Behavioral significance of motion direction causes anisotropic flash-lag, flash-drag, flash-repulsion, and movement-mislocalization effects

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Motion from periphery to central vision (foveopetal motion) causes a greater flash-lag effect than motion in the opposite direction (foveofugal motion). In order to examine the factors that contribute to the motion direction-based anisotropic flash-lag effect, we investigated the mislocalization of the flash caused by motion and the mislocalization of the moving object per se. We observed that for foveofugal motion, flashes were perceived shifted in the direction of motion but mislocalized in the opposite direction for foveopetal motion. Additionally the mislocalization of the moving object was larger in foveopetal motion than in foveofugal motion. Thus, both factors contribute to the anisotropic flash-lag effect. We interpret these findings in terms of greater behavioral significance of foveopetal motion in relation to foveofugal motion.

Keywords: flash lag, flash mislocalization, foveopetal motion, foveofugal motion, vision, position

Introduction

The flash-lag effect is a well-studied phenomenon in which observers see a flash co-localized with a moving as spatially lagging behind the moving object (Fröhlich, 1923; Hazelhoff & Wiersma, 1924; Mateeff & Hohnsbein, 1988; Metzger, 1932; Nijhawan, 1994). The magnitude of the flash-lag effect is known to vary across individuals and across different displays. Displays with different shapes and sizes of moving objects and flashes (Nijhawan, 2001), and different modes of presentation (Khurana, Nieman, Nijhawan, & Shimojo, 2006), have yielded a relatively wide range of magnitudes of the flash-lag effect as measured in units of time (spatial-lag/velocity). Variations in the magnitude of the effect are also known to occur within a single observer and a single display type. Mateeff and Hohnsbein (1988) manipulated the direction of object motion in relation to the observer's fixation point. In their experiment the object either moved from the periphery to central vision (foveopetal motion) or moved in the opposite direction (foveofugal motion). These authors found that the flash-lag effect for foveopetal motion (FP-Motion) was much stronger than that for foveofugal motion (FF-Motion) (also see Mateeff et al., 1991). The interpretation offered by these authors was that the FP/FF-Motion anisotropy in the magnitude of the flash-lag effect reflects a shorter processing delay for objects approaching the retina as compared to objects moving away from the retina.

Although there is still debate as to which account most successfully explains the flash-lag effect, Mateeff and Hohnsbein's (1988) suggestion of FP/FF-Motion-based anisotropy in the flash-lag appears consistent with the "differential latency" account of the flash-lag effect, which suggests that the flash-lag effect occurs due to shorter latency for moving objects in relation to flashes (Metzger, 1932; Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney & Murakami, 1998). However, there could be other causes of the observed FP/FF-Motion-based anisotropy in flash-lag, which have not been explored. The main purpose of the present experiments is to investigate alternative factors that might contribute to the strong FP/FF-Motion-based anisotropy in the flash-lag effect.

A second phenomenon that has been the focus of several recent investigations, which we shall refer to as motion-based flash-mislocalization effect, or simply flash-mislocalization effect, is observed when flashes are presented in the vicinity of moving objects. The typical effect is that moving objects cause nearby flashed objects to be dragged in the direction of motion (Whitney & Cavanagh, 2000). This effect is extremely robust and has been investigated with various types of motion, including motion viewed through a slit. In one study, in which the retinal image movements (of small elements) were orthogonal to the perceived motion of a diamond-shaped object, flash-mislocalization followed perceived motion and not retinal image motion, i.e., the flash-mislocalization effect occurred in the direction of the perceived motion of the diamonds (Watanabe, Nijhawan, & Shimojo, 2002).

It has been shown that there is anisotropy in the flash-mislocalization effect that depends on which part of the moving object (its leading or trailing end) the flashed object is presented closest to (Shi & de'Sperati, 2008; Watanabe, 2005); the flash-mislocalization effect is much stronger for the leading edge of a moving object.

Recent studies showed that the flash-mislocalization effect, in which moving objects cause the flashes to appear displaced in the motion direction, can dilute the flash-lag effect leading to a reduced magnitude flash-lag (Eagleman & Sejnowski, 2007; Shi & de'Sperati, 2008). However, it is not known whether the flash-mislocalization effect itself depends on the direction of the motion. Here we specifically use the observed FP/FF-Motion anisotropy in the flash-lag effect to address this question. Thus, we ask if the condition that produces a weaker flash-lag effect, that is the FF-Motion condition, also produces to a stronger flash-mislocalization effect, and vice-versa. Can the full FP/FF-Motion-based anisotropy in flash-lag be accounted for in terms of the difference of flash-mislocalization effects in the two conditions, or does an anisotropic mislocalization of the moving objects per se also contribute to the anisotropic flash-lag?

In order to address the cause of the FP/FF-Motion-based flash-lag anisotropy, we first measured this anisotropy by using the standard flash-lag paradigm with the exception that objects moved either toward the point of eye fixation of the subjects or moved away from this point. In the second and third experiment, we measured the flash-mislocalization effect in the FP/FF-Motion conditions. In the fourth experiment, we measured the mislocalization of the moving item per se in relation to a static reference line ("fixed flash").

General methods

Apparatus

Stimuli were presented on a Datacheck oscilloscope with very fast P15 phosphor. The P15 phosphor ensured that on-screen image persistence was reduced to 10% of normal image intensity within 2.8 μs of image termination (Bell, 1970). Event timing, data collection, and stimulus generation were controlled by a Pentium PC, which also controlled oscilloscopic image presentation by means of a Cambridge Research Systems D300 card with 16 MB memory. The response device was a two-button parallel keypad.

Subjects

The same five subjects participated in Experiments 1, 2, and 4. One of them was an author (Z.S.) and three of the remaining four participants were naive to the purpose of the experiments. Four additional naïve subjects and the author (Z.S.) participated in Experiment 3. All participants had normal or corrected-to-normal visual acuity.

Data analysis

All psychometric curves were fitted by logistic regression with the data pooled over all participants in a given experiment. The point of subjective equality (PSE) was obtained by estimating the 50% point via a logistic function. For the purpose of comparison, all PSEs are stated in terms of visual angle. In addition, we estimated the confidence intervals (CI) of individual PSEs by using a bootstrap method with 1000 iterations (Efron & Tibshirani, 1993; Kanai, Sheth, & Shimojo, 2004).

Experiment 1

Flash-lag anisotropy with foveopetal and foveofugal motions

The purpose of Experiment 1 was to replicate previous findings (Kanai et al., 2004; Mateeff & Hohnsbein, 1988; Müsseler & Aschersleben, 1998), which reported that there is a large magnitude difference in the flash-lag effect for FP- versus FF-Motion.

Methods

Stimuli

The stimulus configurations are illustrated in Figure 1. Four conditions were tested in the experiment: FP-Motion and FF-Motion in combination with the presentation of the stimuli in the left visual field (LVF) and right visual field (RVF). In all conditions, two vertical collinear lines (0.1° × 1°) moved horizontally at 6°/sec. They were placed symmetrically 1.2° above and below the fixation cross. The initial position of the moving lines was 4.8° to the left or right from the fixation cross for the FP-Motion condition and 0° (i.e., at fixation) for the FF-Motion condition. The flashed line (0.1° × 1°) was presented 2.4° to the left or right of the fixation cross. The vertical separation between the lines (i.e., their nearest tips) was 0.2°. The duration of the flash was set to 5 ms in all conditions. The luminance of the moving lines and the flash were set to 0.97 cd/m^2 and 8.48 cd/m^2, respectively; the luminance of the flashed line was measured when it
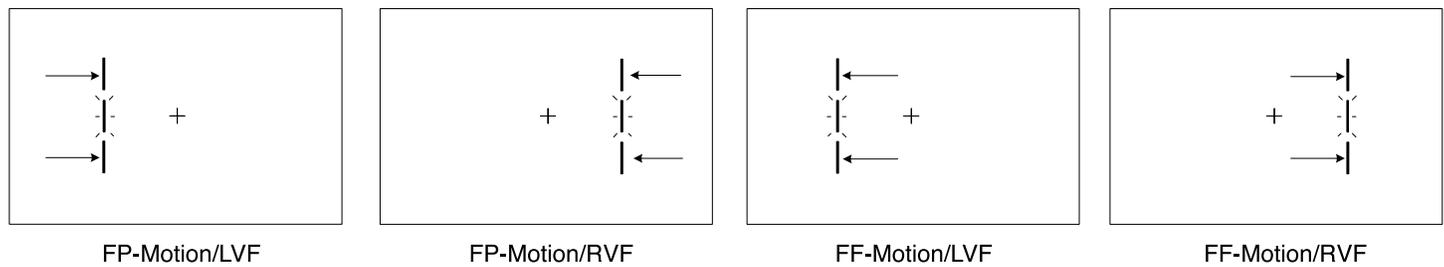
Figure 1. Schematic illustration of the four conditions used. A fixation cross ("plus" sign) was provided for fixation of gaze. In the left two panels, the lines move from periphery toward central fovea (foveopetal conditions, FP-Motion); in the right two panels, the lines move away from central fovea (foveofugal conditions, FF-Motion). In the first and third panels all stimuli were presented in the left visual field (LVF), while in the second and fourth panels stimuli were presented in the right visual field (RVF).

was presented continuously. The average surrounding luminance in the experimental cabin was 0.04 cd/m^2.

Procedure

In order to optimally measure psychometric functions, coarse PSEs for individual observer were quickly estimated by a multiple random staircase method (Cornsweet, 1962). The entire procedure was completed in 30 to 70 trials. After that, a method of constant stimuli was used. The position of the flash was 0, ±10.8′, ±21.6′, and ±32.4′ relative to the previously estimated PSEs. There were 20 trials per condition for a total of 560 (4 × 7 × 20) trials per observer.

Participants sat in front of the oscilloscope at a viewing distance of 57 cm. Head movements were limited by a chin rest. Each trial was initiated with a 250-ms tone and a fixation cross. After a randomly determined interval between 1000 and 1100 ms, the lines appeared and started to move. During the movement of the two lines, a third line was flashed for 5 ms. The onset time of the flash was varied on each trial. The moving lines vanished after moving a distance of 4.8°. Participants were instructed to fixate on the central fixation cross during stimulus presentation. The participants performed a two-alternative forced choice (2AFC) task, in which they pressed one of two buttons to indicate whether the flashed line appeared to the right or to the left of the moving lines.

Results and discussion

Typical psychometric curves from one participant are plotted in Figure 2A. Individual flash-lag effects for four conditions from five participants are shown in Figure 2B.

The figures indicate large asymmetric lag effects for FP- and FF-Motion conditions. The largest lag-effect was in the FP-Motion (RVF) condition (mean: 29.3′). The smallest flash-lag effect (actually a slight lead-effect) was in the FF-Motion (RVF) condition (mean: −2.4′). A paired *t*-test showed that a very strong FP/FF-Motion-based flash-lag

anisotropy for the stimuli presented in the right visual field ($p < 0.01$). For FP/FF-Motion conditions presented in the left visual field (LVF) there was also significant flash-lag anisotropy (means: 24.8′ and 3.9′, respectively, paired *t*-test: $p < 0.05$). The mean flash-lag effects for the FP- and FF-Motion conditions regardless of visual field were 27′ and 0.8′, respectively. Further paired *t*-test indicated significant asymmetry of the flash-lag effect for FF- and FP-Motion conditions ($p < 0.01$). These results replicate the previous such findings (Kanai et al., 2004; Mateeff & Hohnsbein, 1988).

In addition to the anisotropic flash-lag effects depending on FP/FF-Motion conditions, flash-lag magnitude was also found to vary depending in which visual field, left or right, the display was presented (similar asymmetric effect was also demonstrated by Kanai et al., 2004). The flash-lag effect was more sensitive to the direction of motion in the right visual field (flash-lag difference between FP- and FF-Motion conditions: 31.5′; 95% CI: 29.39, 33.71) than in the left visual field (flash-lag difference between FP- and FF-Motion conditions: 20.9′; 95% CI: 18.82, 22.95). The cause of the asymmetric effect in the left and right visual fields is unclear. It has been reported that localization error for a brief light stimulus is larger when the stimulus is presented in the right visual field (Mateeff & Gourevich, 1983).

Experiment 2

Flash-drag and flash-repulsion effects

The results of Experiment 1 showed that the FP/FF-Motion conditions produced flash-lag effects of different magnitudes, with the FP-Motion condition producing a much larger effect. However, from these results it is not clear what the source of the anisotropy is.

A number of researchers have shown that visual motion can bias the visual localization of stationary objects (De Valois & De Valois, 1991; Nishida &
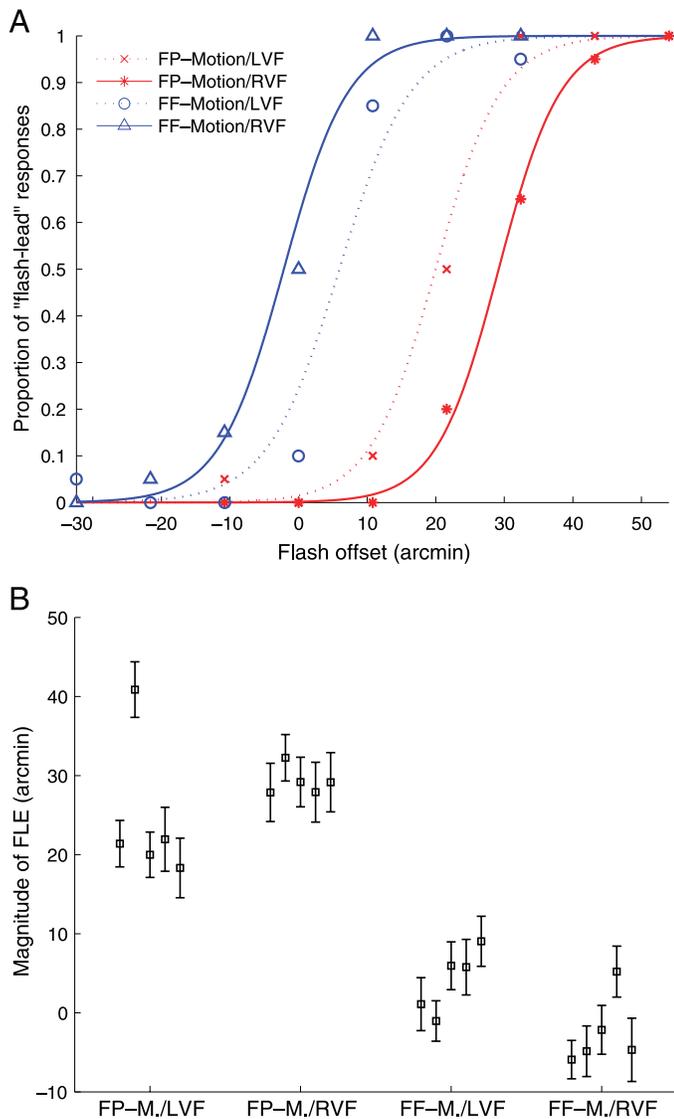
Figure 2. Psychometric functions and PSEs of Experiment 1. (A) Psychometric curves for the four conditions of one participant. The specifications of data points and psychometric curves are shown in legends. The rest four data sets were similar. (B) Individual flash-lag effects for the four conditions (*N* = 5). In each condition, the five data points plotted from left to right represent participants 1 to 5. Error bars indicate 95% confidence intervals.

Johnston, 1999; Ramachandran & Anstis, 1990; Whitney & Cavanagh, 2000), and several researchers (Eagleman & Sejnowski, 2007; Linares, López-Moliner, & Johnston, 2007; Snowden, 1998; Watanabe et al., 2002) have recently suggested that this motion-based position bias can contribute to the flash-lag effect. Although it has been suggested that the flash-drag effect could contribute to the diluting of the flash-lag effect (Eagleman & Sejnowski, 2007; Whitney & Cavanagh, 2000), it is not known if the flash-mislocalization effect contributes to the FP/FF-Motion-based anisotropy in the flash-lag effect observed in Experiment 1. For the flash-mislocalization effect to be a factor, this effect itself should show an anisotropy in relation to FP/FF-Motions, with the FF-Motion producing a stronger flash-mislocalization effect than the FP-Motion. In Experiment 2, we examined how the magnitude of the flash-mislocalization effect varies as a function of FP/FF-Motion conditions.

Methods

Stimuli

We used the same configurations of moving and flashed lines as in Experiment 1. The onset time of the flash was set to the moment when the three lines were physically aligned. In addition, two collinear reference lines (0.1° × 0.5°) were presented vertically positioned 2° above and below the fixation cross. The initial position of the reference lines was 0′, ±12′, ±24′, and ±36′ (left or right) away from the flash. The reference lines stayed on during the presentation of moving stimuli and vanished together with the offset of the moving stimuli. The position of the flash was fixed at 2.4° to the left or right of fixation (Figure 3).

Procedure

A method of constant stimuli was used for the experiment. The same four conditions as in Experiment 1 were tested in the current experiment. Seven different offsets of reference lines (see above) were used for each condition. The trial structure was the same as that in Experiment 1 except for a change in the task of the participant. Here in a
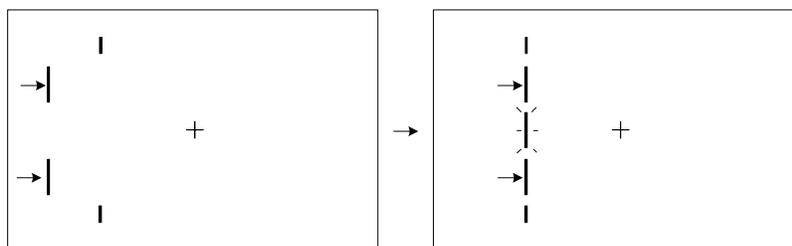

Figure 3. Schematic illustration of stimuli settings in Experiment 2. In addition to the stimulus elements used in Experiment 1, two short reference lines were present above and below the moving lines. The left panel depicts the initial motion of lines for the FP-Motion (LVF) condition. The right panel depicts the moment of the flash.

2AFC task, the participants judged whether the flashed line appeared to the left or right of the reference lines, while "ignoring" the moving lines. There were 15 trials for each condition for a total of 420 (4 × 7 × 15) trials per participant.

Results and discussion

The results, pooled over five participants, are shown in Figure 4. As is clear, the perceived position of the flash in relation to the reference lines was shifted in opposite directions for FP-Motion versus FF-Motion. For the FF-Motion condition the flash appeared shifted in the direction of motion, specifically the shifts for LVF and RVF were 2.3′ (95% CI: 0.43, 4.23) and 7.6′ (95% CI: 5.87, 9.4), which are consistent with the standard flash-mislocalization, or flash-drag, effect (see, e.g., Whitney & Cavanagh, 2000). However, for FP-Motion condition the flash appeared shifted in the direction opposite to object motion, specifically the shifts for LVF and RVF were −6.9′ (95% CI: −8.88, −5) and −3.3′ (95% CI: −5.23, −1.29). Furthermore, the magnitude of this "flash-repulsion" effect was almost the same magnitude as the flash-drag effect for the FF-Motion.

A further analysis was executed on the individual participants' data in order to examine if the opposing flash-mislocalization effects were also present in the individual data. Mean flash-mislocalizations are shown in Figure 4C. Separate t-tests were conducted on the four conditions. The results showed that the "flash-repulsion" effects for the FP-Motion were significant for RVF ($p < 0.05$) and marginally significant for LVF ($p = 0.058$). The standard flash-mislocalization effect for the FF-Motion in RVF was also significant ($p < 0.05$) while it was not significantly different from zero in LVF ($p > 0.1$). Thus, the analyses of individual data further confirmed the anisotropic pattern of the flash-mislocalization effect.

Analogous to the results of Experiment 1, we found an asymmetry for left and right visual fields. The mislocalization of the flash was more sensitive to the motion direction in the right visual field (difference of flash-mislocalization between FP-Motion and FF-Motion: 14.63′; 95% CI: 12.04, 17.22) than in the left visual field (difference of flash-mislocalization between FP-Motion and FF-Motion: 5.60′; 95% CI: 2.80, 8.39).

In summary, this experiment reveals two new results: (1) FP- and FF-Motions produce opposite flash-mislocalization effects, and (2) FP-Motion shifts the perceived location of a flash in a direction opposite to that of object motion (flash-repulsion effect). This result is consistent with a previous anecdotal report (Watanabe, 2005) that when the flash is presented far behind in the incoming motion field (similar to foveopetal motion), there is a tendency of the flash to be mislocalized in the direction opposite to motion. In Experiment 2 there are additional factors, which might have contributed to the
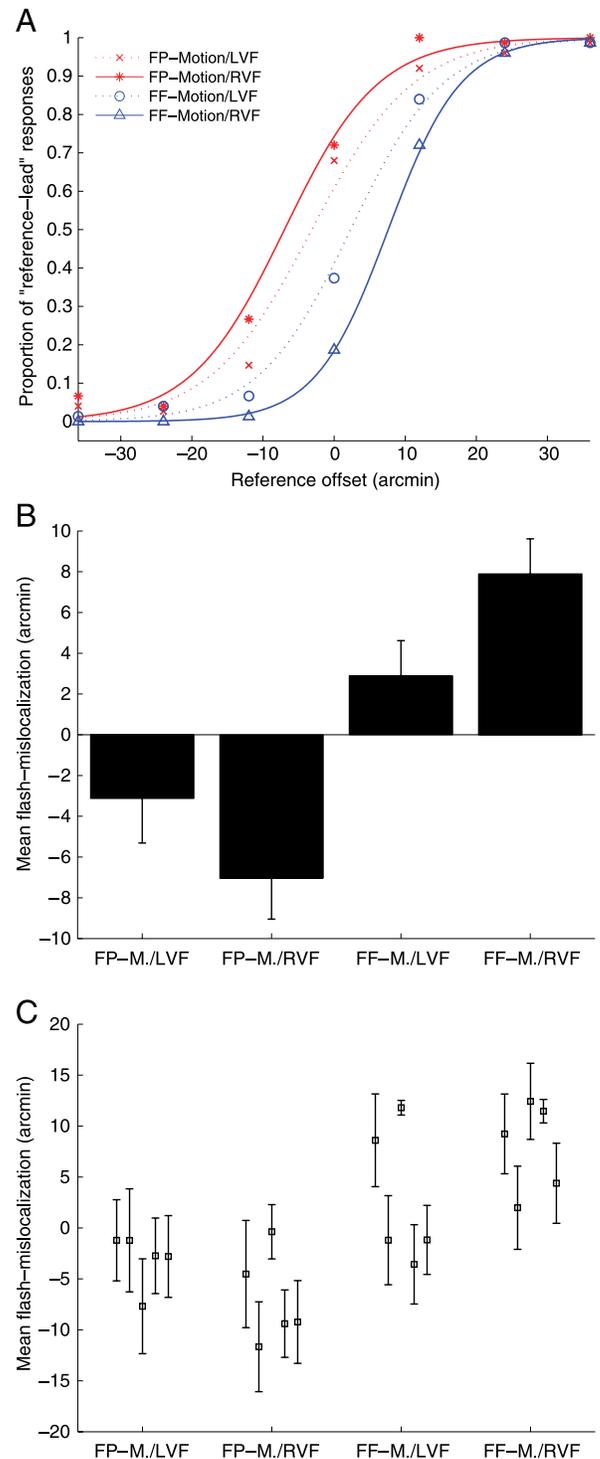

Figure 4. Psychometric functions and mean flash-mislocalization effects of Experiment 2. (A) Psychometric curves as a function of the four conditions. The specifications for the data points and psychometric curves are shown in the legends. (B) Mean flash-mislocalization effects relative to the direction of motion are plotted for all four conditions. Error bars indicate 95% confidence intervals. (C) Individual flash-mislocalization effects for the four conditions ($N = 5$). In each condition, the five data points plotted from left to right represent participants 1 to 5.

flash-mislocalization, that have not been fully controlled. Mislocalization of flashes has been observed when the experimental display contains a flash in the absence of moving stimuli (Eggert, Ditterich, & Straube, 2001; Mateeff & Gourevich, 1983). In these previous studies, the flashes appear shifted in relation to fixation, which could explain the results of Experiment 2. In addition, a few studies have demonstrated that the motion after the flash may matter more than the motion before the flash for the flash-mislocalization effect (Durant & Johnston, 2004; Eagleman & Sejnowski, 2007; Whitney & Cavanagh, 2000), which is not controlled in Experiment 2 in the FF- and FP-Motion conditions. In Experiment 3, we controlled for these factors.

Experiment 3

Flash-mislocalization with no motion and equated motion

In Experiment 3A, we removed the moving lines. If simple mislocalization in relation to fixation is responsible for inducing the anisotropic flash-mislocalization, then we should find similar results as in Experiment 2. If not, then this will provide evidence that the anisotropic flash-mislocalization depends on the direction of motion. Experiment 3B controlled for the trajectory of the motion after the flash for FF- and FP-Motion conditions. Perceptual localization may be influenced by motion signals over 60–80 ms after the flash (Durant & Johnston, 2004; Eagleman & Sejnowski, 2007). To disentangle the effects of the direction of motion from the trajectory of motion, the trajectory of motion over 60 ms after the flash covered the same spatial extent for FP and FF motion in Experiment 3B.

Methods and procedure

Experiment 3A was identical to Experiment 2, except that moving lines were removed. In Experiment 3B, the position of the flash was set at 2.58° to the left or right of fixation for the condition of FP-Motion and at 2.22° for the condition of FF motion. Thus, the trajectories of motion covered the same spatial extent over 60 ms after the flash. The rest of the settings were identical to Experiment 2.

Results and discussion

The mean results of the flash-mislocalization for the individual data from Experiment 3A are shown in Figure 5A. The mean results of flash-mislocalization for RVF and
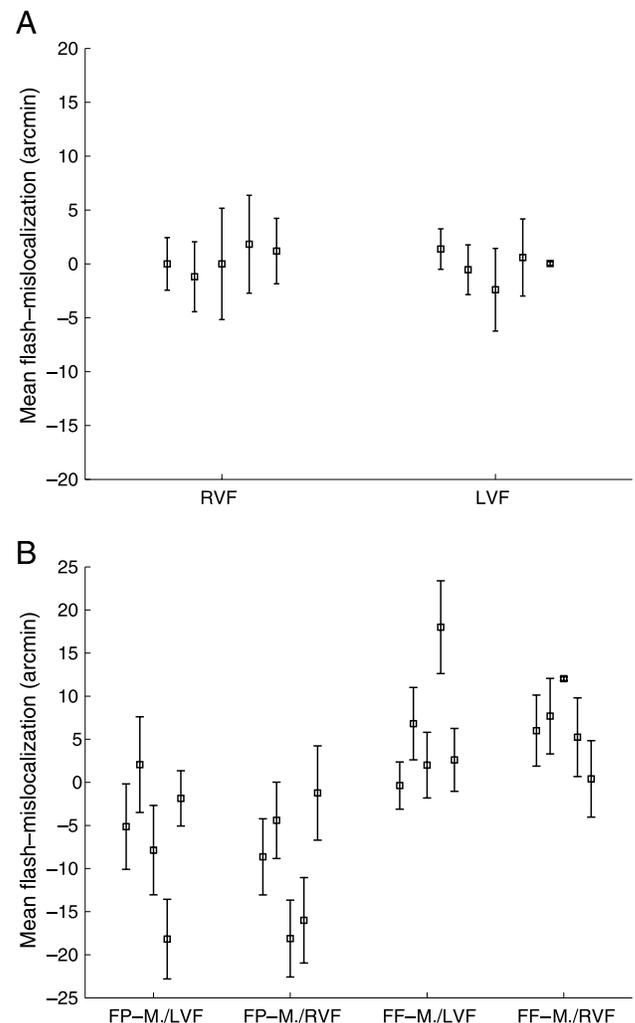

Figure 5. (A) Individual data on shifts in the position of the flash in the absence of motion for the LVF and RVF (N = 5). Error bars indicate 95% confidence intervals. In each condition, the five data points plotted from left to right represent participants 1 to 5. (B) Individual flash-mislocalization effect data for the four conditions (N = 5) with motion after the flash equated. In each condition, the five data points plotted from left to right represent participants 1 to 5.

LVF were 0.37′ and −0.19′, respectively. Thus, there were no significant mislocalization effects (p = 0.52 and 0.78, respectively). Unlike the influence of motion in Experiment 2, the flash alone is not subject to any significant perceptual mislocalization. In some cases, for example where there is large separation between the flash and the fixation and in the absence of landmarks, mislocalization in relation to the fixation has been observed (Eggert et al., 2001; Mateeff & Gourevich, 1983). However, in our case, the flash was relatively near the fixation (2.4°) and there was a nearby landmark (reference lines). This resulted in an insignificant mislocalization of the flash. This result supports our claim that the anisotropic flash-mislocalization effect in Experiment 2 was indeed due to the direction of motion.

The individual mean flash-mislocalization from Experiment 3B are shown in Figure 5B, where the overall pattern is similar to that in Figure 4C from Experiment 2. The mean flash-mislocalizations were $-6.19'$, $-9.68'$, $5.81'$, and $6.27'$ for LVF, RVF of FP-Motion, LVF, and RVF of FF-Motion, respectively. The results showed a strong flash-repulsion effect for the FP-Motion condition ($p < 0.01$) and a strong flash-drag effect for the FF-Motion condition ($p < 0.01$). The experiment replicated the anisotropic flash-mislocalization effect under the conditions in which the motion trajectories covered the same spatial extent over the 60 ms after the flash. This confirmed that the anisotropic flash-mislocalization effect observed in Experiment 2 was not due to the motion after the flash being unequal for the FF- and FP-Motion conditions.

These two control experiments ruled out the possible confound factors in Experiment 2 and demonstrated that the opposite flash-mislocalization effects were mainly due to the direction of motion. Typically, the flash-mislocalization effects we observed in the FF-Motion conditions are referred to as "motion capture" or "flash-drag" effect. However, our results in the FP-Motion condition causing a flash-repulsion effect leave little doubt that a more appropriate term to use may indeed be flash-mislocalization, as the effect can occur in a direction opposite to the direction of motion.

As shown by the results of Experiments 2 and 3B, a strong FP/FF-Motion-based anisotropy exists for the flash-mislocalization effect, and that this must contribute to the anisotropic flash-lag we observed in Experiment 1. However, the observed flash-mislocalization anisotropy is not sufficient to completely account for the flash-lag anisotropy. This suggests that there must be FP/FF-Motion-based anisotropic mislocalization of the moving object per se. In the next experiment we investigate this possibility.

Experiment 4

Anisotropic mislocalization of the moving object in relation to a "fixed flash"

In Experiment 4, we investigated the FP/FF-Motion-based anisotropy of the mislocalization of the moving object per se. We examined the mislocalization of the moving object for the LVF and RVF presentations, as in the previous experiments.

Methods
Stimuli

The moving stimulus was the same as in Experiment 1. In order to measure the mislocalization of the moving object per se (movement-mislocalization), we had to use a time marker to mark the instantaneous position of the moving object, and yet this marker could not be a flash because Experiments 2 and 3B revealed that the flash itself is susceptible to mislocalization. In order to fix the position of the time marker we used a "fixed flash," an object that consisted of both continuous and flashed components. The time marker consisted of a reference line ($0.1° \times 0.5°$) that was presented horizontally away from fixation at various distances ($\pm1.5°$, $\pm1.8°$, $\pm2.1°$, $\pm2.4°$, $\pm2.7°$, $\pm3.0°$ and $\pm3.3°$; minus refers to stimuli in the left visual field). When the moving lines crossed the horizontal position $\pm2.4°$, the reference line increased in length from $0.5°$ to $1°$ for 5 ms (Figure 6). Because the reference line was present all the time, the positional signal of the reference was constantly available. As a result, the brief length increment of the line was always perceived in the same location as the shorter reference line. With this stimulus, we eliminated the flash-mislocalization effect observed in Experiments 2 and 3B.

Procedure

A method of constant stimuli which consisted of four conditions of motion and 7 different offsets of reference lines (see above) was used. The trials were identical to Experiment 1 except for a change in the task and the initial visibility of the reference line segment. In a 2AFC task, the participants were instructed to press one of two keys depending on whether the reference line appeared to the left or to the right of the moving lines at the time it increased in length. There were 15 trials per condition for a total of 420 ($4 \times 7 \times 15$) trials per participant.
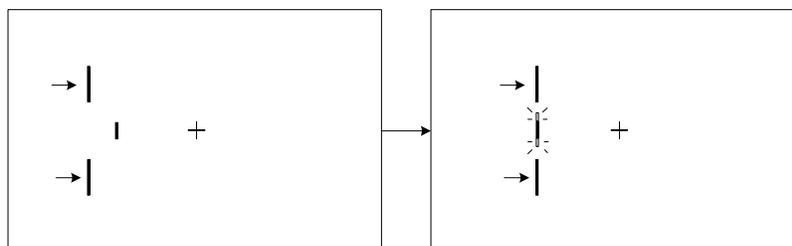

Figure 6. Schematic illustration of stimuli used in Experiment 3. The left panel depicts the initial motion of lines for the FP-Motion (LVF) condition. A short reference line was presented that briefly increased in length (right panel). For illustration purposes, the parts added to the reference line are shown as unfilled. In the display, the line was uniform.

Results and discussion

Figures 7A and 7B show data from this experiment. In Experiment 4, for all four conditions the movement-mislocalization effect was positive, such that the position of the moving object appeared shifted in the direction of motion. Interestingly, as in Experiment 1, there was a FP/FF-Motion-based anisotropy in the movement-mislocalization effect, i.e., the movement-mislocalization was larger for FP-Motion than for FF-Motion (means: 18.37′, 7.41′, respectively, paired *t*-test: *p* < 0.01). The maximum and minimum movement-mislocalization effects were found in the right visual field (23′, 95% CI: 20.24, 25.66 for FP-Motion and 3′, 95% CI: 0.16, 5.8 for FF-Motion, paired *t*-test: *p* < 0.01). In the left visual field, the movement-mislocalization effects were almost the same for the FP- and FF-Motion conditions (14.3′, 95% CI: 11.75, 16.84 and 11.9′, 95% CI: 8.62, 15.18, respectively,

p = 0.72). In contrast to the results of Experiment 1, a large anisotropy in the movement-mislocalization was found only in the right visual field. Compared with the results of Experiment 1, the magnitudes of movement-mislocalization were overall smaller than flash-lag effects. The anisotropy effect (difference between FP-Motion and FF-Motion) was also smaller than it in Experiment 1 (10.96′ and 26.04′ for movement-mislocalization and flash-lag effects, respectively).

General discussion

We examined the cause of the strong anisotropy in the flash-lag effect as a function of motion direction in relation to the fovea. We first obtained a measure of the anisotropy in Experiment 1, replicating previous results (Mateeff & Hohnsbein, 1988). Experiments 2, 3, and 4 investigated the source(s) of this anisotropy. In Experiments 2 and 3, we asked to what extent the flash-lag anisotropy is caused by an anisotropy in the flash-mislocalization effect. In Experiment 4, we asked to what extent the flash-lag anisotropy is caused by an anisotropy in the movement-mislocalization effect. Our results indicate that the FP/FF-Motion-based anisotropy in the flash-lag effect is due to anisotropies observed both in the flash- and the movement-mislocalization effects. For example, the small flash-lead effect we found in the FF-Motion (RVF) condition of Experiment 1 was a combination of a large flash-drag effect (Experiment 2) with a small movement-mislocalization effect (Experiment 4). Similarly, the large flash-lag effect for the FP-Motion (RVF) condition is a combination of large movement-mislocalization (Experiment 4) and flash-repulsion (Experiment 2) effects. The flash-repulsion effect we observed in Experiment 2 was approximately of equivalent magnitude, but opposite sign, to the previously observed flash-drag effect (Whitney & Cavanagh, 2000).

Previous research has shown anisotropies in the flash-lag effect depending on whether the flashed object was presented close to the leading or the trailing edge of the moving object (Watanabe, Nijhawan, Khurana, & Shimojo, 2001). In addition, flash-mislocalization has been found to be anisotropic depending on whether the flash was presented ahead or behind the moving object (Durant & Johnston, 2004; Shi & de'Sperati, 2008; Watanabe, 2005; Watanabe & Yokoi, 2006, 2007). As far as we are aware, the present study is the first report of a strong modulation of the flash-mislocalization effect (so much so that it leads to a flash-repulsion effect) and of movement-mislocalization effect (where flash-mislocalization has been controlled) caused by movement direction relative to the fovea. Most of the previous studies have reported a flash-mislocalization effect in which the flashes are displaced in the direction of the nearest moving object,
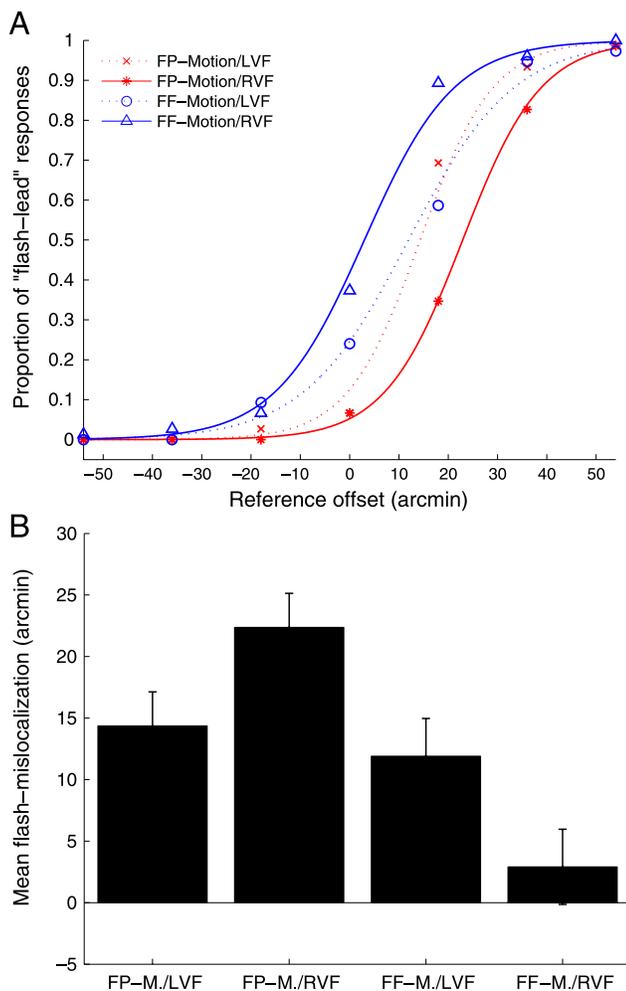
Figure 7. Psychometric functions and PSEs from Experiment 4. (A) Psychometric curves for the four conditions. The specifications of the data points and the psychometric curves are shown in the legends. (B) Magnitudes of flash-mislocalizations are shown for all four conditions. Error bars indicate 95% confidence intervals.

i.e., the flash-drag effect. A previous study reported that the magnitude of flash-mislocalization depended on the size and duration of flashes, but the mislocalization always occurred *in* the direction of motion (Whitney & Cavanagh, 2000). A tendency of flash-mislocalization in the direction opposite to motion direction has been anecdotally observed previously, but only when the flash was presented far behind the moving object (Watanabe, 2005) or beyond the apparent motion end point (Shim & Cavanagh, 2006). In our experiments, the retinal position of the flash was identical in the FP- and FF-Motion conditions, and in both cases the flash was near the moving object, and yet the two motion directions produced opposite flash-mislocalization effects.

Our results clearly show that two factors contribute to the FP/FF-Motion-based anisotropy in the flash-lag effect: anisotropic flash- and movement-mislocalization effects. We calculated the correlation of the flash-lag magnitudes observed in different conditions of Experiment 1 with "difference" scores based on flash- and movement-mislocalization effects (difference score = movement-mislocalization effect − flash-mislocalization effect). The correlation of 0.94 (p = 0.06), plotted in Figure 8, suggests that the flash-mislocalization and the movement-mislocalization effects can together almost completely account for the FP/FF-Motion-based anisotropy in the flash-lag effect observed in Experiment 1. We should mention that since the flash-lag effect measured in Experiment 1 was by the point of subject equality (PSE),
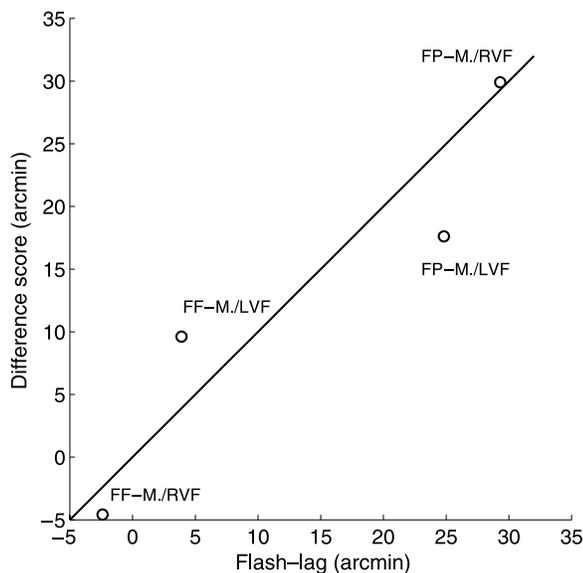
in the cases of the positive flash-lag effect the position of the "aligned" flash was close to the leading edge of the moving object. Similarly, the position of the "aligned" flash was close to the trailing edge of the moving object in the cases of flash-lead effect. It has been demonstrated in previous studies (Durant & Johnston, 2004; Watanabe, 2005) that the flash-drag effect is larger when the flash is presented ahead of the moving object and smaller when the flash is presented behind the moving object. As the flash-drag effects in Experiment 2 were measured when the flash was physically aligned with the moving object the actual reduction in the magnitude of the flash-lag effect in Experiment 1 due to the flash-drag effect was slightly different from that estimated by Experiment 2. As shown in Figure 8, this deviation may indeed be reflected in the FF-Motion conditions producing the flash-drag effect; for these conditions, the difference score is a bit overestimated (above the diagonal line) for the positive flash-flag effect and a bit underestimated (below the diagonal line) for the flash-lead effect.

Our results cannot be accounted for by previous observations that the perceived position of a flash presented in the retinal periphery has a tendency to shift toward the fovea, when the position is judged with respect to a fixation spot (Eggert et al., 2001; Mateeff & Gourevich, 1983). First, we showed that in the presence of nearby reference lines such foveal shift bias is small (Experiment 3A). Even without the reference lines, such a bias is not a strong influence; we ran an additional control experiment that was identical to Experiment 3A except without the reference lines. The mean foveal bias, even with the reference lines removed, was only $-0.25' \pm 1.33'$ in the left visual field and $-2.4' \pm 1.28'$ in the right visual field. This result is consistent with a previous report (Mapp, Barbeito, Bedell, & Ono, 1989) that the tendency of flashes to appear shifted toward the fovea is not a strong factor. Most importantly, however, the small foveal bias we observed in the control experiment was in the direction opposite to the flash-mislocalization observed in Experiment 2. Thus, the movement-based mislocalization effects probably dominated any foveal shift bias, which consequently made little net contribution to our results.

Anisotropies both in the flash- and movement-mislocalization effects contribute to the anisotropic flash-lag effect. What might be the cause of the FP/FF-Motion-based anisotropy in the flash- and the movement-mislocalization effects? An earlier suggestion may partially explain the anisotropy in the movement-mislocalization effect. Mateeff and Hohnsbein (1988) suggested that the FP/FF-Motion-based anisotropy in the flash-lag effect was due to shorter processing latency for objects moving toward the fovea. This suggestion is related to the differential latency explanation of the flash-lag effect (Kirschfeld, 2006; Kirschfeld & Kammer, 1999; Metzger, 1932; Purushothaman et al., 1998; Whitney & Cavanagh, 2000; Whitney & Murakami, 1998). Both logic and findings support the "differential latency" explanation of

Figure 8. Correlation plot of the flash-lag effect in Experiment 1 with difference scores (difference score = movement-mislocalization effect − flash-mislocalization effect). The diagonal line indicates the virtual complete correlation. The points that lie above the line indicate that the difference score is larger, and the points that lie below the line indicate that the difference score is smaller, than flash-lag effect.

the FP/FF-Motion-based anisotropy in the flash-lag effect. When an animal moves forward (which is the more typical direction of movement), the retinal image motion is of an "expanding" pattern consisting of FF-Motion. Thus, it may be argued that animals are more adapted to FF-Motion, and as a consequence more sensitive to FP-Motion (Harris, Morgan, & Still, 1981). Due to higher relative sensitivity, the latency for FP-Motion may be smaller. In addition, there is neurophysiological evidence that the latency for periphery to center motion is shorter than for center to periphery motion (Jancke, Erlhagen, Schöner, & Dinse, 2004).

Differential latency has been used before to explain position lags and shape distortions of moving objects. The well-known Pulfrich pendulum effect, in which the motion of a swinging bob in the frontal plane is perceived as movement along a curved path in depth, is one such example. This effect is thought to be due to the slightly longer delay in the processing of object motion by the eye with a filter (which the observer wears) relative to the eye without the filter. The longer processing delay turns into a spatial lag, which is interpreted by the visual system as translation in depth (Burr & Ross, 1979; Morgan & Thompson, 1975). Other experiments have shown the impact of neural delays on the perceptual distortion of shape of moving objects (Roufs, 1963; Williams & Lit, 1983; Zanker, Quenzer, & Fahle, 2001). Both the Pulfrich and shape deformation effects, however, require a rather modest time difference to account for the psychophysical results. For example, Zanker et al. (2001) found a luminance dependent shape distortion for moving objects corresponding to about 3 ms. Jancke et al. (2004) found that the latency for FP-Motion was, on average, 4 ms shorter than for FF-Motion. The FP/FF-Motion-based anisotropy in the movement-mislocalization we found in Experiment 4 corresponds to 31 ms. Thus, we propose that the movement-mislocalization anisotropy is likely to involve additional factors.

From a biological point of view, production and perception of movement in nature are not only frequent but also play an important role in the survival of the individual and the species (Walls, 1942). Movement has been recognized as a fundamental sensory dimension (Nakayama, 1985). The amount of neural activity invoked by a stimulus depends on the relevance of the stimulus to the animal (Desimone & Duncan, 1995), and responses of neurons in primate area MT and MST to motion are strongly modulated by attention and the behavioral state of the animal (Treue & Maunsell, 1996). We suggest that there is an asymmetry in the behavioral significance of visual movement depending on whether the object is traveling foveopetally or foveofugally. Consequently the two movements stimulate the visual system with different strengths.

In animals that have fovea, such as humans, moving objects of interest are frequently tracked with pursuit eye-movements. However, there are many situations in which the object of interest is not tracked by eye-movements but by attention. Considering situations in which the animal is not engaged in pursuit eye-movements, a scenario where an object's image is "approaching the fovea" is much more reflective of the animal's interest in the object than the scenario where the object's image is "moving away from the fovea." Furthermore, image motion in the direction away from the fovea (e.g., an expanding visual pattern) has more to do with the position of the observer moving forward (see below) than with the position of the stimulus moving laterally across the visual field (Warren & Hannon, 1988). Irrespective of whether an animal's interest in an object is responsible for the object's image approaching the fovea, or the image of an object approaching the fovea causes greater interest (attention) in the animal, we suggest that the FP-Motion stimulus causes heightened neural activity in comparison to the FF-Motion stimulus. The FP-Motion stimulus invokes a greater facilitation (and inhibition) of neurons, and the activation travels further ahead of the leading edge of the moving stimulus (see below), while the FF-Motion stimulus modulates the neural response to a lesser degree.

In order to explain the flash-lag effect, Kirschfeld and Kammer (1999) invoked the mechanisms of attentional enhancement and metacontrast suppression (Kirschfeld, 2006; Kirschfeld & Kammer, 1999). According to this model (Figure 9A), a moving stimulus acts as a cue to the position that it will occupy in the next moment, which leads to a bow wave of attentional facilitation toward the leading edge of the moving object and a "wake of opposite polarity" on the trailing side of the moving object. Kanai and coworkers (2004) proposed a similar model based on neural excitation and inhibition. Both models support spatial extrapolation, though the former suggests the extrapolation on perceptual level and the latter invokes it on a neuronal level (Kirschfeld, 2006). The inhibitory hypothesis has been further confirmed by recent visual contrast study, which demonstrated that the brightness of a flash was suppressed in the vicinity of a moving stimulus (Chappell, 2007). However, the excitation hypothesis has not been observed by using a flash probe. Chappell (2007) speculated that there is a possibility that the excitation might be specific to the moving stimuli, which cannot be observed by the test flash. Here we adapted the excitation and inhibition account to explain the movement-mislocalization data.

We suggest that the "attentional facilitation" toward the leading side of the moving object does not set the stage for processing of new retinal signals generated by the moving object with shorter time delay but rather for "spatial extrapolation" of the delayed retinal signals (Nijhawan, Watanabe, Khurana, & Shimojo, 2004). The facilitation and inhibition act as weighting functions, which assign different weights for the positions. Stronger facilitation and inhibition provide larger asymmetrical weights for the leading and trailing edges of the moving object. As a consequence, the positional distribution is
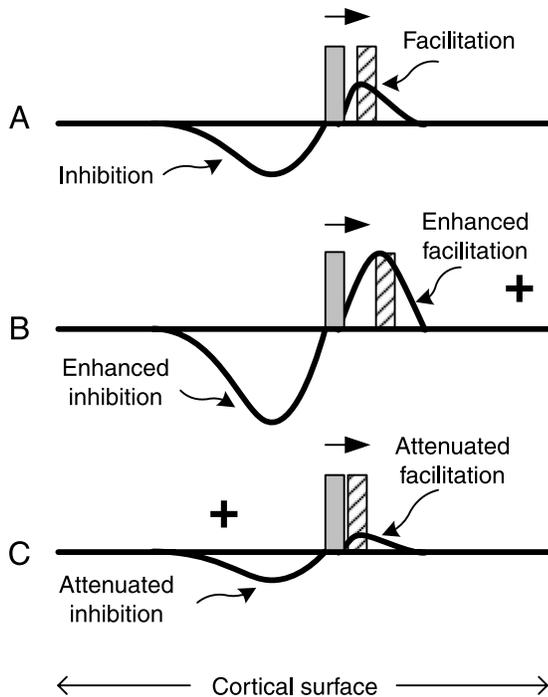
Figure 9. (A) Adapted from Kirschfeld and Kammer (1999). The peak of facilitation and trough of inhibition shows two sets of cortical neurons whose responsiveness to stimulation is affected by the moving object. The neurons ahead in the path of motion are facilitated while neurons trailing behind the moving object representation are inhibited. The crosses in panels B and C depict the fixation point. The gray rectangles represent the actual position of the moving objects, and the rectangles with diagonals represent the extrapolated positions of the moving objects. (B) The FP-Motion stimulus is represented by enhanced facilitation and inhibition. (C) The FF-Motion stimulus is represented by attenuated facilitation and inhibition.

skewed more in the direction of motion, thus effectively shifting the average position of the moving object further forward (Figure 9B). A horizontal segment of the pathway can carry out the spatial extrapolation with a small additional delay (Nijhawan, 2008a) over and above the baseline afferent delay of about 100 ms (De Valois & De Valois, 1991). We suggest that the requirement to localize an object undergoing FP-Motion more accurately for action, particularly in the light of the significant afferent visual delays that should cause the moving object to appear to lag its physical position (Nijhawan, 1994), causes a greater movement-mislocalization effect for FP-Motion stimulus than for FF-Motion stimulus observed in Experiment 4 (Figure 9B and 9C).

In order to explain the flash-mislocalization effects, where motion (direction) has opposite effects on the coding of flash position, we consider two functional requirements for reliable motion processing: disambiguation of motion signals and detection of small velocity differences. These two functions have been referred to as

assimilation and contrast and seem to be served by opposite neural processes. Assimilation reduces the variation of velocity signals emanating from different parts of the visual field by averaging, which solves problems such as the "aperture problem" (Adelson & Movshon, 1982), while contrast enhances small velocity differences leading to image segmentation and phenomena such as destruction of camouflage (Braddick, 1993). Different classes of cells in area MT contribute to two these separate functions (Born & Tootell, 1992). Depending on the stimulus conditions the assimilation or the contrast processes are maximally engaged (Nawrot & Sekuler, 1990). We suggest (see below) that motion assimilation is likely to be more active during FF-Motion and the motion contrast process more active during FP-Motion.

Whitney and Cavanagh (2000) first reported the flash-drag effect. Consistent with their proposal, we suggest that the flash-drag effect occurs because of motion assimilation; the coding of flash position is influenced by motion signals arising in areas of the visual field at some distance from the flashes. The "spreading of perceived motion" (Braddick, 1993) impacts flashed objects as flashes are ambiguous in the moving/nonmoving stimulus space (Nijhawan, 2008b). Other perceptual phenomenon such as "motion capture" (Mackay, 1961; Ramachandran, 1987) and motion-based position bias effects (De Valois & De Valois, 1991; Ramachandran & Anstis, 1990) may also be explained in terms of motion assimilation processes. The flashes appear displaced in the direction of motion because motion is known to have an impact on the position of nonmoving objects (Nishida & Johnston, 1999), and because motion assimilation processes are more active during FF-Motion (see below).

Experiments 2 and 3B yielded previously unreported observations in which the flash appeared displaced in a direction opposite to motion direction of a nearby object (flash-repulsion effect). In light of the flash-drag effect, one may conjecture that a common localization mechanism codes for the position of moving and stationary objects. As far as we are aware, there are no clear cases where moving objects are perceived as shifted in the direction opposite to motion direction, so the observation of a flash-repulsion effect argues against a common location coding mechanism for moving and flashed stimuli. The flash-repulsion effect immediately suggests a contrast process. When two small dots are presented next to each other, and one of the dots is moving while the other is stationary, then instead of the stationary dot appearing to shift in the direction of motion it is frequently seen as moving in the direction opposite to the actually moving dot. This is a version of the well know phenomenon of induced motion (Duncker, 1929). Because motion contrast processes are more active during FP-Motion, the flashes appear displaced in the direction opposite to motion direction.

Why might motion assimilation processes be more active during FF-Motion and motion contrast processes

be more active during FP-Motion? Previous research has shown that when movement direction is orthogonal to the fovea-periphery axis, such as a rotating motion pattern, the flash location is typically shifted in the direction of motion (Whitney & Cavanagh, 2000). Our research suggests that FF-Motion has a similar influence on the position of flashes as does orthogonal motion. If we consider the observer in the natural environment (away from TV screens), then a rotating (orthogonal motion) or expanding (FF-Motion) pattern of retinal stimulation is typically generated by rotation of the head or by forward movement of the observer, respectively. Furthermore, when rotating and expanding image motions are present, then excluding the axis of rotation or focus of expansion these motions are present everywhere in the image. So, under this condition, the assimilation process is more operational and is applied to the flashes as well. In comparison, FP-Motion stimulus is more likely to result from an object moving in the environment, so in this case the process that enhances the detection of objects and segmentation, that is the motion contrast process, is more operational.

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