Motion signal and the perceived positions of moving objects

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When a flash is presented in spatial alignment with a moving stimulus, the flash appears to lag behind (the flash-lag effect). The motion of the object can influence the position of the flash, but there may also be a reciprocal effect of the flash on the moving object. Here, we demonstrate that this is the case. We show that when a flash is presented near the moving object, the flash-lag effect does not depend greatly on the duration of the preflash trajectory. However, when the flash is presented sufficiently far from the moving object, the flash-lag effect increases with the duration of the preflash trajectory, until it reaches an asymptotic level. We also show that the interaction of the near flash can occur when it is task irrelevant. Finally, using the motion aftereffect, we demonstrate that motion signals are involved in the time evolution of the flash-lag effect.

Keywords: flash-lag effect, temporal mechanisms, spatial mechanisms, motion aftereffect

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Introduction

Localization of objects in visual space is one of the primary functions of the visual system. Spatial localization depends not only on position in retinotopic maps but also on other influences (Schlag & Schlag-Rey, 2002), like the motion signal (Whitney, 2002). For example, it has been shown that the perceived location of a stationary envelope filled with a moving pattern is biased in the direction of motion (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). Moreover, if after prolonged viewing, the pattern stops, then not only is the stationary pattern perceived as moving in the opposite direction—the motion aftereffect (MAE)—but also, the perceived position of the envelope is also shifted in the direction of the MAE (Nishida & Johnston, 1999; Snowden, 1998), indicating that position shifts can arise from internally generated motion. Interestingly, it has been shown (Nishida & Johnston, 1999) that the shift induced by the MAE gradually increases over the first 1 or 2 s postadaptation, suggesting that the representation of position is influenced by a dynamic system that integrates motion information over time.

The flash-lag effect (Nijhawan, 1994) has also been used extensively to study the perceived location of moving objects. When a flash is presented in spatial alignment with a moving stimulus, the flash appears to lag behind. The cause of the illusion is still a matter of debate (Krekelberg & Lappe, 2001; Nijhawan, 2002; Ögmen, Patel, Bedell, & Camuz, 2004; Whitney, 2002). Some investigators support the view that the flash-lag mislocalization is caused by purely temporal mechanisms: attentional delays (Baldo & Klein, 1995), differential latencies (Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000), temporal integration (Krekelberg & Lappe, 2000), and position sampling (Brenner & Smeets, 2000). Others propose spatial mechanisms (motion extrapolation) that directly influence the coded location of the moving object, shifting its apparent position in the direction of motion (Nijhawan, 1994; Snowden, 1998). If this is the case, given that it has been shown that motion information is integrated over time (Nishida & Johnston, 1999), one might also expect the magnitude of the flash-lag effect to evolve over time. Specifically, one would predict that the flash-lag effect magnitude should increase as the duration of the preflash trajectory increases.

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Previous empirical work on the flash-lag effect, however, does not support this prediction. Several studies have compared the magnitude of the flash-lag effect when the presentation of the flash coincides with the onset of the moving object against conditions in which the flash is presented during continuous object motion. Although some studies found that the magnitude of the effect for continuous object motion and for flash-initiated motion is the same (Baldo & Klein, 1995; Eagleman & Sejnowski, 2000; Nijhawan, Watanabe, Khurana, & Shimojo, 2004), others found a larger effect for the flash-onset presentation (Chappell, Hine, Acworth, & Hardwick, 2006; Müsseler, Stork, & Kerzel, 2002; Ögmen et al., 2004).

We believe that the apparently incongruous results, with respect to the temporal dependence of spatial position shifts, between the MAE and flash-lag experiments may be explained if, in the flash-lag effect, the sudden appearance of a near flash influences the perception of the moving object. To test this hypothesis, we measured the time evolution of the flash-lag effect with different distances between the flash and the moving object.

General methods

The stimuli were displayed on a 21-in. CRT monitor (Sony Trinitron GM 520) at a refresh rate of 100 Hz and were viewed binocularly from a distance of 50 cm in a dimly lit room. Observers reported normal or corrected-to-normal visual acuity. They were instructed to maintain fixation on a dot presented at the center of the display.

We presented observers with a pair of dots diametrically opposed to each other, rotating about the fixation point. We measured the perceived position of the pair at several intervals from their motion onset (flash presentation time) in the visual field by flashing another pair of diametrically

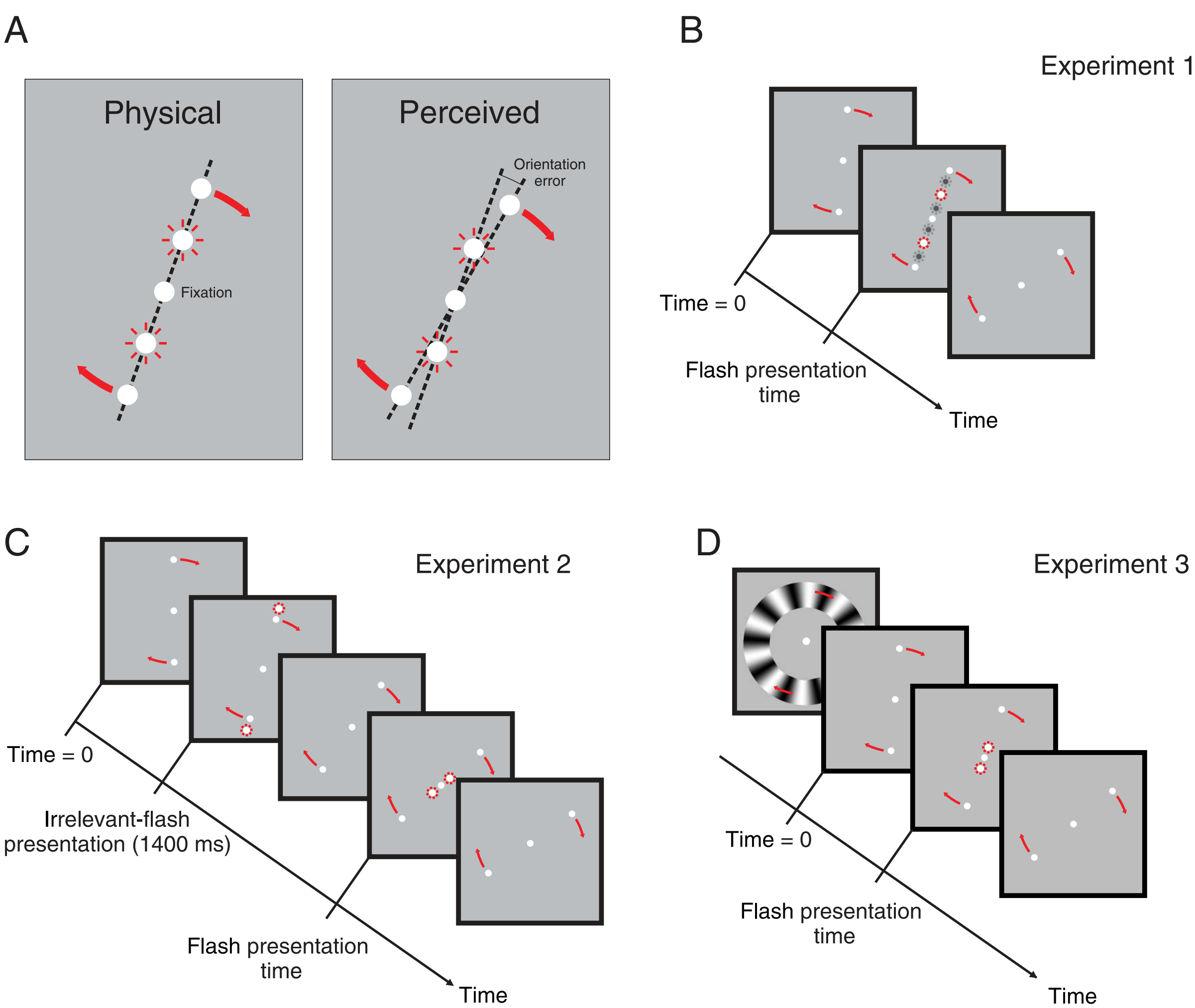

Figure 1. (A) Illustration of the flash-lag effect. (B) Experiment 1. Three different positions for the flashed dots were tested. (C) Experiment 2. In addition to the flashed dots used to measure the flash-lag effect, another two flashed dots completely irrelevant for the task were displayed. (D) Experiment 3. Before each trial, a sinusoidal grating was displayed to produce adaptation.

opposed dots and asking observers for relative position judgments (Figure 1). The initial angular position of the moving dots was randomized across trials.

Both the moving and the flashed dots subtended 0.8° of visual angle. They were displayed on a dark background. The moving dots (luminance = 23 cd/m^2, angular speed = 60°·s^{-1}) were presented at an eccentricity of 7.5° of visual angle. The direction of rotation varied at random from trial to trial between clockwise and counterclockwise. The flashed dots (luminance = 93 cd/m^2) were displayed for 10 ms. The luminance of the flashed dots was greater to equate the perceived luminance. The fixation dot was the same size as the flashed dots (luminance = 23 cd/m^2).

Participants judged whether the flashed dots were displayed behind or ahead of the moving dots. We expressed the spatial misalignment as an orientation difference between the imaginary lines that pass through the moving dots and the flashed dots (Figure 1A). Their relative position (orientation) was varied according to the method of constant stimuli. Nine relative orientations ranging from −3.6° to 25.2° in increments of 3.6° were used to derive a psychometric function. Positive values corresponded to the flashed dots presented ahead with respect to the moving dots. Each psychometric function provided distributions of the proportion of trials in which the moving dots were seen behind the flashed dots as a function of their relative orientation. We fitted cumulative Gaussians to derive the points of subjective equality (the means of the underlying Gaussian distributions), which served as measures of the flash-lag effect. Measurements were made for several flash presentation times in each of the three reported experiments.

We used the parametric bootstrap method (Efron & Tibshirani, 1993) to obtain the 95% confidence intervals for the parameters of the cumulative-Gaussian functions. When conclusions could not be drawn by merely looking at the overlap between two confidence intervals, parametric bootstrap and Monte Carlo simulations were used to compare two given psychometric curves by testing the null hypothesis that the observed difference between points of subjective equality is not different from zero. To accomplish this, we used the procedure implemented in pfcmp (Wichmann & Hill, 2001a, 2001b).

Experiment 1

In the first experiment, we investigated the dependency of the flash-lag effect on the timing of the motion trajectory. Because we suspected that the proximity of the flash might also affect the perceived position of the moving object, we also varied the distance between the flashed dots and the moving dots.

Methods

Three observers participated in the experiment: the first author and two psychophysically trained observers who were naive as to the purposes of the study. We measured the flash-lag effect at various time points (flash presentation time: 200, 400, 800, and 1,600 ms) as a function of the distance between the flash and the moving object (1°, 2.5°, and 5°). Each observer conducted five sessions. The experimental conditions were randomized within each session. For each flash presentation time, each relative distance was sampled 20 times. Thus, each orientation error was calculated using 60 measures (20 × 3 observers).

Results

Figure 2A shows the orientation error as a function of the flash presentation time and the relative distance between the flashed and moving dots. The flash-lag effect was greater when the flash was presented 800 ms as compared with 200 ms after the onset of motion ($p < .05$) for each of the three relative distances. The difference between these two flash presentation times, however, was larger for the 5° separation (orientation error difference: 4.00°) than for the 2.5° (orientation error difference: 1.47°) or the 1° (orientation error difference: 1.23°) separation.

For the three relative distances, the flash-lag effect was very similar for the 800- and 1,600-ms latencies, although only for the 1° separation condition did the difference reach significance ($p = .036$).

Discussion

The results (Figure 2A) show the typical flash-lag effect: The moving dots appear ahead of the flashed dots when they are physically aligned (Figure 1A). We also found that the magnitude of the lag decreased as the eccentricity of the flashed dots increased (red, green, and blue lines in Figure 2A). Baldo and Klein (1995) used a similar display, but they presented the flashes more peripherally than the moving objects. They showed that the flash-lag effect increased as the eccentricity of the flashes increased. Therefore, our findings complement theirs showing that the critical factor is the relative distance between the flashes and the moving objects, rather than the absolute eccentricity of flashes.

Interestingly, we found that the lag gradually increased with the duration of the preflash trajectory until it reached an asymptotic level (Figure 2A), indicating some temporal recruitment of the apparent shift in spatial position (Nishida & Johnston, 1999).

The effect of the preflash trajectory is substantially reduced for flashes presented near moving objects (green and blue lines in Figure 2A), suggesting an interaction between flashes and moving objects. Because in flash-lag experiments, flashes are typically presented relatively close to moving objects, this result is consistent with studies showing no differences between the flash-onset and the continuous flash-lag effects (Baldo & Klein, 1995;

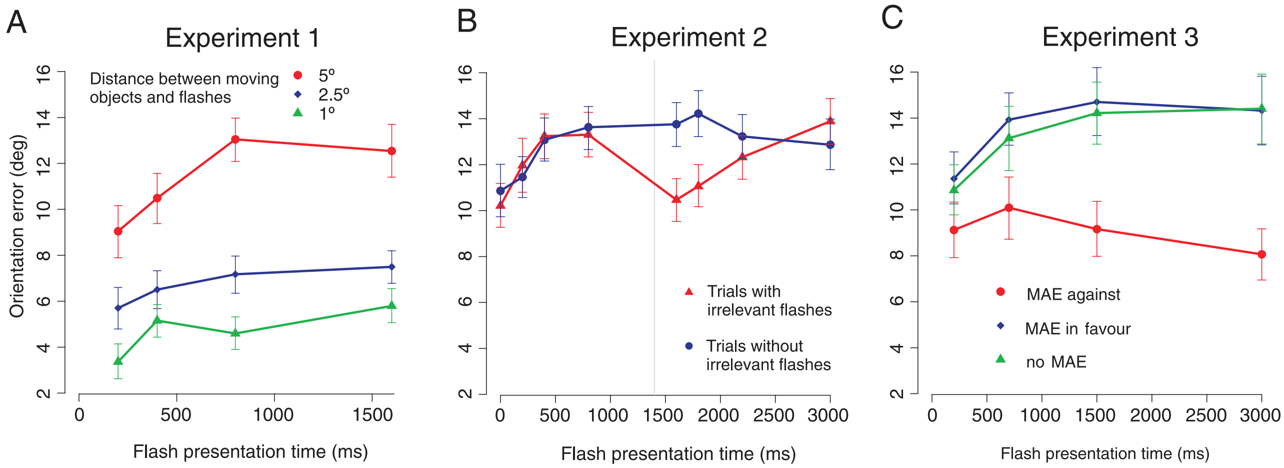

Figure 2. (A) Results of Experiment 1. (B) Results of Experiment 2. The vertical gray line represents the presentation time for irrelevant flashes (1,400 ms). (C) Results of Experiment 3. The error bars represent a 95% confidence interval estimated by using the bootstrap method.

Eagleman & Sejnowski, 2000; Nijhawan et al., 2004). As mentioned in the Introduction section, others studies, however, have found a greater flash-lag effect for the flash-onset condition than for the continuous motion condition (Chappell et al., 2006; Müsseler et al., 2002; Ögmen et al., 2004). We did not measure the flash-lag effect at flash onset, but extrapolating our results, one would predict the opposite result: a smaller flash-lag effect for the flash-onset condition. In Experiment 2, we included a flash-onset condition to test this prediction.

Experiment 2

It has been shown that a moving object can influence the perceived position of a flash (Durant & Johnston, 2004; Whitney & Cavanagh, 2000), but the results of Experiment 1 suggest that there is also a reciprocal effect of the flash on the moving object.

To determine whether the flash has a direct effect on the apparent position moving patterns, we explored the influence of task-irrelevant flashes. In each trial, two types of flashes were presented: Task-irrelevant flashes were displayed near the moving objects 1,400 ms after the onset of motion, and, to measure the flash-lag effect in different instants of time (in this experiment, we included a 0 relative timing), task-relevant flashes were displayed far from the moving objects.

Methods

The first author and two psychophysically trained observers who were naive as to the purposes of the study participated in the experiment. We measured the flash-lag effect using the most remote flashes of Experiment 1 at different points in time (flash presentation time: 0, 200, 400, 800, 1,600, 1,800, 2,200, and 3,000 ms). In half of the trials, 1,400 ms after the onset of motion, we presented a pair of flashed dots (irrelevant flashes) close to the moving dots, instructing the observers to ignore them. The eccentricity of the irrelevant flashed dots was 8.5°. Each observer performed eight sessions. The experimental conditions were randomized within each session. Each flash presentation time was sampled 32 times (16 times with irrelevant flashes and 16 times without). Thus, each orientation error was calculated using 48 measures.

Results

Figure 2B shows the orientation error as a function of the flash presentation time. The red line corresponds to the condition in which the task-irrelevant flashes were displayed, and the blue line corresponds to the condition in which they were not displayed. Before the presentation of task-irrelevant flashes (flash presentation times: 0, 200, 400, and 800 ms), the confidence intervals for these two conditions completely overlapped. However, at 200 and 400 ms after the presentation of the task-irrelevant flashes (flash presentation times: 1,600 and 1,800 ms), the flash-lag effect was significantly smaller ($p < .05$) in the presence of irrelevant flashes. No differences were found when the flash lag was measured 800 and 1,600 ms after the occurrence of the task-irrelevant flashes (flash presentation times: 2,200 and 3,000 ms).

Because task-irrelevant flashes presented before 1,400 ms (flash presentation times: 0, 200, 400, and 800 ms) had no effect, we included the data from these conditions in an analysis of the change in the flash-lag effect over time. The flash-lag effect measured at 400 and 800 ms after motion onset did not differ significantly, and both were greater than the flash-lag effect at 0 ms.

When the task-irrelevant flashes were not presented, there were no significant differences for the flash-lag effect measured from 400 ms (flash presentation times: 400, 800, 1,600, 1,800, 2,200, and 3,000 ms). When the task-irrelevant flashes were presented, some differences appeared: The flash-lag effect at 1,600 ms was not significantly different from that at 1,800 ms, but it was smaller than for the 800-, 2,200-, and 3,000-ms conditions.

Discussion

The flash-lag effect measured before 1,400 ms was not influenced by the occurrence of the irrelevant flashes (Figure 2B). This was expected because trials with and without irrelevant flashes are identical for this time interval. Crucially, the occurrence of the irrelevant flashes affected the measured lag for around 1 s after presentation (Figure 2B), showing a clear interaction between flashes and moving objects that seems to consist of restarting the process of spatial repositioning of the moving objects.

Except for the postdiction account (Eagleman & Sejnowski, 2000) for which the flash resets a motion signal, the other explanations assume no interaction between the moving object and the flash (Krekelberg & Lappe, 2001; Nijhawan, 2002; Ögmen et al., 2004; Whitney, 2002). The flash, therefore, is considered for most of the accounts as just a spatiotemporal marker that indicates when position judgments should be made. Here, contrary to this view, we demonstrate an interaction between flashes and moving objects that occurs even for task-irrelevant flashes. This is consistent with a very recent investigation (Chappell et al., 2006) showing that both the onset and the reversal trajectories of a moving object are affected by the presentation of an adjacent task-irrelevant flash. Chappell et al. (2006) proposed attention "capture" as an explanation, but this cannot explain our results because it would be expected to enhance the lag. In addition, we show that the effect of irrelevant flashes lasted for around 1 s after the flash.

As expected, we found the smallest flash-lag effect for the flash-onset condition. In previous studies, flashes and moving objects are presented near each other. For this situation, it has been shown that the flash-lag effect at flash onset is greater (Chappell et al., 2006; Müsseler et al., 2002; Ögmen et al., 2004) or the same (Baldo & Klein, 1995; Eagleman & Sejnowski, 2000; Nijhawan et al., 2004) as the effect for continuous object motion. Here, we showed that when flashes are presented far from the moving objects, the flash-lag effect could also be reduced in the flash-onset condition.

Experiment 3

In the previous experiments, we showed that the flash-lag effect evolves over time. We think that this time dependence is caused by the motion signal of the moving object itself. In this experiment, we study the influence of motion signals that do not arise from the moving object. For this purpose, we added an extra motion signal in the form of a MAE. To generate a MAE, before each experimental trial, we presented a rotating ring that covered the area in which the moving dots subsequently appeared. MAE was generated in one of two directions: in favor and against the direction of the moving objects. This way, we can control for simple contrast adaptation effects.

Methods

Two psychophysically trained observers who were naive as to the purposes of the study participated in the experiment. We measured the flash-lag effect at different instants in time (flash presentation time: 200, 700, 1,500, and 3,000 ms) using the most remote flashes of Experiment 1. Observers conducted two types of sessions: with and without adaptation. Before each trial of the adaptation sessions, a ring (smallest radius = 4.5°, biggest radius = 9.5°) carrying a sinusoidal grating was displayed for 10 s (60 s for the first trial of each session) at an angular speed of $60° \cdot s^{-1}$. The direction was maintained in each session. After adaptation, the direction of the motion of the moving dots was chosen at random between clockwise and counterclockwise. Each observer completed 15 sessions with adaptation and 5 without adaptation. Each orientation error was calculated using 30 measures.

Results and discussion

The results (Figure 2C) show that a MAE signal in the direction of the moving dots has no effect. However, a MAE whose direction was against the dot motion globally reduced the flash-lag effect and eliminated its temporal dependence, confirming that motion signals mediate the flash-lag effect. This result would not be predicted on the basis of a purely temporal mechanism (Baldo & Klein, 1995; Brenner & Smeets, 2000; Krekelberg & Lappe, 2000; Purushothaman et al., 1998; Whitney & Murakami, 1998; Whitney et al., 2000). The implication of direction-selective mechanisms suggests that the standard flash-lag effect for visual moving objects and the flash-lag effect generalizations (Alais & Burr, 2003; Sheth, Nijhawan, & Shimojo, 2000) may share mechanisms but are not exactly the same phenomenon.

At the neural level, it has been suggested that spatial mechanisms could be implemented by backprojections from area V5/MT to V1 (McGraw, Walsh, & Barrett, 2004; Nishida & Johnston, 1999; Whitney & Cavanagh, 2000), which have been proposed to support visual awareness of motion (Pascual-Leone & Walsh, 2001; Silvanto, Cowey, Lavie, & Walsh, 2005).

In the flash-lag literature, spatial accounts are primarily associated with the motion extrapolation hypothesis (Nijhawan, 1994). According to this explanation, the visual system uses the motion signals to extrapolate the position of the moving object and, in this way, compensates for neural delays. Within this view, the moving object is seen at its true physical position. It is proposed that the sudden appearance of the flash undermines the temporal corrections of perception, which results in the flash-lag effect. The motion extrapolation hypothesis assumes an independence of the processing of the moving object and the flash, which is not supported. We do demonstrate, however, the modification of spatial representations. It remains to be seen as to whether this modification participates in sensory compensation.

Because we were able to demonstrate with this experiment that the progressive lag involves motion signals, the results of Experiment 2 imply that in the flash-lag effect, the flash not only captures attention (Chappell et al., 2006) but also influences how motion alters the code for spatial location.

Conclusions

Here, we demonstrate that spatial mechanisms contribute to the flash-lag mislocalization. Temporal explanations are not sufficient. Importantly, these spatial mechanisms might go unnoticed if flashes are presented near moving objects, indicating that flashes cannot be considered as innocuous spatiotemporal markers.

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