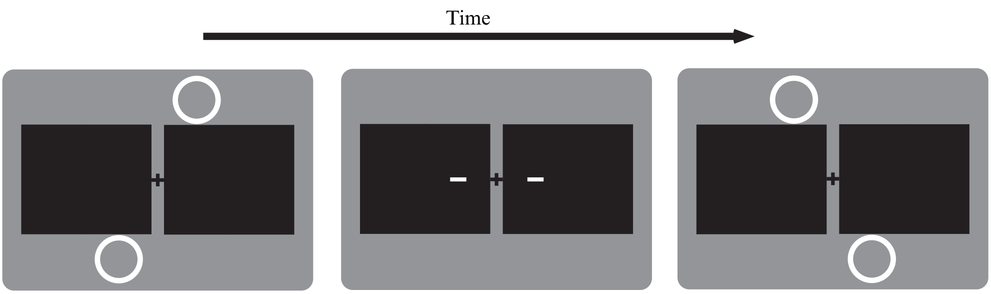


Figure 5. Stimulus sequence in experiment 3 (attentional repulsion).

4.1 *Method*

The two circles were flashed for one frame at 5.85 deg above and below and 2.95 or 7.95 deg to the left and right of the fixation cross. Then, 17 frames ($\sim$824 ms) later, the circles were flashed at the orthogonal locations (figure 5). This corresponded to presenting only the first and last frames of the motion trajectory in experiment 1. Note that the full-view condition and the implicit-occlusion condition were indistinguishable in experiment 3. Therefore, there were only two conditions: without-surface and with-surface conditions. The observers, other stimulus settings, and procedure were identical to those in experiment 1.

4.2 *Results and discussion*

The results of experiment 3 are shown in figure 6, together with those of experiment 1. Although no spatial relationship could be defined between the circle and bar in experiment 3, for presentation and comparison purposes the results are plotted in the same manner as in previous experiments, with the assumption that the circles moved from the first to second locations with a constant speed of 14.2 deg s^{-1}.

The flashed bar in experiment 3 appeared displaced to the location opposite to the circle that was presented first. This result could be consistent with attentional repulsion (Suzuki and Cavanagh 1997). However, the magnitude of the perceived shift was generally smaller than in experiment 1 and, more importantly, the effect exhibited no dependence on the relative timing/position in both full-view and occlusion conditions

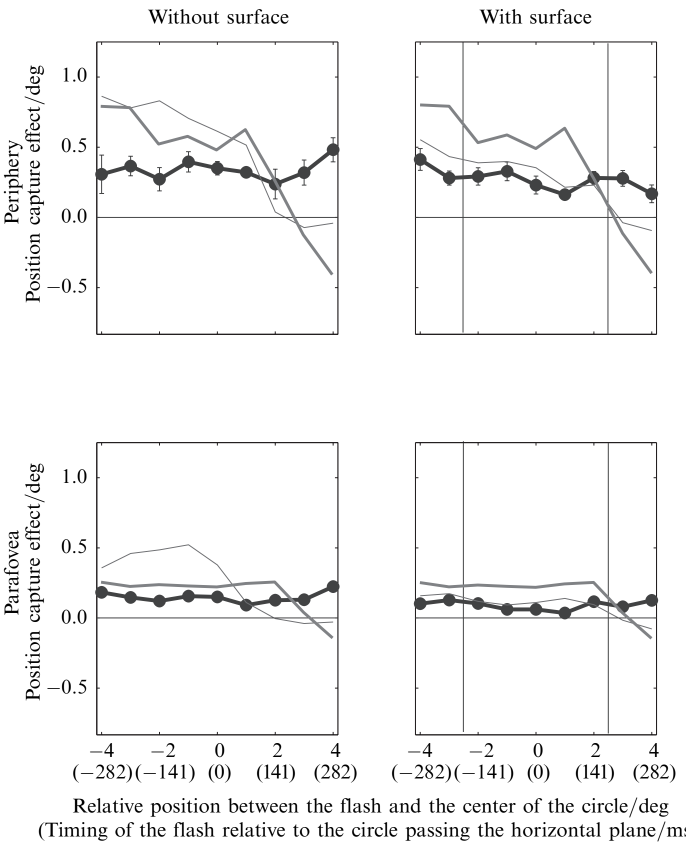


Figure 6. The results of experiment 3 (attentional repulsion; thick lines with disk symbols). Thin lines in the left panel show the results in the full-view condition from experiment 1. Thin lines in the right panel show the results in the explicit-occlusion condition from experiment 1. Thick gray lines without symbol in both panels show the results in the implicit-occlusion condition from experiment 1. These are plotted for comparison purposes.

($F_{8,24} = 1.4$, $p = 0.19$). Similar to previous experiments, the larger eccentricity of the flashes led to larger position capture ($F_{1,3} = 106.8$, $p < 0.001$) and the black rectangle surface reduced the magnitude of the position-capture effect ($F_{1,3} = 12.3$, $p < 0.01$). No interaction was significant (eccentricity–occlusion: $F_{1,3} = 0.10$, $p = 0.75$; eccentricity–timing: $F_{8,24} = 0.41$, $p = 0.91$; occlusion–timing: $F_{8,24} = 1.76$, $p = 0.09$; three factors: $F_{8,24} = 1.09$, $p = 0.38$). Thus, the perceived shift caused by attentional repulsion was not sufficient to explain the magnitude and characteristics of the position-capture effect observed in previous experiments. Therefore, it is unlikely that attentional repulsion is the primary cause of the perceived shift of the flashed bar in the present experimental paradigm.

5 Experiment 4: Position capture by an invisible moving object depends on the expected trajectory of the moving object

The results of experiment 3 indicate that the position-capture effect in the occlusion conditions is not due to attentional repulsion, which favors the idea that it is indeed caused by the invisible (implied) object motion behind the occluding surface. The motion of the 'hidden' circle in experiments 1 and 2 was implied most likely because observers saw how the circle behaved in the full-view condition and the occlusion conditions, with being intermixed with the full-view condition, simulated the situation that the same event occurred behind the surface. In other words, the perceptual anticipation that the circle would move straight could contribute to the position-capture effect in the occlusion conditions. It follows that, if observers know that the circle will reverse its direction of motion while it is hidden and the visual display simulates such a situation, the direction of the perceived shift of the flash would change accordingly. In experiment 4, we examined this case.

5.1 *Method*

Three new naïve observers and one of the authors, KW, took part in experiment 4. A different experimental setup was used in a different laboratory, but the visual display and procedure were carefully made to be the same as those in experiment 1. Experiment 4 differs from experiment 1 in that the circle reversed the direction of motion when the centre of the circle reached the horizontal plane with the fixation (at the 0 deg position; figure 7).

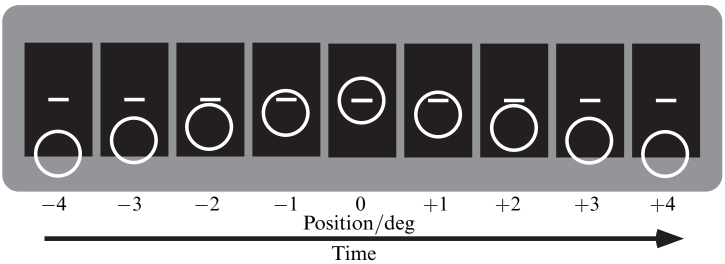


Figure 7. Relative positions between the circle and bar in experiment 4 (motion reversal).

5.2 *Results and discussion*

The results of experiment 4 are shown in figure 8. The position-capture effect depended on the relative position/timing of the flash ($F_{8,,24} = 117.3$, $p < 0.01$). It was larger with the larger eccentricity ($F_{1,3} = 7.7$, $p < 0.01$), and was reduced with the presence of occlusion ($F_{2,6} = 8.3$, $p < 0.01$). All interactions were significant (eccentricity – occlusion: $F_{2,6} = 5.2$, $p < 0.01$; eccentricity – position: $F_{8,24} = 25.3$, $p < 0.01$; occlusion – position: $F_{16,48} = 17.1$, $p < 0.01$; three factors: $F_{16,48} = 2.9$, $p < 0.01$). Note that, in figure 8, at negative values of relative position, a positive value on the ordinate means a position-capture effect, whereas at positive values of relative position a negative value means a position-capture effect.

In the full-view condition, the initial positional shift of the flash was in the direction of the motion of the circle before the reversal of motion. But, around the time of the motion reversal, the direction of positional shift was reversed, making U-shape functions. The bar appeared shifted in the opposite direction to the motion before the reversal, and in the same direction as the motion after the reversal. Thus, the position-capture effect in the full-view condition clearly depended on the trajectory (and reversal) of the object motion. Interestingly, the reversal of perceived shift of the flash position was observed even before the circle changed its motion direction (at the −1 deg position; figure 8; see also figure 7). One possible account is that there may be a longer delay for assigning positions to the flash than for registering motion direction of the object (Whitney and Cavanagh 2000). But we currently do not have a definitive explanation for this result and further investigations are necessary.

The results in the occlusion conditions were most important as to the purpose of experiment 4. Although the results look rather variable, it is clear that the pattern of results is different from that of experiment 1. Since the accretion/deletion event before the flash was identical between experiment 1 and experiment 4, it is the accretion/deletion event *after* the flash that made the results different. The perceived shift

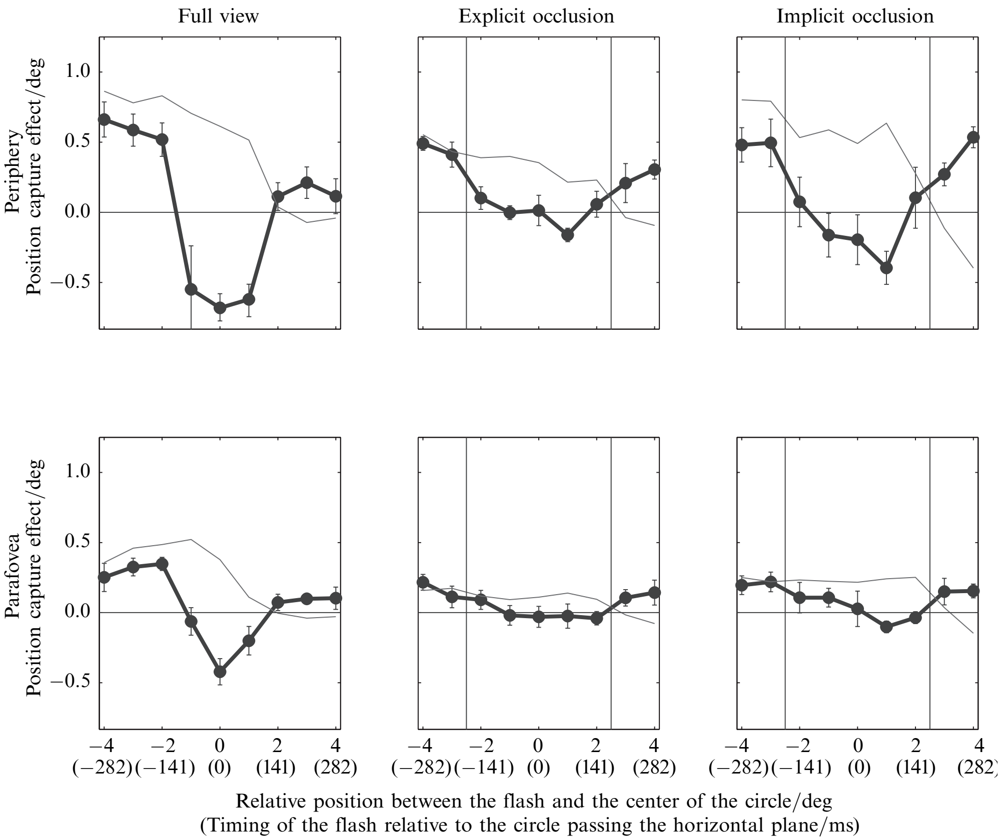


Figure 8. The results of experiment 4 (motion reversal; disks with thick lines). The results of experiment 1 are also shown for comparison purposes (thin lines). The motion reversal occurred when the center (or implied center) of the circle and the bar were aligned (ie at the 0 deg position). Hence, at negative values of relative position, a positive value on the ordinate means a position-capture effect, whereas at positive values of relative position, a negative value means a position-capture effect.

of the flashed bar was reversed broadly according to the direction reversal of implied object motion, resembling that in the full-view condition. This suggests that the experience of the motion-reversal event in the full-view condition could have an influence on the position capture in the occlusion conditions. Thus, overall, the results of experiment 4 support the idea that the position-capture effect by a 'hidden' moving object depends on the implied behavior of the moving object behind an occluding surface. It is also worth noting that the U-shape functions in the occlusion conditions are skewed toward the positive side of the relative position/timing, compared with those in the full-view condition. This could mean that, in the occlusion conditions, the reversal of the position-capture effect occurred slightly later than in the full-view condition. This delay of reversal of the position-capture effect is in agreement with the phenomenal dilatation of the time for amodally moving objects (Burke 1952).(4)

(4) This idea was also supported by the following observation. We modified the visual display of experiment 1 such that the circle never reappeared in the occlusion condition. The position capture persisted for a fair period of time, depending on observer, but eventually disappeared as a delay from the disappearance of the circle and the flash presentation increased. We thank an anonymous reviewer for pointing out this control.

6 General discussion

The present study concerned two main questions: (i) whether the perceived positions of a flash ahead of and behind a moving object suffer mislocalization in different magnitudes, and (ii) whether an invisible object implied to be moving behind an occluding surface can produce a shift of the perceived position of the flash. We obtained affirmative results for both.

6.1 *Position shift of flashed stimuli by visible object motion*

Our results showed that the position-capture effect can be observed well before the moving circle came close to the location of the flash. This result clearly parallels the previous study showing that the distance between moving and flashed stimuli has little effect on the magnitude of the position-capture effect (Whitney and Cavanagh 2000). The new finding is that the position of a flash is perceived differently between spaces *ahead of* and *behind* a moving object. However, it should be noted that the stimulus employed in the present study was rather different from the stimulus used by Whitney and Cavanagh (2000), where motion signals were generated such that there was no position change of the stimulus that contained motion signals (eg by rotating a radial grating). They found that a substantial shift of the relative positions of the flashed stimuli occurred only when the motion stimulus was presented between the comparison flashes. With the motion stimulus that changes its location (ie object motion), a flash ahead of a moving object appears displaced in the direction of the object motion, whereas a flash behind the moving object does not.

The differential mislocalization observed in the present study is analogous to the mislocalization of flashes during smooth-pursuit eye movements, where flashes ahead of the eye are perceived displaced in the direction of pursuit but flashes behind the eye are not (van Beers et al 2001; Matsumiya and Uchikawa 2000; Mitrani and Dimitrov 1982). The present study shows that the asymmetric mislocalization effect does not require eye movements. It is possible that the visual system attentively tracks moving objects (eg Pylyshyn and Storm 1988) and it is this attentive tracking that produces the asymmetric position-capture effect. This may nicely explain both the eye-movement and the moving-object cases, although the underlying mechanism of the asymmetric position-capture effect remains to be investigated.

In addition, we found that the position-capture effect by a visible moving object is sensitive to the spatial contact of flashed stimuli with moving stimuli. The position-capture effect occurs when a flash is presented physically *on* the moving circles. This sensitivity to spatial overlap implies that some interaction between motion and form processing may be involved in the position-capture effect.

6.2 *Position shift of flashed stimuli by invisible object motion*

If an object that moves toward an occluding surface disappears for a period of time and re-emerges at another location, observers usually report a compelling impression that the object moved continuously behind the occluding surface (tunnel effect—Burke 1952; Michotte 1950, 1963). The occlusion conditions in the present study simulated such a situation, and our results showed that an invisible, but phenomenally persisting, moving object can affect the perceived position of a flash. In the present experiments, however, the position capture by the invisible motion differed from that by the visible motion in that the magnitude of the position capture was smaller and it seemed to depend less on the spatial relationship between the flash and the implied location of the hidden object. The latter is probably because the speed of a hidden object behind an occluding surface tends to be underestimated (Burke 1952).

Neurons that respond to moving stimuli that are no longer in sight have been reported in neurophysiological studies. For example, some neurons in the macaque parietal cortex maintained directionally selective responses during the temporary absence of visual stimuli (Assad and Maunsell 1995). More recently, a population of neurons in the temporal cortex of the macaque has been shown to be tuned to the occlusion of objects (Baker et al 2001). The results of the present study suggest that the neuronal representations of hidden objects in these areas may affect neuronal representations of the relative positions of stationary objects.

Finally, different types of invisible motion have been examined in psychophysical and modeling studies: motion under binocular rivalry (Blake et al 1999; Wiesenfelder and Blake 1991), path-guided apparent motion (Shepard and Zare 1983), and trajectory motion behind occluding barriers (Watamaniuk and McKee 1995; Watamaniuk et al 1995). It will be interesting to investigate the relationship between these phenomena of invisible motion and the position-capture effect observed in the present study.

7 Conclusion

In the present study, we asked whether the position-capture effect depends on the spatial relationship between moving and flashed stimuli and whether 'hidden' object motion can produce the position-capture effect. Having obtained positive results for both, we conclude that the perceived position of flashed stimuli is affected not only by nearby retinal motion signals, but also by the representation of 'objects in motion' in higher levels of visual processing (Watanabe 2002; Watanabe et al 2001, 2002).

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