Dynamic distortion of visual position representation around moving objects

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The relative visual positions of briefly flashed stimuli are systematically modified in the presence of motion signals (R. Nijhawan, 2002; D. Whitney, 2002). Previously, we investigated the two-dimensional distortion of relative-position representations between moving and flashed stimuli. The results showed that the perceived position of a flash is not uniformly displaced but shifted toward a single convergent point back along the trajectory of a moving object (K. Watanabe & K. Yokoi, 2006, 2007). In the present study, we examined the temporal dynamics of the anisotropic distortion of visual position representation. While observers fixated on a stationary cross, a black disk appeared, moved along a horizontal trajectory, and disappeared. A white dot was briefly flashed at various positions relative to the moving disk and at various timings relative to the motion onset/offset. The temporal emerging-waning pattern of anisotropic mislocalization indicated that position representation in the space ahead of a moving object differs qualitatively from that in the space behind it. Thus, anisotropic mislocalization cannot be explained by either a spatially or a temporally homogeneous process. Instead, visual position representation is anisotropically influenced by moving objects in both space and time.

Keywords: motion, position, flash-lag, onset, offset


Introduction

The localization of visual objects is one of the primary tasks of the visual system. Therefore, it is not surprising that visual localization is performed efficiently without errors in most of everyday situations. However, visual mislocalizations do occur (Schlag & Schlag-Rey, 2002), particularly in the presence of motion signals (Nijhawan, 2002; Whitney, 2002). For example, when a visual stimulus—one that is physically aligned with another moving stimulus—is flashed, observers perceive the flashed stimulus to be spatially lagging behind the moving stimulus. This phenomenon is referred to as the “flash-lag” effect (e.g., Krekelberg & Lappe, 2001; Nijhawan, 1994, 2002). There exist various explanations for the flash-lag effect (for reviews, see Krekelberg & Lappe, 2001; Nijhawan, 2002; Whitney, 2002), which include, but is not limited to, those that focus on anticipatory process (Nijhawan, 1994), differential latency (Oğmen, Patel, Bedell, & Camuz, 2004; Purushothaman, Patel, Bedell, & Oğmen, 1998; Whitney & Murakami, 1998), temporal integration (Krekelberg & Lappe, 1999, 2000; Lappe & Krekelberg, 1998), attention (Baldo, Kihara, Namba, & Klein, 2002; Baldo & Klein, 1995), postdiction (Eagleman & Sejnowski, 2000a, 2000b), spatial and temporal uncertainty (Brenner & Smeets, 2000; Brenner, van Beers, Rotman, & Smeets, 2006; Eagleman & Sejnowski, 2000b; Kanai, Sheth, & Shimojo, 2004; Vreven & Verghese, 2005), and cognitive factors (Moore & Enns, 2004; Watanabe, 2004; Watanabe, Nijhawan, Khurana, & Shimojo, 2001).

With the objective of generalizing the flash-lag effect, we investigated the two-dimensional mislocalization pattern of a visual flash relative to a moving object. The results indicated that the perceived position of a flash is not uniformly displaced but that it appears to be shifted toward a fixed convergent point behind the moving stimulus (Watanabe & Yokoi, 2006, 2007; Figure 1). This unexpected finding provides a clear counterexample to a spatially homogeneous mechanism for the effect and implies that the flash-lag effect may be a special case of anisotropic mislocalization. In addition, another recent study has revealed that both temporal and spatial
mechanisms contribute to the flash-lag effect (Linares, López-Molinear, & Johnston, 2007). Having proposed that the anisotropic mislocalization is a spatially generalized form of the flash-lag phenomenon, we sought to examine the similarities between the conventional flash-lag effect and anisotropic mislocalization. One of the main debates over the flash-lag phenomenon concerns its dynamic aspect. It was reported that the flash-lag phenomenon occurs even when the onset of a moving object coincides with the onset of a flash, whereas it does not occur when the motion offset coincides with the flash onset (Khurana & Nijhawan, 1995), although recent investigations revealed that the magnitude of flash-lag in these cases is dependent on various factors (e.g., Eagleman & Sejnowski, 2000a, 2000b; Kanai et al., 2004; Kerzel & Gegenfurtner, 2004; Müsselfer, Stork, & Kerzel, 2002; Oğmen et al., 2004; Watanabe, 2004). If the anisotropic mislocalization and the flash-lag effect are based on a common mechanism, they will exhibit similar dependencies on the flash timing relative to the onset and the offset of a moving object.

On the other hand, anisotropic mislocalization also signifies several characteristics that are not found in the conventional flash-lag phenomenon. More specifically, the effect implies that the visual processes of position representation in the space ahead of a moving object may differ qualitatively from those behind the moving object. In this context, an investigation on the temporal emerging-waning pattern would be beneficial in obtaining more detailed information with regard to the underlying mechanisms of anisotropic mislocalization.

Experiment 1: Dynamic distortion of position representation

In Experiment 1, we examined the manner in which the anisotropic pattern of mislocalization changed over time. The basic method was similar to the one used in our previous studies (Watanabe & Yokoi, 2006, 2007). However, a visual flash was presented at various timings relative to the motion onset and offset.

Methods

The experiment involved five observers: the authors and the three psychophysically trained observers who were unaware of the purposes of the study.

A stationary fixation cross (white, 61.0 cd/m², 0.63 deg) appeared at the center of a gray background (8.2 cd/m²). From an observation distance of 57 cm, the observers viewed a CRT display (100 Hz) and fixated on the fixation cross for 200 ms (20 frames). For two observers, the eye movements of both eyes were recorded using an Eye-Link II gaze tracker (SR Research, Ontario, Canada), and the fixation was confirmed to be stable during experimental sessions. A black disk (0.01 cd/m², 0.50 deg in diameter) appeared on the left or on the right (randomly determined) side of the screen (5.00 deg above the fixation cross) and began moving after a brief pause (from 200 to 500 ms). It moved along a horizontal trajectory toward the other side of the screen at a constant speed of 12.50 deg/s. When the disk reached the final position, it became stationary for 200 to 500 ms before disappearing.

A white dot (61.0 cd/m², 0.25 deg) was flashed for one frame (10 ms) at various timings relative to the onset and the offset of the disk’s motion (with stimulus onset asynchrony; SOA of −300, −200, −100, −50, 0, +50, +100, +150, +200, and +300 ms from the moment at which the motion started and stopped). The initial starting position of the disk and the length of the trajectory were adjusted so that the flash always occurred when the moving disk was 2.50 deg to the left or to the right of the fixation cross. The initial starting position of the disk and the length of the trajectory were adjusted so that the flash always occurred when the moving disk was 2.50 deg to the left or to the right of the fixation cross (consequently the positions of the motion onsets and offsets were unpredictable for each trial). This was done to make the position and the timing of the flash unpredictable (occurring when the moving disk was either in the left or in the right visual field) while the eccentricity of the moving disk at the time of the flash...
presentation constant. The positions of the white dot relative to the moving disk are shown in Figure 2.

After the presentation of the stimulus sequence, the black disk reappeared at the center of the screen (but did
not move) together with a continuously visible white disk (identical to the flash) at a similar relative position as in
the stimulus sequence (jittered by 0.63 deg). Using the computer mouse, the observers adjusted the position of the
white disk to indicate the perceived position of the flash relative to the black disk (Movie 1). The next trial began
500 ms after the observer’s response.

In a session, two trials were repeated for each combination of flash timing (11), onset/offset condition (2), and flash position (25) in a counterbalanced manner. Each observer performed six sessions (6,600 trials), which resulted in 12 trials for each condition.

Results and discussion

The results obtained from all the observers showed a similar pattern; therefore, the data were averaged. Figure 3 shows the results of Experiment 1, wherein the perceived flash positions are plotted relative to the black disk corresponding to the origin. A positive value on the horizontal axis indicates that the flash was presented ahead of the black disk. The pattern of results indicated that there was a general central bias toward both the stationary and the moving stimuli (i.e., observers always underestimated the distance of the flash from the reference stimuli), although it was much enhanced with the moving stimuli (Watanabe & Yokoi, 2006, 2007). There are two possible reasons for this general central bias in the present data. Firstly, it has been known that observers mislocalize the positions of targets toward the fovea (foveal bias; Mateeff & Gourevich, 1983; Mitrani & Dimitrov, 1982). Secondly, the perceived position of a flashed stimulus has been reported to be biased toward a stable frame of reference (e.g., Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999; Sheth & Shimojo, 2001). During the response phase, the stationary black disk that was centrally presented might act as the fixation stimulus and the stationary frame of reference.

In addition to the central bias, the perceived positions of flashes were distorted anisotropically, confirming our previous findings (Watanabe & Yokoi, 2006, 2007). Flashes presented ahead of the moving object produced large mislocalization effects, while those presented behind the moving object showed only minor effects. In addition, the mislocalization seemed to follow different temporal patterns at different relative positions of the flash (Movie 2).

Although the mislocalization pattern was fairly complex, the most noticeable characteristic of anisotropic mislocalization was the difference between the spaces ahead of and behind the moving object. Therefore, for simplicity, we plotted the horizontal positions of centroids of perceived flashes within the spaces ahead of or behind the moving object as a function of SOA (Figure 4). The centroid was calculated as the averaged coordinate of 10 flashes ahead of and behind the moving
Results of Experiment 1. The coordinates are shown at the bottom-left corner, with the origin being the position of the black disk. The other panels show the perceived positions of the flashes relative to the black disk, averaged for all observers separately for SOAs and the onset/offset conditions. Results of the leftward and the rightward motions were collapsed and presented as if the black disk moved rightward. The inhomogeneity of the mislocalization effect was apparent. In particular, the flashes presented ahead of the moving object produced large mislocalization effects while the flashes behind the moving object showed only minor effects. Also, the mislocalization seemed to follow different temporal patterns at different relative positions of the flash.
The results of Experiment 1 confirmed anisotropic mislocalization around a moving object (Watanabe & Yokoi, 2006, 2007) and further indicated that the temporal characteristic of mislocalization differs among different relative positions between flashed and moving stimuli, particularly between the spaces ahead of and behind the moving object.

In the space ahead of the moving disk, the main effects of SOA were significant both for the motion onset and the motion offset (one-way ANOVA, $F(10, 40) = 33.09$, $p < 0.05$ for motion onset, $F(10, 40) = 54.51$, $p < 0.05$ for motion offset). Post hoc Newman–Keuls tests revealed that the significant distortion of the relative position representation emerged 150 ms before the motion onset ($p < 0.05$) and reached the asymptote level at the timing of the onset. In addition, the anisotropic distortion began to indicate a significant decrease 150 ms before the motion offset ($p < 0.05$) and ceased to exist at the moment of the motion offset. This pattern is reminiscent of the temporal characteristic of the conventional flash-lag effect. The temporal emerging-waning pattern of the flash-lag effect around the onset and the offset of a moving stimulus has been reported (Eagleman & Sejnowski, 2000a; Khurana & Nijhawan, 1995; Whitney, Cavanaugh, & Murakami, 2000; Whitney, Murakami, & Cavanaugh, 2000). However, the present study is the first to demonstrate asymmetric mislocalizations around motion onsets and offsets and to examine how these vary over time.

In the space behind the moving disk, the main effect of SOA was significant for the motion onset ($F(10, 40) = 2.69$, $p < 0.05$) and motion offset ($F(10, 40) = 4.39$, $p < 0.05$). However, the position representation of the flash was relatively stable, with the exception of the moment of motion onset and motion offset; the transient flash-lag effect occurred at the motion onset and the transient flash-lead occurred at the motion offset (Newman–Keuls tests, $p < 0.05$).

The position representation of flashes in the space ahead of the moving disk change gradually toward the onset and the offset of motion and became stable at the onset and the offset. The position representation of flashes in the space behind the moving disk exhibited the transient flash-lag and flash-lead at the motion onset and offset.
Experiment 2: Effects of the speed of a moving object

The results of Experiment 1 indicated that the mislocalization magnitude increased gradually until the disk began to move and decreased until it finally stopped as though the visual system knew the exact moment when the motion would start and stop. These temporal patterns are in agreement with several explanations provided for the flash-lag phenomenon; according to these explanations, events following the flash determine the flash-lag magnitude (cf., for a counter-example, see Chappell & Hine, 2004). For example, Eagleman and Sejnowski (2000a) proposed that the relative position representation between moving and flashed stimuli is determined by the position information of the moving stimuli 80–100 ms after the flash (postdiction hypothesis). A qualitatively similar account had been proposed by the temporal averaging account (Krekelberg & Lappe, 1999, 2000; Lappe & Krekelberg, 1998). According to these accounts, the mislocalization magnitude increases with the speed of the moving object; however, it is expected that the flash-lag effect would reach the asymptote level at the motion onset and cease to exist just at the moment of motion offset, irrespective of the motion speed. The purpose of Experiment 2 was to examine whether this would be the case for anisotropic mislocalization. Moreover, in Experiment 1, the flashes ahead of the moving disk exhibited a temporal pattern similar to the typical flash-lag effect, whereas the flashes behind the moving disk showed the transient mislocalization at the motion onset/offset. This suggests that the localization processes may differ and that the effect of motion speed would differ between the spaces ahead of and behind the moving stimulus. An additional purpose of Experiment 2 was to examine this possibility.

Methods

The observers, stimuli, and procedure were identical to those of Experiment 1, with the exception of the speed of the moving disk—which was set 6.25, 12.50, 18.75, or 0 deg/s and the flash that occurred at 4 horizontal positions ahead of and behind the moving disk with no vertical offset (−2.50, −1.25, +1.25, +2.50 deg; Figure 5). Again, the initial starting position of the disk and the length of the trajectory were adjusted so that the flash always occurred when the moving disk was 2.50 deg to the left or to the right of the fixation cross. As in the case of Experiment 1, all the conditions were randomized.

Results and discussion

Figure 6 shows the perceived positions of the flashes in Experiment 2. The broken lines indicate the perceived position of the flash with respect to the stationary disk (0 deg/s condition). The final magnitude of mislocalization (the asymptote level) was larger with greater speed of the motion (speed dependency of the flash-lag phenomenon; Krekelberg & Lappe, 2001; Nijhawan, 1994, 2002). As in the case of Experiment 1, the flashes ahead of the moving disk began to be mislocalized before the motion onset and ceased at the moment of motion offset, irrespective of the motion speed. Two-way ANOVAs (SOA × Motion speed) were performed separately for the different relative positions and the onset/offset conditions. The main effects of SOA and motion speeds, as well as the interaction, were significant for all the cases (SOA, $F(10,40) > 4.18$, $p < 0.05$; motion speed, $F(2,8) > 6.94$, $p < 0.05$; interaction, $F(20,320) > 2.31$, $p < 0.05$), except for the −2.50-deg behind condition. In this far-behind condition, only the interaction was significant for the motion onset condition ($F(20,320) = 3.27, p < 0.05$), and the main effect of SOA was significant for the motion offset condition ($F(10,40) = 2.76, p < 0.05$).

For the flashes presented ahead of the moving disk, post hoc Newman–Keuls tests ($p < 0.05$) showed that the mislocalization magnitude became significant between 150 and 50 ms (depending on motion speed) before the motion onset and started to decrease 150 to 50 ms before...
the motion offset and did not change after the motion onset/offset for all motion speed conditions. This pattern of mislocalization dynamics fits well with the idea that the mislocalization phenomena, including the flash-lag effect, do not simply reflect instantaneous sensory signals but include integration processes of position signals over time (Krekelberg & Lappe, 2001), particularly the integration process after a transient signal (e.g., a visual flash; Eagleman & Sejnowski, 2000a, 2000b).

The flashes behind the moving disk tended to show the transient mislocalization only at the motion onset/offset (post hoc Newman–Keuls tests, $p < 0.05$). Further, the speed dependency was much less pronounced. In the highest speed (18.75 deg/s) condition, there seemed to be a rebound of mislocalization after the motion onset; however, it was not observed in the other conditions. Thus, the mislocalization magnitude with the flashes behind the moving disk exhibited a quite different temporal pattern and did not show a clear dependency on motion speed. This suggests that the clear velocity dependency may indicate that the temporal explanation for the flash-lag effect holds only for the space ahead of the moving stimulus and that the localization process in the space behind moving stimuli may be qualitatively different from that in the space ahead of moving stimuli.

**General discussion**

The present study aimed to investigate the emerging and the receding pattern of anisotropic mislocalization (Watanabe & Yokoi, 2006, 2007). The results of this study revealed the following: First, the anisotropic mislocalization pattern gradually emerges 150 ms before the motion onset and begins to decrease 150 ms before the motion offset. Second, the magnitude of mislocalization reaches the plateau just at the time of motion onset and levels out just at the time of motion offset. Third, the temporal patterns similar to the typical flash-lag effect are observed when the flash appears ahead of the moving object. Fourth, for the flash behind a moving object, however, the flash-lag phenomenon occurs only at the moment of motion onset and the transient flash-lead is observed at the moment of motion offset. However, these transient mislocalization effects in the space behind the moving object were nowhere near as great as those in the space ahead of the moving object. Fifth, the mislocalization magnitude depends on motion speed when the flash is presented in the space ahead of the moving disk. The mislocalization magnitude with flashes in the space behind the moving disk does not show a clear speed dependency. In sum, the detailed temporal mapping of anisotropic mislocalization suggested that the localization processes in the spaces ahead of and behind a moving object differ qualitatively. In the context of the present findings, we briefly outline the implications of the present results for current theories of the flash-lag effect and speculate the possible mechanism for differences in position representation between the space ahead of and behind a moving stimulus.
Existing theories of the flash-lag effect and anisotropic mislocalization

Similar temporal patterns between the conventional flash-lag effect and anisotropic mislocalization (for flashes ahead of the moving object) strengthen our proposal that anisotropic mislocalization is a spatially generalized form of the flash-lag phenomenon. However, no current theories of the flash-lag effect fully explain anisotropic mislocalization. For example, current versions of differential latency theories do not specify how the visual latency for a flashed object differ between the space ahead of a moving object and that behind it (Oğmen et al., 2004; Purushothaman et al., 1998; Whitney & Murakami, 1998). Similarly, current theories of positional averaging have no mechanism for incorporating anisotropies (Krekelberg & Lappe, 1999, 2000; Lappe & Krekelberg, 1998; but for partial incorporation of spatial asymmetry, see Kanai et al., 2004). The postdiction model posits that the object’s position is estimated at each moment by integrating positional information forward in time and that the flash resets all the integrals so that only those starting immediately after the flash will produce a position estimate (Eagleman & Sejnowski, 2000a). This may explain why, regardless of motion speed, the mislocalization magnitude reaches the maximum level at the moment of motion onset and wanes out at the moment of motion offset. The postdiction model is yet to incorporate the spatial anisotropies. To account for the anisotropies in mislocalization data, theories would have to assume at least one spatial mechanism.

Differential position representation processes in space ahead of and behind a moving stimulus

The present findings underscore the possible differential processing of position representation between spaces ahead of versus behind a moving object. What is different between these locations? One possibility is the differential behavioral significance. The space ahead of a moving object is the space where the object will arrive in the near future. In contrast, the space behind the moving object is the space that observers have already seen. Therefore, it may make sense to process the space ahead of a moving object differently from the space behind it. In fact, 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 (Tanaka, Yoshida, & Fukushima, 1998; van Donkelaar, 1999; van Donkelaar & Drew, 2002). A similar pattern was also found in the attentive tracking of a moving object (de'Sperati & Deubel, 2006). Perhaps, motion is associated with anticipative mechanisms (Kerzel & Gegenfurtner, 2003; Nijhawan, 1994; Verghese & McKee, 2002) so that locations ahead of a moving object are made more salient through attentional enhancement. However, it is generally believed that more attention leads to enhanced detectability through signal enhancement and/or uncertainty reduction (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Lu & Dosher, 1998; Verghese & McKee, 2002), which in turn would result in the reduction of the flash-lag effect (Baldo & Klein, 1995; Baldo et al., 2002). This is contrary to what was found in the present study, namely, the enhancement of the flash-lag effect in the space ahead of a moving object.

Some researchers hypothesize that spatial and/or temporal uncertainty would play a key role in the flash-lag phenomenon. Several studies showed that the positional uncertainty of a moving object affects the flash-lag magnitude (e.g., Kanai et al., 2004; Vreven & Verghese, 2005), whereas other studies reported little effect of the positional uncertainty of a moving object (Murakami, 2001a, 2001b; Whitney, Cavanaugh, et al., 2000; Whitney, Murakami, et al., 2000). On the other hand, results from studies of flash predictability are consistent: Making the flash spatially predictable decreases the mislocalization magnitude (Brenner & Smeets, 2000; Baldo et al., 2002; Eagleman & Sejnowski, 2000b). Given this, it may be inferred that the positional uncertainty of a visual flash is larger in the space ahead of a moving object than the space behind the moving object. One interesting possibility is that the mislocalization may be caused by an active process imposing positional uncertainty (or noise) in the space ahead of a moving object. Positional uncertainty may be enforced because the perception of motion necessitates positional uncertainty. In other words, higher positional confidence would contradict the dynamic representation of motion; the more concretely an observer knows where an object is, the less vividly the observer perceives the motion of the object.

Another possibility is that the differential position representation may be related to the differential levels of dependence on the anticipative model for actions (Kerzel & Gegenfurtner, 2003; Nijhawan & Kirschfeld, 2003; Wolpert, Ghahramani, & Jordan, 1995). As mentioned previously, the behavioral relevance of the spaces ahead of and behind a moving object may differ. Observers could potentially take action (making eye, head, hand movements, and so on) toward it if something important occurs in or around the moving object. It is essential for the localization system to deliver an effector to a desired location by predicting the future positions of the moving object because actions taken with respect to the moving object would otherwise fall short (Brenner, Smeets, & de Lussanet, 1998; Kerzel & Gegenfurtner, 2003; Nijhawan, 1994; Nijhawan & Kirschfeld, 2003). Then, the space ahead of a moving object may be a more relevant region for predictive models. Indeed, it has been shown that the visual motion system anticipates the appearance of similar motion signals along motion trajectories because physical objects in motion, in general, do not abruptly change direction (Nakayama & Silverman, 1984; Ramachandran
The larger flash-lag effect in the space ahead of a moving object might be considered as a manifestation of the “prediction error”; although the visual system anticipates similar motion signals, it encounters a stationary flash. The difference between expected and actual stimulation may be experienced as a motion (error) signal in the opposite direction. This might cause the motion-induced position capture, wherein the perceived position of a stationary object appears to be shifted in the direction of motion signals with (Watanabe, 2005a; Whitney & Cavanaugh, 2000) and without awareness (Harp, Bressler, & Whitney, 2007; Whitney, 2005).

The two possibilities proposed above are the subject of future studies. With respect to the idea of differential behavioral relevance, it is worth mentioning that, during a smooth pursuit eye movement, flashes ahead of gaze direction are mislocalized in the direction of pursuit (in the egocentric frame of reference) but flashes behind the eye are not (Matsumiya & Uchikawa, 2000; Mitrani & Dimitrov, 1982; van Beers, Wolpert, & Haggard, 2001). Moreover, a similar pattern was found even without smooth pursuit eye movement (Watanabe, 2005b). However, the manner in which these egocentric mislocalizations are related to the anisotropic distortion of the relative position between moving and flashed objects also remains to be investigated (Watanabe, 2005b).

**Conclusions**

The flash-lag situation is not as simple as it appears at the outset. It is essentially a dual task situation in the sense that observers concurrently perform two localization tasks (one for a flash and the other for a moving stimulus) and that they must isolate in time and space a non-terminal position of a moving stimulus with reference to flash timing and position (Brenner et al., 2006; Eagleman & Sejnowski, 2000a; Kanai et al., 2004; Kreegipuu & Allik, 2003, 2004). By demonstrating the complex pattern of interaction in position representation between moving and flashed visual stimuli, the present findings support the view that the assignment of visual position in space and time is rather a complicated process in the human perceptual system (Brenner et al., 2006; Eagleman & Sejnowski, 2000a; Kreegipuu & Allik, 2003, 2004). Future investigation must not exclude the inescapable complexity of position representation in the human visual system.

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