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Saccades reveal that allocentric coding of the moving object causes mislocalization in the flash-lag effect

Stefanie I. Becker
University of Queensland, Brisbane, Queensland, Australia

Ulrich Ansorge
University of Vienna, Vienna, Austria
and University of Osnabrück, Osnabrück, Germany

and

Massimo Turatto
University of Trento, Trento, Italy

The flash-lag effect is a visual misperception of a position of a flash relative to that of a moving object: Even when both are at the same position, the flash is reported to lag behind the moving object. In the present study, the flash-lag effect was investigated with eye-movement measurements: Subjects were required to saccade to either the flash or the moving object. The results showed that saccades to the flash were precise, whereas saccades to the moving object showed an offset in the direction of motion. A further experiment revealed that this offset in the saccades to the moving object was eliminated when the whole background flashed. This result indicates that saccadic offsets to the moving stimulus critically depend on the spatially distinctive flash in the vicinity of the moving object. The results are incompatible with current theoretical explanations of the flash-lag effect, such as the motion extrapolation account. We propose that allocentric coding of the position of the moving object could account for the flash-lag effect.

The flash-lag effect is a visual misperception in which the position of a flash is perceived as shifted relative to that of a continuously moving stimulus: When observers are asked to report their percept at the time the flash occurred, they typically report that the flash was lagging behind the moving object—even when both were presented simultaneously at the same position. This tendency to misperceive the relative locations of flash and moving stimulus has been reported to be impressively robust and common: Over the past years, Nijhawan (2001) has informally tested over 200 subjects, all of them showing the flash-lag effect.

In the present study, we explored whether the flash-lag effect can also be obtained when observers do not have to explicitly judge what they see, but instead have to make a motor response to the stimuli. More often than not, motor responses that are not made on the basis of explicit judgments have proven to be immune to visual illusions, such as, for example, the Titchener–Ebbinghaus illusion, the Ponzo illusion, or the Müller-Lyer illusion. For example, Aglioti, DeSouza, and Goodale (1995) found a large Titchener illusion in perceived stimulus size, but no effect of the illusion on grip scaling when observers had to grasp the stimulus. Similarly, the illusion of seeing induced motion leaves pointing movements unaltered (Bridgeman, Kirch, & Sperling, 1981). The fact that the motor system is not susceptible to visual illusions has been explained by the hypothesis that perceptual and motor systems operate on representations with different spatiotemporal characteristics (Goodale & Milner, 1992). In the two-visual-systems hypothesis, visual information is processed in two different streams, with the ventral pathway (which projects from the primary visual cortex to the inferotemporal cortex) subserving conscious perception, and the dorsal stream (which projects from the primary visual cortex to the posterior parietal cortex) subserving action. In accordance with the affordances of each visual system, the vision-for-action system processes stimuli very fast and yields representations that contain information about the physical properties of an object (e.g., its physical size or its absolute position, relative to the observer). These representations are also supposed to decay very fast when they are not used (see, e.g., Hu & Goodale, 2000). In contrast, vision for perception is presumably based on longer lasting representations that are invariant to the observers' actual positions. The processing speed is also not critical. Correspondingly, the

S. I. Becker, s.becker@psy.uq.edu.au

processing of stimuli in the vision-for-perception system is slower, but it yields representations in which stimuli are represented in relation to other stimuli, which makes this system more susceptible to visual illusions.

Subsequent studies comparing the effect of visual illusions on simple motor responses (e.g., pointing movements, saccades, grasping) versus perceptual judgments have mainly shown that perceptual judgments are affected more strongly by visual illusions than are motor responses—a result that is consistent with the two-visual-systems hypothesis (e.g., Franz, 2001). However, to date it is unclear whether a similar dissociation can be found for perceptual judgments and eye movements in the flash-lag effect.

The Flash-Lag Effect

A multitude of different explanations has been put forward to account for the flash-lag effect. Most of the proposed explanations are agnostic with respect to the question of whether the flash-lag effect occurs only on the level of perception, or whether it will also be found in motor responses—for instance, pointing, grasping, or eye movements. However, in the extrapolation hypothesis (Nijhawan, 1994, 2008), the flash-lag effect should occur on both the level of perceptual judgments and motor responses. Indeed, on the extrapolation hypothesis, the flash-lag effect exists on the level of perceptual judgments because of an extrapolation mechanism that subserves actions. As Nijhawan (1994, 2008) pointed out, the perception of all objects is beset with a neuronal delay of about 100 msec. This neuronal processing delay would hamper our actions specifically with regard to fast-moving objects. As a solution, the visual system constantly extrapolates the position of a moving object forward in time, to compensate the neuronal processing delay and to enable us to deal successfully with fast-moving stimuli (e.g., catching or hitting a ball; e.g., Nijhawan, 1994). Since the same delay is not a problem for actions concerning stationary objects, the extrapolation mechanism is specific to moving objects so that only the position of moving stimuli is extrapolated forward in time.

The flash-lag effect is due to the fact that the perception of the flash cannot be extrapolated forward in time, so that perception of the flash is subject to the neuronal delay of 100 msec. Simultaneously, however, the position of the constantly moving object in the display is constantly extrapolated forward in time. Therefore, at the moment the flash is perceived, the moving object has already traveled further along the trajectory of motion. Hence, the moving object is seen at a position displaced in the direction of motion, and this leads to the impression that the flash lags behind the moving object, even when both were presented concomitantly at the same location (Nijhawan, 1994, 2008).

In sum, the extrapolation view attributes the flash-lag effect, which appears on the level of conscious perception, to an extrapolation mechanism that is needed to allow successful actions with fast-moving stimuli: "The goal of visual prediction [or extrapolation] cannot be solely to inform perception. Rather, visual prediction must impact the behavior of animals and ultimately contribute to a survival advantage" (Nijhawan, 2008, p. 192). Thus, the extrapolation account assumes that extrapolation is carried out in the dorsal pathway that subserves action, and that the extrapolated information is then communicated to the ventral pathway, where it causes the visual illusion ("compensation for visual delays is not carried out in the feedforward ventral pathway serving perception. . . . The perceptual consequences of extrapolation are there due to crosstalk between the dorsal and the ventral pathways at a late stage." [Nijhawan, 2008, p. 194]).

As a consequence, the extrapolation account would predict no dissociation between perceptual and motor responses in the flash-lag effect, contrary to what has been found for other visual illusions (Nijhawan, 1994, 2001; see also Nijhawan & Kirschfeld, 2003).

In the present study, we tested this prediction by assessing the flash-lag effect in the perceptual judgments of observers, and in their saccades to the position of the flash and the moving object. On the basis of the two-visual-systems hypothesis, we expected that the flash-lag effect would occur only when observers had to make a perceptual judgment, whereas it would be absent when they had to respond by making an eye movement. On the other hand, on the extrapolation account, we expected flash-lag effects of equal magnitude in both the perceptual judgment and eye-movement conditions.

So far, there has been only a single study investigating saccadic responses to a flash, but in this study, the eyes were in smooth self-motion (Blohm, Missal, & Lefevre, 2003). The results showed that saccades to the flash were systematically misplaced in a direction corresponding to the error in the perceptual judgments (Blohm et al., 2003; see also Nijhawan, 2001). However, because observers in this study were not aware that their eyes were moving at all, the endpoint of the first saccade on each trial reliably failed to end on the intended position, and observers needed to make 1–2 corrective saccades to fixate the remembered position of the flash. Blohm et al. also speculated that the first saccade was probably not affected by the visual illusion, whereas the final saccades were made in accordance with the perceived stimulus position and thus reflected the illusion. However, this hypothesis could not be tested in the design of Blohm et al.; thus, it is still an open question as to whether saccades to the flash are susceptible to the flash-lag effect.

EXPERIMENT 1

Experiment 1 was designed to investigate whether eye movements show a flash-lag effect. The precision of saccades was measured in two different tasks. In the first task, subjects were required to saccade to the position at which a flash had appeared, whereas in the second task, subjects were asked to saccade to the position where the moving ring had been at the time of the flash. A third task verified the illusion of the flash-lag effect. In this judgment task, subjects reported whether they saw the flash lagging behind, at the same location as, or leading the moving ring.

On the extrapolation account, we would expect that saccades to the position of the flash should be precise, whereas saccades to the remembered position of the moving object (at the time of the flash) should be offset in the direction of motion. Naturally, on the extrapolation account, observers should, in general, be able to make precise online saccades to moving objects, because extrapolation compensates for the neuronal delay in processing the current position of moving objects. Our task, however, involved an offline, or memory-guided, saccade to the perceived position of the moving stimulus at the time the flash was seen. Because there is no compensation for delayed neuronal coding of the flash, and because the moving stimulus continued to move after the flash, a saccade error was predicted under offline saccade conditions. The reason for this is that during coding of the flashed position, the moving object moves further along the trajectory of motion. Thus, the position of the moving object at the time of the flash appears to be offset in the direction of motion (whereas an offline saccade to the position of the flash should show no offset).

On the other hand, in the two-visual-systems hypothesis, perceptual and motor systems are dissociated, and the motor system generally operates on veridical position information. Motor responses are largely unaffected by visual illusions even when they involve a remembered feature of an object that is presented only briefly and that does not remain visible during the motor response (Bridgeman et al., 1981; Goodale & Milner, 1992; Wong & Mack, 1981). Thus, in the two-visual-systems hypothesis, we would expect observers to make precise saccades to the positions of the flash and the moving ring, despite apparent displacements on the perceptual level (see, e.g., Aglioti et al., 1995; Bridgeman et al., 1981; Goodale & Milner, 1992).

Method

Subjects. Six practiced observers—2 men and 4 women—at the University of Trento, Italy, took part in the experiment. One of the authors (S.I.B.) was a subject as well. The mean age of all subjects was 29 years (age range from 26 to 32).

Materials. An Intel Pentium 4 computer (Dell) with a 19-in. SVGA color monitor (Ilyama) controlled the timing of events and generated the stimuli. Stimuli were presented with a resolution of 1,024 × 768 pixels and a refresh rate of 99.9 Hz. For recording of eye movements, a video-based infrared eyetracking system (EyeLink II, SR Research, Ontario, Canada) with a spatial resolution of 0.1° and a temporal resolution of 500 Hz was used. Subjects were seated in a dimly lit room, with their heads fixated by a chinrest and two cheek pads, and they viewed the screen from a distance of 65 cm. For the registration of manual responses, a standard keyboard was used. Event scheduling and reaction-time measurement were controlled by the Presentation software (Neurobehavioral Systems).

Stimuli. The moving ring consisted of a black ring with an outer diameter of 2.4° and an inner diameter of 1.1°. It moved with a speed of 41.7 rpm on the outline of an imaginary circle with a diameter of 6.2°. The movement was created by successively shifting the ring 2.5° from its preceding position with every refresh (10 msec), starting at the 12 o'clock position. The flash was a filled white circle with a diameter of 1.1°. Figure 1 depicts an example of the stimulus display.

Design. Performance was measured in three blocked tasks. In the judgment task, subjects were asked to report what they saw by pressing one of three keys. In the second and third tasks, observers had to perform a memory-guided saccade either to the position of the flash, or to the position at which the moving ring was seen at the time the flash occurred. The order of blocks was balanced across all subjects, so that each subject got a unique order of blocks.

In each block, the same experimental contingencies obtained: The position of the flash was randomly determined on each trial, and the flash could be located either inside the ring, or 5° in front of or behind the moving ring, relative to the motion direction (displacement conditions). Since the critical measures concerned the flash and the moving ring being located at the same position, subjects completed 45 trials in this condition and 15 trials in each displacement condition.

Procedure. Each trial started with the presentation of a small, white fixation point. Subjects were instructed to fixate the center of this point throughout the trial. At the beginning of each trial, we controlled fixation. The flash was presented only if tracking was stable (no blinks) and gaze was within 1° of the center of the fixation point, for at least 350 msec (within a time window of 3 sec). Otherwise, a drift correction was made. If drift correction failed, subjects were calibrated anew (5-point calibration), and the next trial started again with the fixation control.

On each trial, the ring completed two revolutions, with the flash presented on the second revolution for one refresh (10 msec). In the saccade task, a blank gray screen with a small, white fixation cross followed the completion of the second revolution for 500 msec, in which subjects could saccade to the designated target and back to the fixation point. The next trial started with the presentation of the white fixation point and the fixation control.

In the judgment condition, an extra response display was presented between trials. The display depicted the key-to-response mapping and asked subjects to press a key according to whether the flash was perceived to be located (1) inside the ring, (2) displaced in the direction of movement, or (3) displaced against the direction of movement. Figure 1 depicts examples of both displays.

Before each block, subjects were calibrated with a 5-point calibration and were given written instruction about the next task. Moreover, subjects were instructed to try to be as accurate as possible. After each block, subjects were encouraged to take a short break. On average, it took 45 min to complete the experiment.

Results

Data. Eye-movement data were parsed into saccades and fixations using Eyelink's standard parser configuration. An eye movement was classified as a saccade when it exceeded 30°/sec velocity, 8,000°/sec^2 acceleration, or when the eyes were displaced more than 0.1° from the previous position. Saccades were excluded from the analysis when the deviation between the direction of the target object and the direction of the saccades exceeded 30°, which, in Experiment 1, led to a loss of 7.22% of the data.

Accuracy. Figure 2A depicts the mean proportion of judgments for each relative position between flash and moving ring in those conditions in which the flash was located exactly at the center of the ring. As can be seen, despite the flash being located exactly inside the moving ring, it was judged as lagging behind the moving object. Statistical analysis revealed a significantly higher mean proportion of judgments that the flash was being displaced against the movement of the ring than of judgments that the objects were at the same position [$t(5) = 4.3, p < .008$], or that the flash was being displaced in the direction of movement [$t(5) = 4.06, p < .010$]. The latter two judgment frequencies did not significantly differ from one other ($p = .8$). Figure 2B displays the mean proportion of judgments for each individual observer. As can be seen in the figure, all observers—with the exception of the 5th subject

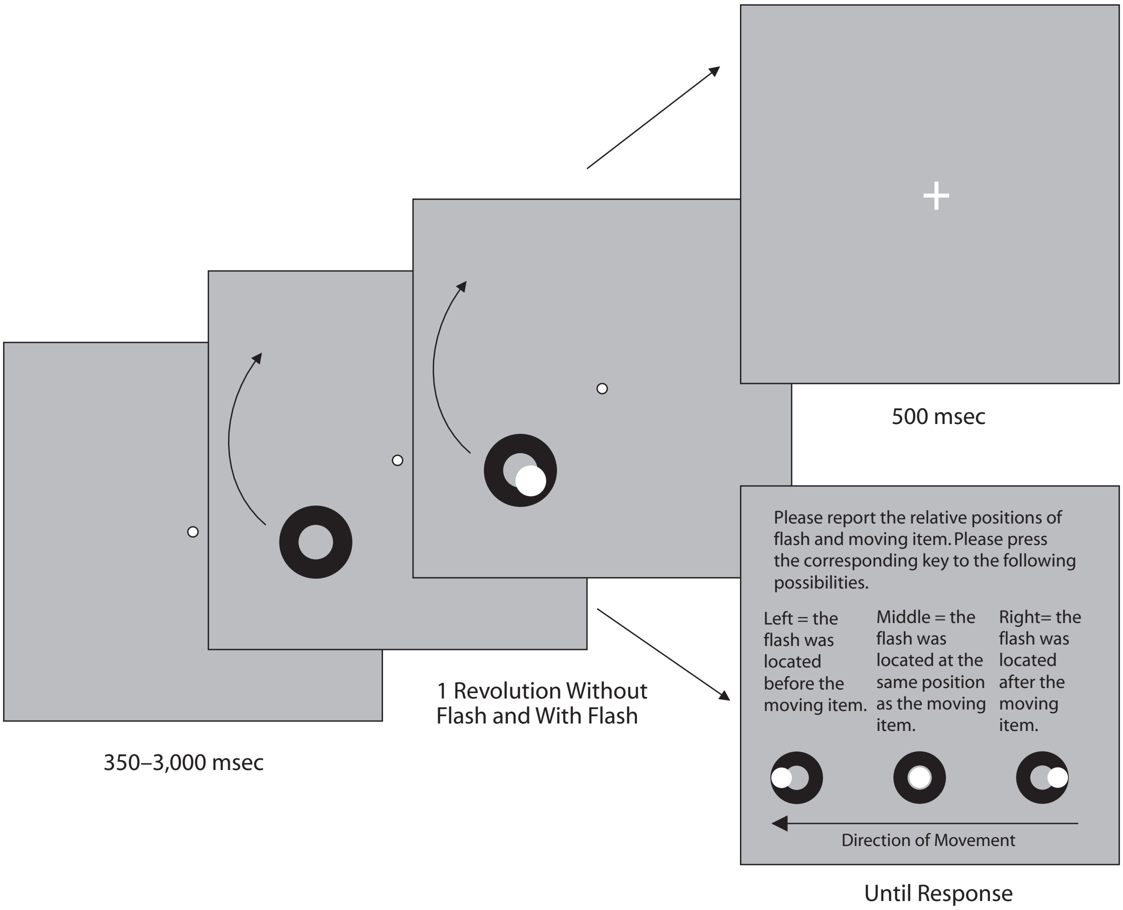

Figure 1. An example of a trial: The left frame illustrates the display with the dot used for the fixation control. The second and third frames show the moving ring, and the flash when it was displaced by 5º. After that, displays in saccade and judgment tasks differed. The top panel depicts a display during the saccade task, and the bottom panel depicts a display in the judgment task.

(Sj 5)—showed a significant flash-lag effect; that is, they reported that the flash had lagged behind the moving ring when the ring and the flash were spatially aligned.

The mean results from both saccade tasks are depicted in Figure 3, separately for saccades to the flash and to the ring (i.e., to the position at which the moving ring was at the time the flash appeared). As can be seen, memory-guided saccades to the position of the flash were precise, with no significant deviation of the saccade from the actual position of the flash ($p = .40$). However, saccades aimed at the position of the moving ring at the time the flash appeared were significantly shifted in the direction of the ring's movement [$t(5) = 3.28$, $p < .022$]. Figures 4A and 4B, moreover, show the endpoints of saccades directed to the flash and the position of the moving ring individually for each observer. As can be seen from the figures, the offset in saccadic endpoints of saccades to the ring is not due to some extreme outliers, but to a shift of the whole distribution of saccadic endpoints (see Figure 4B).[1]

Discussion

The results indicate, first, that under flash-lag conditions, saccades can be precisely directed to the flash. However, saccades that were directed to the remembered position of the moving object at the time the flash appeared were systematically displaced in the direction of movement. This indicates that the computation of the saccadic endpoint was susceptible to the same kind of direction shift reflected in the flash-lag effect.

Thus, the flash-lag effect does not show a dissociation between perceptual and motor system effects, contrary to many effects in which the motor system was apparently spared from impacts of visual illusions (see, e.g., Aglioti et al., 1995; Bridgeman et al., 1981).

The observed pattern of results is in line with the extrapolation account, according to which the flash-lag effect reflects a mislocalization of the moving item, but not of the flash. Moreover, as was predicted on the basis of the extrapolation hypothesis, the flash-lag effect is not restricted to perceptual judgments; it also influences processes on the motor-response level. This is an interesting finding, because previous studies have found that saccades are usually executed with high precision to the veridical position of the target, even in the presence of strong perceptual illusions.[2] For instance, in the study of Wong and Mack (1981), observers were asked to saccade to the

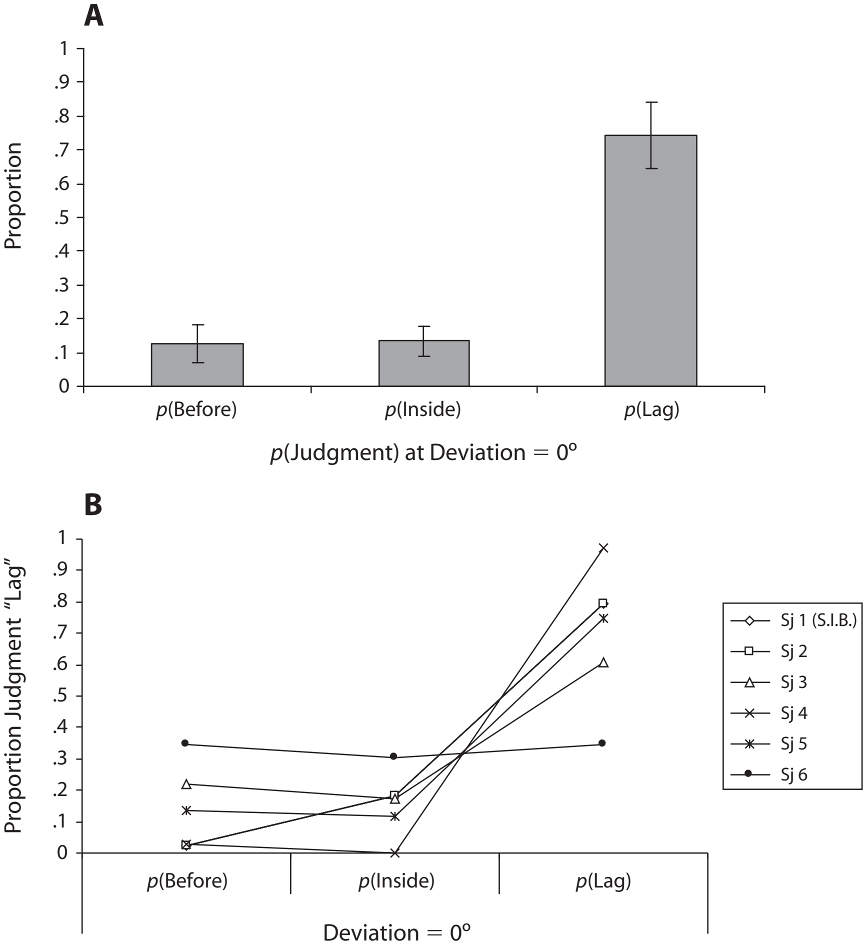

Figure 2. The mean proportion of manual responses in Experiment 1, when the flash was presented inside the moving ring. *p*(Before) illustrates the mean probability that subjects reported the flash position before the position of the moving ring. *p*(Inside) and *p*(Lag) signify the probability that subjects reported the flash as being located inside or behind the position of the moving ring at the time the flash occurred. Error bars represent ±1 *SEM*. Sj, subject.

remembered position of a target that had undergone an illusory displacement between frames. The illusory displacement was induced by moving the frame surrounding the target. Despite the fact that altering the position of the frame resulted in a strong perceptual illusion that the target had moved, and that the saccades had to be executed to a remembered position, saccade precision was unaffected by the perceptual illusion (Wong & Mack, 1981). The observation made in the present study—that saccades to the remembered position of the moving ring were displaced—is consistent with the view that the flash-lag effect originates in the dorsal pathway, which subserves actions, and that this information is later transferred to the ventral pathway, where it causes the visual illusion. However, the results are also compatible with alternative views—for instance, that the flash-lag effect arises from very early visual processes that compute the position of objects before the ventral/dorsal division (see, e.g., Krekelberg, 2003; Nijhawan, 1997, 2001).

Intriguingly, the results are also compatible with an alternative explanation of the dorsal/ventral dissociation in visual illusions. According to the frame of reference explanation, differences between perceptual and motor responses obtained in previous studies are not due to dissociations between the corresponding systems, but rather to the type of encoding strategies used in the task (see, e.g., Bernardis, Knox, & Bruno, 2005; Bruno, 2001; Schenk, 2006). In particular, it has been proposed that visual illusions result from an allocentric encoding of stimuli, whereas immunity from visual illusions stems from an egocentric encoding strategy. The motor task typically requires an encoding of object size, length, or position in an egocentric manner, taking the agent's position in space as the sole reference point. Conversely, the perceptual task usually requires a comparison of the target with other, nontarget objects, thus requiring an allocentric frame of reference for encoding. Since the frame of reference (allocentric or egocentric) and the type of processing system (perceptual vs. motor) are mostly confounded, both the two-visual-systems hypothesis and the frames-of-reference hypothesis can explain the observed dissociations between perceptual illusions and motor processing.

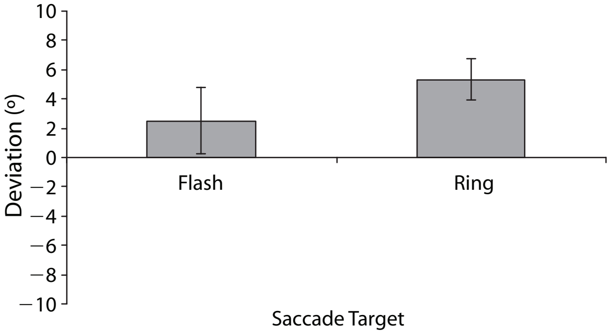

Figure 3. Mean deviation in the direction of saccades, depicted separately for saccades targeted at the flash and at the position of the ring. Deviations of 0 indicate that the saccade was precise; positive values indicate that saccadic endpoints were shifted into the direction of motion. Error bars represent ±1 *SEM*.

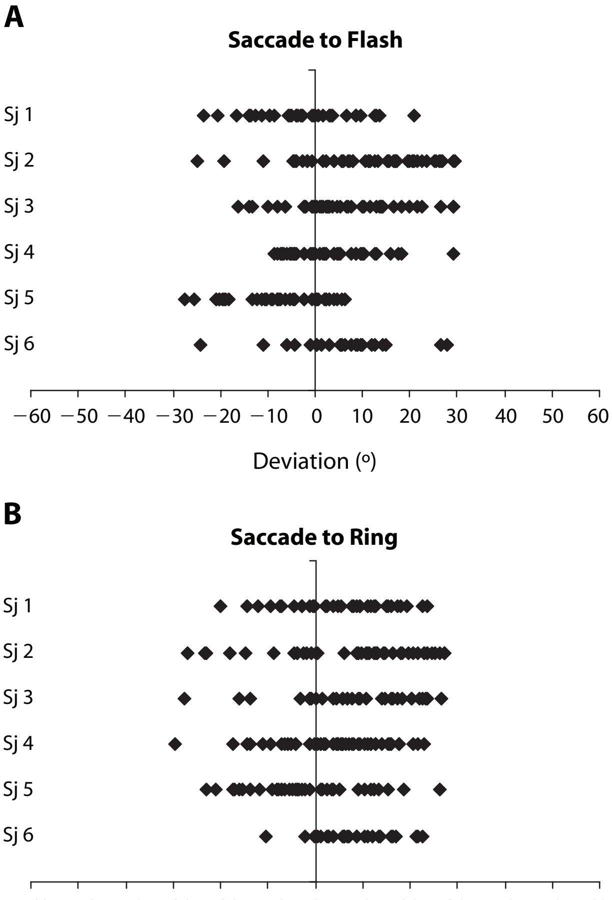

Figure 4. Results from individual trials, depicted separately for each subject. (A) The deviation of saccadic endpoints for saccades directed to the flash. (B) The deviation of saccades directed to the moving ring. Deviations of 0 indicate that the saccade was precise; positive values indicate that saccadic endpoints were shifted into the direction of motion. Sj, subject.

However, in the frame-of-reference hypothesis, there is no strict dissociation between the processing systems themselves, so it is possible to observe illusions of the same magnitude with perceptual judgments and motor responses, provided that the task induced observers to encode objects in an allocentric frame of reference (e.g., Franz, Fahle, Bülthoff, & Gegenfurtner, 2001).

Although it was originally developed to present an alternative explanation for the observed dissociation between perceptual illusions and motor responses, the frame-of-reference hypothesis might even account for the flash-lag effect itself. It is, for example, conceivable that saccades to the flash and moving ring are programmed using different encoding strategies: Whereas saccades to the flash are programmed directly, within an egocentric frame of reference, saccades to the moving ring might be programmed on the basis of encoding the position of the moving stimulus relative to the position of the flash, thus using an allocentric coding strategy. In this case, the visual system would first determine the position of the flash, and then compute the position of the moving ring relative to the flash, taking the position of the flash as a reference or anchor point. Processing of the relative positions would, however, be a time-consuming process, which in turn would lead to a delay in further processing the moving stimulus. Thus, at the time the visual system starts processing the position of the moving object, it has already moved on to another location, which explains the offset of saccades targeted at the moving ring as well as the flash-lag effect itself (i.e., the misperception that the flash appears to lag behind the moving object).

This explanation is akin to the attentional capture explanation of the flash-lag effect, which proposes that the flash captures attention to its position and that the processing of the motion stimulus is halted until attention can be (re)directed to the moving target. At the point in time that attention is deployed to the moving target, however, the moving target has moved on and is thus perceived as being shifted in the direction of motion (see, e.g., Baldo, Kihara, & Namba, 2002; Baldo & Klein, 1995; Carbone & Pomplun, 2006; cf. Müsseler & Aschersleben, 1998; Müsseler & Neumann, 1992). Although the allocentric coding account is similar to the attentional capture account of the flash-lag effect (insofar as allocentric encoding of the flash and moving item require sequential processes), it also differs in important respects. Specifically, the flash-lag effect does not occur (only) as a consequence of time-consuming attention shifts to the position of the flash. Rather, the delay occurs because observers first encode the nominally irrelevant position of the flash, which is then taken as an anchor point, or point of reference, from which the position of the moving ring is computed. In line with this allocentric encoding account of the flash-lag effect, Priess, Becker, Ansorge, Carbone, and Scharlau (2009) found that when they asked their subjects for temporal order judgments about which of two changes occurred first (the flash or a change of the moving target), the flash was perceived as temporally preceding a simultaneously occurring change of the moving target. This sequence of perceived events is fully in line with the hypothesis that attention is first directed to the location of the peripheral flash, and then only afterward (back) to the moving ring (Priess et al., 2009; but see also Eagleman & Sejnowski, 2000).

Contrary to other hypotheses, such as the extrapolation view, the allocentric coding explanation proposes that the position of a continuously moving stimulus is not misperceived per se; rather, allocentric encoding of the position of the moving stimulus accounts for the mislocalization. If this hypothesis is correct, then subjects should be able to make precise saccades to the moving stimulus if the flash serves as a temporal signal but cannot be used as a spatial marker. This account was tested in Experiment 2.

EXPERIMENT 2

The main purpose of Experiment 2 was to test the allocentric coding explanation. To that aim, a further condition was introduced, in which subjects had to saccade to the position of a moving ring when the whole background flashed. In this background flash condition, the flash served as a temporal signal for committing the position of the moving ring to memory; it was impossible to use the background flash as a spatial reference. Consequently, the position of the moving ring should have been encoded correctly within an egocentric frame of reference.

Thus, if allocentric coding of the moving stimulus accounts for the findings of the previous experiment, saccadic responses to the moving ring should be precise with the background flash. In turn, when the flash is presented as a spatially discrete object, as in Experiment 1, saccades to the moving ring should show the same offset as before.

According to the extrapolation hypothesis, on the other hand, saccades to the moving ring should always show the same offset, regardless of whether the whole background or a spatially distinctive object flashes. This hypothesis holds because the position of the continuously moving ring should be extrapolated to its future position in both conditions alike, and because the spatially distinct flash and the background flash should both be subject to neuronal delays that cannot be compensated.

Additionally, Experiment 2 included two different conditions in which the precision of saccades to the spatially distinctive flash were tested: In the speeded saccade condition, subjects were asked to saccade to the memorized position as soon as they detected the flash. In the delayed saccade condition, observers were asked to wait until the ring had completed its second revolution and only then to initiate the saccade to the flash. These two conditions were used in order to exclude the possibility that the previous results were due to differences in the time course of saccades to the flash and the moving ring (see, e.g., van Zoest, Donk, & Theeuwes, 2004; Wong & Mack, 1981).

For example, van Zoest et al. (2004) proposed that saccade programming might be differentially affected by bottom-up and top-down processes at different points in time. Thus, at an early stage, saccade programming is dominated by fast bottom-up processes, whereas top-down processes would only dominate saccade programming at a later point in time (van Zoest et al., 2004). In order to exclude the possibility that the differences between saccades to the flash and to the moving ring that were observed in Experiment 1 were due to differences in the onset or saccadic latencies, in Experiment 2, we directly manipulated the time course of saccades to the flash. If, in the previous experiment, saccades targeted to the flash were precise only because they could be initiated faster than saccades to the moving ring, then only the speeded saccades to the flash should be precise. In turn, delayed saccades to the flash should show the same offset as that of the saccades to the moving ring. If, on the other hand, differences in the time course of saccades cannot explain the observed differences, then saccades to the flash should remain precise in both speeded and delayed saccade conditions.

Method

Subjects. Seven students at the University of Trento participated in this experiment. All subjects were new, with the exception of 1 who had already participated in Experiment 1. One subject was excluded because removing all saccades outside 30º of the direction of the target resulted in removing more than 30% of her data. Afterward, excluding all data in which the direction of the saccade deviated more than 30º from the direction of the target object led to a loss of 9.92% of all data.

Apparatus. The apparatus was exactly the same as that in the previous experiment.

Stimuli, Design, and Procedure. These were the same as in Experiment 1, with the following exceptions: Experiment 2 consisted of two tasks that were distributed over four conditions. As in the previous experiment, one task was to make a fast eye movement to the flash. In the speeded saccade condition, subjects had to saccade to the flash as soon as they detected it; in the delayed saccade condition, this saccade had to be delayed until the moving ring had completed its second revolution and the screen was free of motion. The second task required subjects to saccade to the moving ring. The spatial flash condition was exactly the same as in Experiment 1. In turn, in the background flash condition, the flash consisted of a color change from dark gray to white of the whole background (for one refresh; 10 msec) and back to gray. In both conditions, subjects were instructed to remember the position of the moving ring at the time of the flash, and to perform a memory-guided saccade to this location once the ring had completed its second revolution.

As in the previous experiment, the spatially distinctive flash was located inside the moving ring on 60% of all trials, whereas it was presented with a 5º offset in the motion direction on 20% of all trials, and against the motion direction on 20% of all trials. Subjects completed 60 trials in the condition in which the flash and the moving ring were spatially aligned, and 20 trials in each spatial offset condition. In the background flash condition in which this logic was not applicable, data were nevertheless treated accordingly, so that an equal number of trials was committed to analysis in each condition.

Results

Comparing speeded and delayed saccades with one another revealed that saccadic latencies were significantly higher in the delayed saccade condition ($M = 818$ msec) than in the speeded saccade condition ($M = 332$ msec) [$t(5) = 5.84$, $p < .002$]. This result indicates that subjects followed the instructions to delay or speed up their saccades in the respective conditions. Statistical analysis of the accuracy of saccades in the delayed and speeded saccade condition, however, did not show any significant differences [$t(5) = 0.39$, $p = .71$]. Figure 5 depicts the mean saccadic accuracy in speeded and delayed saccades directed to the flash.

Comparing saccadic accuracy between the conditions in which a background flash or a spatial flash signaled the position of the moving object revealed highly significant differences between the conditions [$t(6) = 5.37$, $p < .003$]. As can be seen in Figure 6, the typical offset in the direction of movement was restricted to the condition in which a spatially distinct flash was present. In turn, with a background flash, saccades directed to the position of the moving ring were not mislocalized in the direction of movement; rather, if anything, they showed a slight offset in the opposite direction. As in the previous experiment, the difference between saccades to the spatially distinctive flash and to the moving ring was also significant [$t(5) = 3.53$, $p < .017$]. As before, saccades to the flash were precise, and their direction did not deviate significantly from the actual position of the flash [$t(5) = 1.66$, $p = .16$], whereas saccades to the moving ring deviated significantly from its actual location once a spatially distinct flash was presented [$t(5) = 3.80$, $p < .013$]. Moreover, as can be seen in Figures 7A–7C, the mean offset in saccadic endpoint of saccades directed to the ring was again not due to outliers, but to a systematic shift of the whole distribution in the direction of motion (see Figure 7B).

Discussion

The results of the second experiment are at odds with the extrapolation account and instead support the allocentric coding account. According to the extrapolation hypothesis, saccades to the moving ring should have shown the same offset in the direction of motion, regardless of whether the flash was a spatially localized event or involved the whole background. In contrast, the results revealed that the moving ring is mislocalized only when the flash is presented as a spatially distinct object. This result is in line with the allocentric coding view, according to which the spatially distinctive flash is detected first and serves as a reference for encoding the position of the moving ring. By contrast, when such an allocentric encoding strategy is rendered impossible by flashing the whole background, the position of the moving object is egocentrically—and with this, correctly—encoded. These results indicate that the position of a moving object can be correctly encoded even when a flash is used as a temporal marker. Contrary to the extrapolation account, the flash-lag effect thus cannot be due to the fact that compensation for the neuronal processing delay is available only for the moving object, and not for the flash.

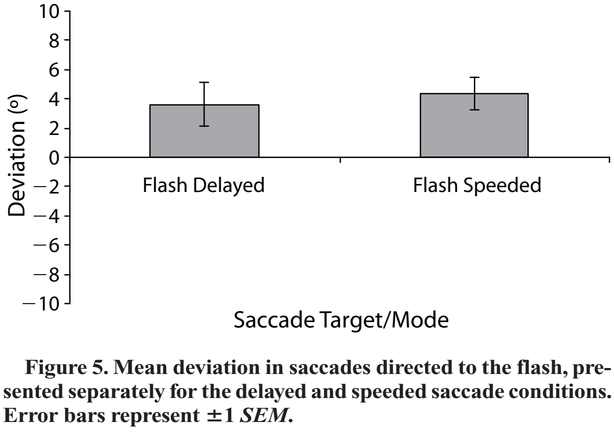

Figure 5. Mean deviation in saccades directed to the flash, presented separately for the delayed and speeded saccade conditions. Error bars represent ±1 *SEM*.

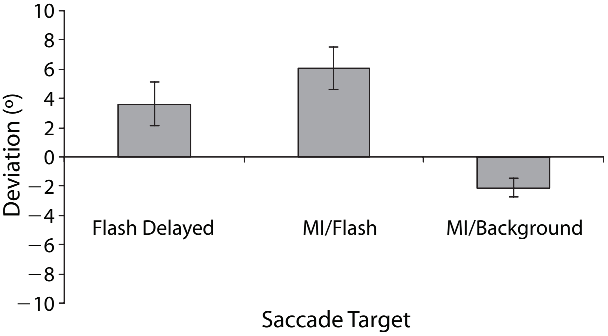

Figure 6. Mean deviation in saccades directed to the positions of the flash (flash delayed) and the moving item (MI; ring–flash) in a classical flash-lag procedure, and also mean deviation of saccades in the new condition, in which saccades should have been directed to the position at which the moving object was located when the whole background flashed (ring–background). Error bars represent ±1 *SEM*.

Furthermore, comparing speeded with delayed saccadic responses to the flash did not reveal any significant differences between saccadic behavior in the two tasks. This result effectively rules out the possibility that differences in localizing the flash and the moving object were due to possible differences in the time course of initiating saccades to the flash and moving object (see, e.g., van Zoest et al., 2004).

GENERAL DISCUSSION

The present study explored saccadic responses directed to the flash and to the moving ring in the disc-ring paradigm standardly used in investigations of the flash-lag effect (see, e.g., Nijhawan, 1997, 2001). The results showed that saccades to the flash were spatially precise, whereas saccades directed to the moving object were significantly offset in the direction of motion. As was shown by a subsequent experiment, saccadic mislocalization of the moving ring critically depends on the presence of a spatially refined flash; the mislocalization could be eliminated when the whole background was flashed. This result pattern presents conflicting evidence for the extrapolation account.

Although many different accounts have been put forward to account for the flash-lag effect, the present results appear to be inconsistent with all of these. This inconsistency arises because most of the extant theories claim that the position of the moving object cannot, in principle, be encoded correctly when a temporally short-lived flash is used as a temporal marker. Conversely, to the best of

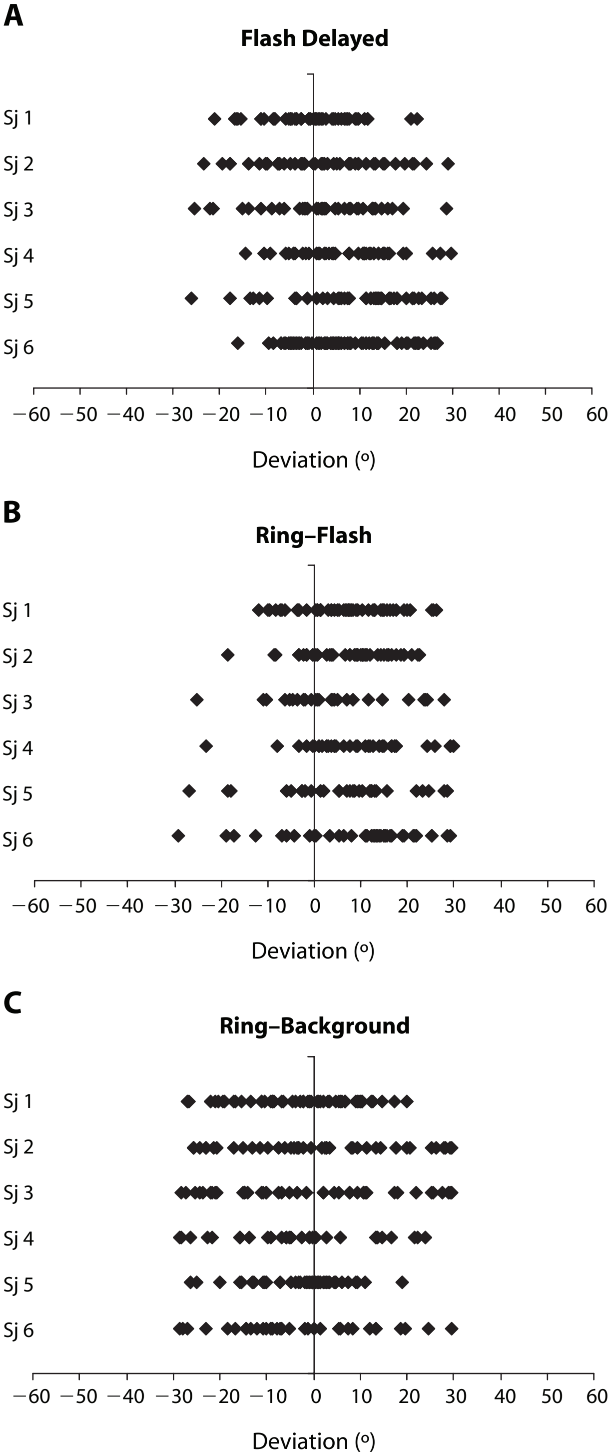

Figure 7. Results from individual trials, depicted separately for each subject. (A) The deviation of saccadic endpoints for delayed saccades directed to the flash. (B) The deviation of saccades directed to the moving ring when the flash was spatially refined. (C) The deviation of saccades directed to the position of the moving ring when the whole background flashed. Deviations of 0 indicate that the saccade was precise; positive values indicate that saccadic endpoints were shifted into the direction of motion. Sj, subject.

our knowledge, most accounts explain mislocalizations of the moving object in the flash-lag effect by the observer's inability to integrate the position information of a moving object correctly with the temporal information of the flash. For instance, according to the extrapolation account, the position of the continuously visible moving ring can be extrapolated forward in time, whereas a corresponding compensation mechanism is not available for the sudden appearing flash. According to the different latency hypothesis, perception of the flash is delayed by longer perceptual processing times. Therefore, at the time the flash is detected, the moving item has already moved onward to its next position, which accounts for the flash-lag effect (see, e.g., Patel & Bedell, 2000; Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney & Murakami, 1998). A different account of the flash-lag effect, the postdiction hypothesis, assumes that the position of a moving object is always a mean value of positions sampled over a longer time interval. The flash resets these motion integration processes, so that only positions after the time of the flash are used for calculating the position of the moving object. As a consequence, the position of the moving object appears to be shifted forward in the direction of motion (see, e.g., Eagleman & Sejnowski, 2000). A related view, the temporal recruitment hypothesis, also assumes that the position of a moving object is always a mean value of positions sampled over a longer time interval (e.g., Krekelberg & Lappe, 2000). Whereas the perception of objects that are continuously visibles benefits from temporal recruitment processes that allow a speeded computation of their position, the computation and integration of position information from the flash is slowed in comparison, which produces the flash-lag effect (Krekelberg & Lappe, 1998).

On the basis of all of these accounts, we would have expected observers to mislocalize the moving ring also in the condition in which the whole background flashed. Current accounts would predict mislocalization errors in this condition because the flash-lag effect is caused by an error in the integration of information from the flash and moving ring, which in turn is due to the temporal characteristics of the flash—that is, its sudden onset and offset. Conversely, the results of Experiment 2 indicate that the moving object can be localized correctly when a background flash with the same temporal characteristics as a standard flash is used as a temporal marker. However, the finding that the position of the moving ring can also be correctly perceived is unanticipated by most current hypotheses designed to explain the flash-lag effect.

One way to reconcile the present findings with these accounts would be to claim that differences in the luminance or the feature contrast modulate the time needed to perceive a flash. It has, for instance, been demonstrated that the flash-lag effect decreases and turns into a flash-lead effect when the luminance of the flash is increased (Purushothaman et al., 1998). This result has been taken to show that the neuronal latencies for perceiving the flash and the moving object depend on their relative luminances, with shorter processing times for bright stimuli than for dim stimuli. Accordingly, it has been shown that the feature contrast of the moving stimulus and the flash plays an important role for the time needed to perceive either stimulus, with shorter neuronal latencies for high-contrast than for low-contrast stimuli (see, e.g., Arnold, Durant, & Johnston, 2003).

To reconcile the present findings with different latency models, it may now be claimed that the background flash condition allowed correct localization of the moving object's position because the neuronal latencies for perceiving this very bright or high-contrast flash were reduced to an extent that they matched the neuronal latencies for perceiving the moving object. Although this possibility cannot be ruled out, it should be observed that this account cannot explain why we observed a flash-lag effect at all under the conditions of the present experiment. In the present study, the moving ring was always black and presented against a dark gray background, whereas the flash was white. Since the moving ring had minimum luminance and feature contrast and the flash was always presented with maximum luminance and feature contrast, we would have expected a flash-lead effect in all experiments, instead of the observed flash-lag effect. Thus, the different latency hypothesis cannot explain the occurrence of a flash-lag effect in the present experiments (see, e.g., Experiment 1).

The failure to find a flash-lead effect could be due to differences in the construction of the stimuli: Differences in brightness were found to modulate the flash-lag effect when near-threshold moving stimuli were used (Purushothaman et al., 1998), whereas suprathreshold stimuli have been reported to produce a reliable flash-lag effect even at complete polarity reversals—that is, both when the flash is black and the moving ring is white and vice versa (Nijahawan, 2001). In the present study, the flash and moving ring were likewise both clearly suprathreshold, which can probably explain the failure to find a flash-lead effect.

In sum, differences in the luminance or feature contrast can at most provide an explanation for finding that the background-flash condition allowed a precise encoding of the position of the moving object. However, neither of these explanations appears to be compatible with the finding of a significant flash-lag effect in the standard condition. Thus, these alternative accounts are less parsimonious than the allocentric encoding account, which can explain both the presence and the absence of a flash-lag effect in the background flash condition by a single underlying mechanism.

Although the results of the present study were taken to be inconsistent with an extrapolation account of the flash-lag effect, they should not be taken to mean that there is no extrapolation mechanism at all. To the contrary, single-cell recordings from ganglion cells in the retinae of a rabbit and salamander showed that moving stimuli cause a wave of neuronal activity that is shifted forward along the path of motion, as was predicted on the extrapolation account (Berry, Brivanlou, Jordan, & Meister, 1999). Whereas it is undisputed that retinal extrapolation mechanisms compensate for neuronal processing delays of moving stimuli (Berry et al., 1999), the results of Experiment 2 indicate that this extrapolation mechanism might not be responsible for the flash-lag effect. Consistent with this view, Schlag, Cai, Dorfman, Mohempour, and Schlag-Rey (2000) showed that the flash-lag effect can also be observed in the absence of retinal motion, when the observer is himself accelerated on a rotating chair (Schlag et al., 2000; see also Blohm et al., 2003). Taken together, these findings indicate that the flash-lag effect cannot be fully explained by a retinal extrapolation mechanism: Apparently, higher level processes on the cortical level are necessary to explain the flash-lag effect (Niemann, Nijhawan, Khurana, & Shimojo, 2006).

Although further research is needed to investigate the compensation mechanism for the flash in more detail, it seems to be clear that the flash-lag effect is not due to an inability to correctly integrate position information of the moving object with temporal information of a suddenly appearing, short-lived flash. However, since almost all extant accounts of the flash-lag effect assume that such an error in information integration processes is responsible for the flash-lag effect, the present results rule out a majority of explanations.

An exception to this rule is the attentional account of the flash-lag effect (see, e.g., Baldo & Klein, 1995). In this view, the displacement of the moving object is due to the fact that the flash inadvertently captures the observer's attention to its position, so that attention needs to be redirected to the moving object in a time-consuming process (Baldo et al., 2002; Baldo & Klein, 1995). The attentional explanation would also be consistent with the results of the present study on the plausible assumption that the background flash is a less spatially defined attention-grabbing event than is the occurrence of the dot onset.

However, it should be noted that the attentional account is not incompatible with the allocentric coding account. Conversely, as was indicated above, it is possible to incorporate attentional effects into the allocentric coding account by claiming that delays in the processing of the moving object's position are caused not only by interference in computing the position of flash and moving object, but also by the need to allocate attention first to the flash, and then to the moving object.

However, previous research indicates that attention only modulates the flash-lag effect; it cannot fully account for the illusion. When the position of the moving object is validly precued in order to allow attention shifts to the relevant position prior to presenting the flash, the flash-lag effect is only reduced, not eliminated (Baldo et al., 2002; Baldo & Klein, 1995; Eagleman & Sejnowski, 2000). Some studies also failed to find significant effects of attention on the flash-lag effect (Khurana & Nijhawan, 1995; Khurana, Watanabe, & Nijhawan, 2000). For this reason, Baldo et al. modified their attentional account of the flash-lag effect to include nonattentional factors, such as purely perceptual processes.

Certainly, further research is also required to investigate the validity of the present allocentric coding account in more detail. So far, however, the proposed explanation seems to be a promising candidate to solve the puzzles about the flash-lag effect, because it avoids the problems of the purely attentional account while simultaneously linking the flash-lag effect to other visual illusions.

With respect to other visual illusions, the present study can possibly also contribute to the ongoing, long-lasting debate as to whether and how conscious perception and the control of action are linked. The relationship between perception and action has been hypothesized to take three different forms. The strong separate representation model proposes that distinct neural representations underlie motor behavior and conscious visual perception. The weak separate representation model likewise posits separate spatial representations for perception and action, but allows for crosstalk, modulated by task demands, to occur between them. Finally, the common representation model holds that conscious perception and visuomotor control proceed from the same mental representation (Franz et al., 2001; see also McCarley, Kramer, & DiGirolamo, 2003).

The results of the present study suggest that with respect to the flash-lag effect, saccadic responses and perceptual judgments did not draw on different spatial representations. In this case, saccades should have been always precisely directed to the moving object, regardless of whether the flash was spatially refined or whether the whole background flashed. In contrast, saccades were accurate only in the latter condition (see Experiment 2), but showed an offset comparable to the illusion in the former condition (see Experiment 1). This indicates that performance was not directly modulated by either the kind of required response (saccade vs. perceptual judgment) or the task demands, because in both conditions, the task was to saccade to the position of the moving ring.

Instead, the present results are consistent with the frame-of-reference hypothesis, which accounts for separate representations by claiming that different spatial representations result from different strategies of encoding. In this view, demands to egocentrically encode the properties of objects will often yield a representation that presents the physical properties of objects veridically, whereas allocentric encoding generally results in representations of relational properties of the target to its surrounding stimuli (see, e.g., Bernardis et al., 2005; Bruno, 2001). Thus, the frequent finding that motor-level responses differ from perceptual responses seems to reside, rather, in a preferred mode of encoding that is applied in a given task; that is, in motor tasks, the preferred mode of encoding is egocentric, whereas in perceptual or judgment tasks, allocentric encoding is preferred.

As Franz, Gegenfurtner, Bülthoff, and Fahle (2000) pointed out, the preferred encoding strategy is often induced by different task demands, so that in the perceptual judgment, subjects have to compare multiple stimuli with each other, whereas in the motor tasks, they can focus on the physical properties of a single stimulus. However, when perceptual and motor tasks are exactly matched, perceptual judgments and motor responses show an equal susceptibility to visual illusions (see also Franz, 2001; Franz et al., 2001).

Additionally, one of the central findings that has been cited in support of the hypothesis that perceptual judgments and motor-level responses are made on the basis of different spatial representations has also been demonstrated to rely on differences in encoding strategies. As Schenk (2006) demonstrated, patient D.F., who suffers a bilateral damage to the ventral stream, is not unable to successfully complete perceptual judgment tasks (while motor-level responses are unimpaired), as was first proposed by Goodale and Milner (1992). Instead, patient D.F. suffers from impaired allocentric encoding, as could be demonstrated by testing perceptual judgments and motor-level responses in both an egocentric and an allocentric encoding condition (Schenk, 2006). Hence, the allocentric encoding account of the flash-lag effect proposed in the present study is well in line with recent findings concerning other visual illusions.

It is also important to note that the allocentric encoding account makes some unique predictions that allow one to distinguish further between this account and other explanations of the flash-lag effect. For instance, on the allocentric encoding account, a spatially distinctive flash should actually be perceived earlier, and its position should be known earlier in time than should the position of the continuously moving object. This prediction is directly contrary to the claims of the alternative accounts (e.g., the extrapolation account, or the different latency hypothesis, but not the attentional account), and allows the allocentric encoding account to be distinguished from these alternative views. On the allocentric encoding account, a flash should be perceived earlier in time than, for instance, the event of the moving object reaching a stationary and consistently visible marker, and this prediction could be tested by assessing the temporal order judgments of the observers. Another possible way to extend the allocentric encoding account would be to test saccades or pointing movements to the moving object at the time of a cue that can (versus cannot) be used as a spatial anchor—for instance, an auditory cue that is simultaneously emitted from loudspeakers around the observer. An auditory cue that can serve as a spatial marker, either for the visual or auditory flash-lag effect, in contrast, should show the typical flash-lag effect, both in perceptual judgments and in pointing movements or saccades (e.g., Alais & Burr, 2003; Arrighi, Alais, & Burr, 2005; Krekelberg, 2003).

AUTHOR NOTE

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NOTES

1. The deviation between the direction of the saccade and the position of the moving ring was also significant for each individual subject, with the exception of Sj 5 (all ts > 2.6, all ps $< .01$, two-tailed).

2. A possible exemption from this rule is the Müller-Lyer illusion, in which eye movements to the endpoints of the figure have been reported to be biased in the direction of the perceptual illusion (see, e.g., McCarley, Kramer, & DiGirolamo, 2003).

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