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Stopping the motion and sleuthing the flash-lag effect: spatial uncertainty is the key to perceptual mislocalization ☆

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Abstract

A moving object is perceived to lie beyond a static object presented at the same time at the same retinal location (flash-lag effect or FLE). Some studies report that if the moving stimulus stops moving (flash-terminated condition or FTC) the instant the flash occurs, a FLE does not occur. Other studies, using different stimuli, report that the FLE does, in fact, occur in the FTC. The FTC is thus a crucial turning point in theories of flash-lag. Unraveling the mystery of the FLE in the FTC will help unravel the mechanisms underpinning flash-lag and perhaps even perceptual localization in general. Our experiments show that eccentricity of the moving stimulus was a contributing factor, as were eccentricity of the flashed stimulus and spatial separation between the two stimuli. Other factors, such as contrast and offset of moving stimulus, also modulate the magnitude of the FLE in the FTC. We surmise that uncertainty in determining the position in space of a moving stimulus is a key requirement for the lag-effect. A lag-effect in the FTC challenges influential models, such as differential latency, motion extrapolation, and postdiction. Based partly on the notion of an asymmetric spread of activity that arises because of the sheer nature of motion and from a combination of established physiological mechanisms, we propose a schematic account of the present findings that subsumes previous psychological models and scaffolds past experimental findings.

Keywords: Flash-lag effect; Motion; Uncertainty; Signal strength

1. Introduction

An object that is flashed at the instant a moving object arrives at the same retinal location is perceived to spatially lag the moving object (flash-lag effect, FLE or lag-effect; MacKay, 1958; Metzger, 1932 in Mateeff & Hohnsbein, 1988; Nijhawan, 1994). A FLE is observed even if the moving object begins moving the instant that the flash occurs (flash-initiated condition or FIC). What is more, the magnitude of the lag-effect is unabated compared with the classical continuous motion condition (CMC) in which the motion both precedes and follows in time the flash (Khurana & Nijhawan, 1995). The converse of the FIC is the flash-terminated condition, or FTC. There is a widespread belief that if the moving object stops moving the instant the flash occurs, no FLE is observed, namely the perceived terminal position of the moving object does not overshoot the perceived position of the static object (Eagleman & Sejnowski, 2000; Nijhawan, 1992). There are several interesting variants of this—sudden changes in speed or direction of the moving object synchronous with the flash (Brenner & Smeets, 2000; Eagleman & Sejnowski, 2000; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000). Nearly all influential models of the lag-effect, including differential latency (Murakami, 2001a, 2001b; Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney & Murakami, 1998; Whitney et al., 2000), temporal integration (Krekelberg & Lappe, 2000a, 2000b, 2001), postdiction (Eagleman & Sejnowski, 2000) and attention (Baldo & Klein, 1995) predict no lag-effect in the FTC (but see Nijhawan, 1994 for an exception. For reviews on this topic, see Krekelberg & Lappe, 2001; Nijhawan, 2002).

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Contrary to these models however, there is empirical evidence for the perceptual overshoot of the final position of a moving stimulus. Fu, Shen, and Dan (2001) demonstrated a clear perceptual overshoot of the final position of a moving stimulus defined by blurred edges. In their study, blurred edges were critical—the effect decreased with increasing edge sharpness. Whitaker, Pearson, McGraw, and Banford (1998) also found a FLE in the FTC. Electrophysiological studies have found a neural substrate for the overshoot in retinal ganglion cells of the tiger salamander and rabbit; it is believed that the overshoot is based on slow retinal processes such as light or contrast adaptation (Berry, Brivanlou, Jordan, & Meister, 1999). On a related note, psychophysical studies of representational momentum have found that human observers' reports of the final position of an implied moving stimulus are biased beyond its actual final displayed position; the magnitude of the bias varies in proportion with implied speed and acceleration (Freyd & Finke, 1984). In studies of motion capture, a somewhat different psychophysical phenomenon, the perceived position of a physically stationary object surrounded by a moving surround is shifted beyond its actual position along the motion direction (e.g. De Valois & De Valois, 1991; Ramachandran & Anstis, 1990; Sheth & Shimojo, 2003). In the aforementioned studies, stimuli and experimental conditions differed but the findings were remarkably similar: the perceived position of an object overshot its physical position.

The seemingly contradictory evidence—some studies show a lag-effect in the FTC, others do not—must be reconciled. Any model that purports to explain the lag-effect must account for the absence of a lag-effect under certain conditions and the presence of one under others. Determining the conditions under which a lag-effect can and cannot be observed will better constrain future accounts of the lag-effect. Here, we investigate the FTC and explore what experimental parameters govern the presence or lack of a lag-effect. We then use our findings and those of past studies to constrain models of the lag-effect and, in general, models of perceptual localization.

Our results show that what is common among the conditions where the FLE is observed in the FTC is enhanced uncertainty of the position of the moving stimulus. Thereupon, we propose a physiologically plausible account, referred to as the asymmetric spread account that has a functional relationship with several of the earlier proposed models. Unlike others' accounts, ours accounts for a lag-effect across a wide spectrum of experimental conditions, and for a lag-effect in the FTC under certain experimental conditions and not others (Sheth, Nijhawan, & Shimojo, 2000). We believe that our simple, straightforward account with its biologically based core can qualitatively explain a wide array of perceptual mislocalization effects in the psychophysical literature.

2. General methods

2.1. Observers and apparatus

In all experiments, observers had normal or corrected-to-normal visual acuity. One of the observers was an author (RK). Remaining observers were naïve. Stimuli were presented on a 22-in. monitor (LaCie Electron; 37.5 cm × 30 cm viewing area) under control of a MAC G4 running MATLAB (Mathworks Inc.) and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Observers sat comfortably in a chair in front of the computer screen at a viewing distance of 57 cm, with their heads partially immobilized in a chinrest (Handaya Co., Japan). Viewing was binocular.

2.2. Analysis

On the data pooled over all the participants in a given experiment, a psychometric curve,

$$F(x) = 0.5 + \frac{(a + bx)}{2\sqrt{1 + (a + bx)^2}}$$

was fitted by minimizing the square error. Free parameters a and b were estimated by a least-squares criterion and point of subjective equality (PSE) was obtained as $(-a/b)$. Confidence intervals were obtained by a basic bootstrap method (Efron & Tibshirani, 1993) instead of classic probit analysis, because studies on the statistical methods for estimating psychophysical thresholds have shown superiority of the bootstrap method over probit analysis (Foster & Bischof, 1991; McKee, Klein, & Teller, 1985; for a thorough comparison between probit analysis and bootstrap method, see Hill, 2001).

We briefly describe the bootstrap method employed in our analysis. We generated a synthetic data set by sampling from the binomial distribution $B(n, p)$, where n is the total number of trials for each condition pooled across all observers, and p is the probability that the moving bar was perceived beyond the reference bar in the direction of preceding motion, i.e. in the direction predicted by the FLE. The PSE for each set of synthetic data was obtained by fitting a psychometric curve. The confidence interval of the PSE obtained from the experimental data was estimated from the distribution of the PSEs for the synthetic data. Based on the distribution, 95% confidence intervals for the PSEs were obtained on a percentile basis for upper and lower limits separately.

3. Experiment 1: The effects of peripheral presentation and large spatial separation

In the first experiment, we used stimuli whose edges were sharply defined, not blurred. Spatial separation between the moving and flashed stimuli was kept rather large, and both stimuli were presented in the periphery. We asked whether the terminal position of a sharply defined, peripherally presented moving stimulus is perceived beyond its true physical location.

3.1. Methods

The stimulus is illustrated in Fig. 1A. A bar drifted horizontally toward the fixation point (FP) and a second bar was flashed in synchrony with the last frame of the motion. Both flashed and moving bars disappeared once the moving bar reached its final position. The horizontal offset between the moving and flashed bars was varied from trial to trial using the method of constant stimuli. The observer had to judge the location of the moving bar with respect to the flashed bar after both bars were extinguished.

Four observers participated. Monitor resolution was 832×624 pixels and the refresh rate was 75 Hz. Moving and flashed bars were the same size (2.65°×0.265°). The speed of the moving bar was 16°/s. The moving bar remained present for 520 ms. The vertical distance between the nearest edges of the bars (bottom edge of the top bar and the top edge of the bottom bar) was 8.5°. The last frame of the moving bar was presented at a constant 3.92° horizontal distance from the FP, whereas the horizontal position of the flash relative to the last frame of the motion was varied between 0′, ±9.54′, ±19.08′ and ±28.62′. The flash was synchronous with the last frame of the moving bar on all trials. Flash duration was 1 frame (13 ms). On half of all trials, the moving bar appeared in the upper visual field (UVF) and the flashed bar in the lower visual field (LVF). On the other half, the arrangement was reversed. Trials of both conditions were randomly intermixed and pooled together for analysis. In a two-alternative forced choice (2AFC) task, observers had to judge whether the top or bottom bar was further right at the moment of the flash. There were 30 trials per condition, for a total of 210 (30×7) trials per observer. A second, similar experiment was conducted, with far less vertical separation (3.18′) between the bars. All other parameters including, for instance, horizontal eccentricity, were kept the same. The order of the two experiments was counterbalanced across observers.

3.2. Results and discussion

The results, pooled over four observers, show that, when the vertical edge-to-edge separation was large (Fig. 1A), the perceived terminal position of the moving bar was beyond the physical terminal position and

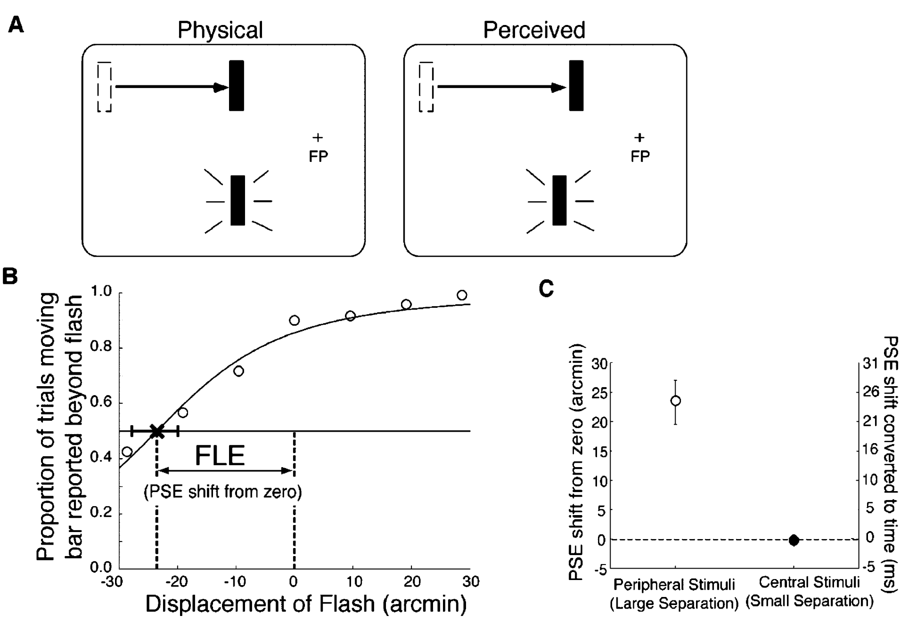

Fig. 1. Flash-lag effect in the flash-termination condition or FTC (motion ends). (A) The left panel illustrates the physical stimulus. The horizontal distance between the fixation point (FP) and the closest edge of the moving bar was 8.5°. The right panel illustrates the typical percept. (B) Results of the spatial judgement task. Each data point consists of 120 samples ($n = 4$). (C) FLE magnitude (PSE shift from 0) for the two sets of conditions (peripheral stimuli with large spatial separation between them versus central stimuli and small spatial separation between them). Error bars indicate 95% confidence intervals.

beyond the perceived position of the flash, in the direction of the bar's motion. That is to say, there was a significant lag-effect. The magnitude of the lag-effect was 24′, which corresponds to the distance that the moving bar traveled in 25 ms. The lag magnitude in the FTC was smaller compared with typical lag magnitudes in the classical CMC (45 ms in Whitney & Murakami, 1998). Of relevance, however, is that there was a lag-effect in the FTC at all. In our experiment, unlike Fu et al.'s (2001), putative key parameters were peripheral location and large vertical edge-to-edge separation of the flashed and moving bars. (Whether peripheral location, edge-to-edge vertical separation, or both, contributed is explored in Experiment 2.) When the two bars were near-foveal and close to one another, there was no lag-effect (Fig. 1C, filled circle), but when the bars were peripherally located and farther apart, there was a significant lag-effect (Fig. 1C, empty circle). In previous studies that failed to find a FLE in the FTC (e.g. Baldo & Klein, 1995; Eagleman & Sejnowski, 2000; Krekelberg & Lappe, 1999; Nijhawan, 1994; Purushothaman et al., 1998), moving and flashed stimuli were close to one another, the moving stimulus was near fixation, or both—all possible reasons why a noticeable FLE in the FTC was not obtained earlier.

Our success in observing a FLE in the FTC in light of past failures prompted us to question whether the lag-effect we observed was a genuine perceptual misalignment, and not merely a product of cognitive factors. It is possible that when forced to choose between two misalignments, observers report the moving bar to be spatially ahead, although both bars may actually be aligned in their perception. In other words, FLE in the FTC is the result of response bias. To control for this possibility, we conducted a 3AFC task in which observers were allowed to report that the termination of motion and the flash appeared spatially aligned. Observers ($n = 10$) perceived motion beyond the flash far more frequently ($64.7 \pm 9.8\%$ s.e.m) than the flash beyond the motion ($13.0 \pm 3.60\%$ s.e.m; $t(9) = 4.42$, $p < 0.001$). The results of the 3AFC task, therefore, support the conclusion that observers truly misperceive motion beyond where the motion physically stops.

4. Experiment 2: What factors are critical for the FLE in the FTC?

The lag-effect was observed under one set of experimental conditions in Experiment 1 and not in another.

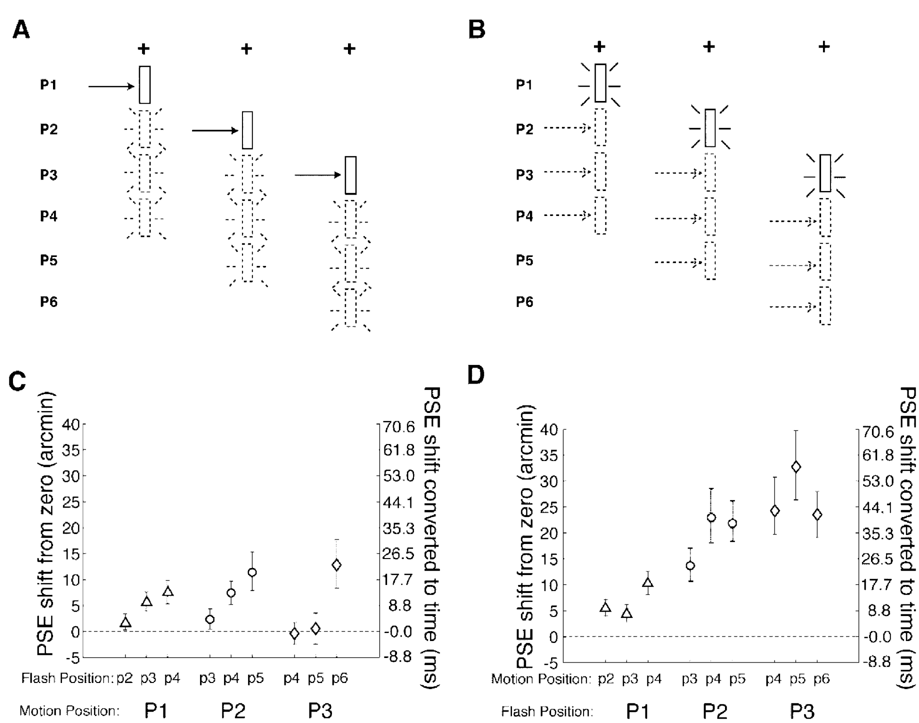

Fig. 2. Relative contribution of peripheral presentation and spatial separation. (A,B) Schematic illustration of the stimulus conditions. (A) The eccentricity of the moving bar (solid rectangles) was varied between P1, P2 and P3, and the flashed bar (dotted rectangles) was presented more peripherally at three different spatial separations for each value of moving bar eccentricity. (B) The eccentricity of the flashed bar (solid rectangles) was varied between P1, P2 and P3, and the moving bar (dotted rectangles) was presented more peripherally than the flashed bar at three different spatial separations for each value of flashed bar eccentricity. (C) FLE magnitudes (PSE shift from 0) of the conditions illustrated in (A). Error bars indicate 95% confidence intervals. (D) FLE magnitude (PSE shift from 0) of the conditions illustrated in (B). Error bars indicate 95% confidence intervals. All conditions (shown in (A) and (B)) were randomly intermixed in the same session.

A variety of factors differed between the experiments, some or all of which could be responsible for the difference in result. Putative factors include moving bar eccentricity, flashed bar eccentricity, and spatial separation of the flashed and moving bars.

In order to discern which of these factors was critical, we varied stimulus eccentricity and the amount of spatial separation, as illustrated in Fig. 2A and B. On half of all experimental trials, the moving bar was more centrally located (Fig. 2A). The flashed bar was presented at three different vertical separations relative to the moving bar. On the other half, the flashed bar was more centrally located, and the moving bar was presented at three different vertical separations from it (Fig. 2B). All trials were randomly intermixed.

4.1. Methods

Two naive observers and one of the authors (RK) participated. The monitor resolution was 1280×1024 pixels and the refresh rate was 85 Hz. Each bar was 1.95°×0.27° in size. The speed of the moving bar was 9.44°/s. The moving bar moved for 424 ms and disappeared after reaching the last frame of its motion. The horizontal eccentricity of the last frame of the moving bar was 0 and presented just below the fixation point. The horizontal position of the flashed bar relative to the last frame of the moving bar was varied (nine values: 0′, ±6.67′, ±13.33′, ±26.67′, ±53.33′) across trials. Onsets of the last frame of the motion and the flash were always synchronous. The moving bar was presented at one of three eccentricities (P1, P2 and P3) below the FP in Fig. 2A. The vertical distance between the FP and the upper edge of a bar positioned at P1 was 0.97°, and from P1, other positions (denoted as P2, P3, and so on) were vertically separated in units of 2.95°, i.e. vertical length of the bar (1.95°) + spatial separation (1.0°). The flashed bar was presented at three different vertical separations relative to the moving bar (1.00°, 3.95°, or 6.90°). The eccentricities of the moving and flashed bars were reversed for the three conditions depicted in Fig. 2B. Thus, there were a total of 18 conditions (Figs. 2A and B). Thirty trials were performed for each of the conditions tested. Thus, there was a total of 4860 (30×9×18) randomly intermixed trials/observer. The entire display appeared either above or below fixation on an equal number of trials (15). On a given trial, the flashed and moving bars were on the same side of fixation, as shown in Fig. 2.

We computed the relative contributions of the three factors (eccentricity of the moving bar, eccentricity of the flashed bar, and spatial separation between the two bars), using multiple linear regression combined with a basic bootstrap method. Data samples were created based on the real response data. The simulated data were then fitted with the following equation

$$w = C_m X + C_f Y + C_{sep} Z,$$

where X, Y and Z denote the eccentricity of the moving bar, the eccentricity of the flashed bar and spatial separation between the two bars, respectively, and C_m, C_f and C_{sep} the respective regression coefficients. We used the numbers that were used to describe the positions of the bar to represent eccentricity (e.g. 1, 2, 3 for P1, P2, P3, respectively) and spatial separation in the equation. The regression coefficients (Fig. 3) were obtained as a solution of the least-squares normal equations (Montgomery, 2001). On the basis of the distribution of the coefficients obtained from 2000 simulated samples, 95% confidence intervals and p-values were estimated (Efron & Tibshirani, 1993).

We conducted an auxiliary experiment described in Fig. 4 to address whether a flash located between a moving stimulus and fixation affects lag-effect magnitude. Two new naïve observers and author RK participated. Stimulus parameters were identical to those in the main experiment, except that, on half of the trials, one of the two stimuli was in the UVF, and the other in the LVF (Fig. 4B). The moving bar was always located at a vertical eccentricity of 3.92°, either in the UVF or LVF. The flash was presented at a vertical eccentricity of 0.97°, again either in the LVF or UVF. There were thus a total of four conditions, two each illustrated in Figs. 4A and B. Trials of the four conditions were randomly intermixed. The horizontal displacement of the flashed bar relative to the final position of the moving bar was one of the same nine values as in the main experiment (0′, ±6.67′, ±13.33′, ±26.67′, ±53.33′). Twenty trials were run per flash location, yielding a total of 720 (20×9 relative flash positions×4 conditions) trials/observer.

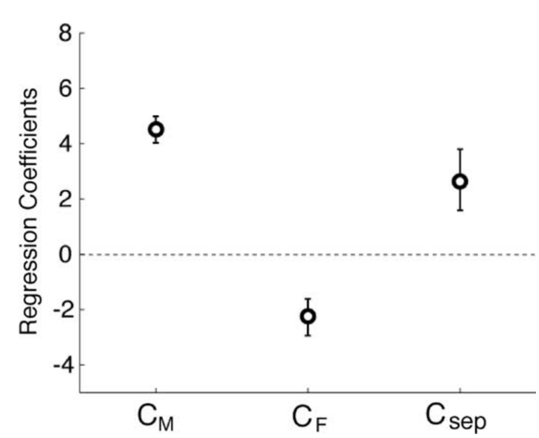

Fig. 3. Results of multiple linear regression analysis. Regression coefficients for the eccentricity of the moving bar (C_m), the eccentricity of the flashed bar (C_f) and the spatial separation between the two (C_{sep}) are plotted.

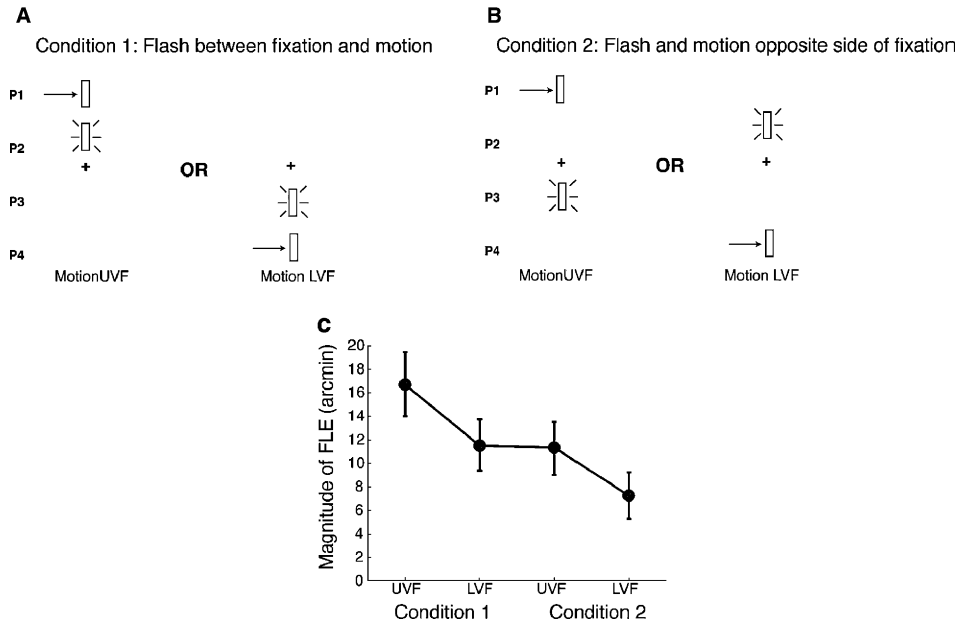

Fig. 4. Dependence of FLE on the position of flash with respect to fixation and moving stimuli. (A) The stimulus configuration in which the flash was presented between fixation and the moving stimulus (condition 1) is illustrated. Both moving and flashed stimuli appeared on the same side of fixation either in the upper visual field (UVF, left) or the lower visual field (LVF, right). (B) The stimulus configuration in which the flash was presented on the opposite side of the moving stimulus with respect to fixation (condition 2) is illustrated. When the moving stimulus appeared in the UVF, the flash appeared in the LVF (left) and vice versa (right). (C) FLE magnitude (PSE shift from 0) is shown for all four sub-conditions. Error bars indicate 95% confidence intervals.

4.2. Results and discussion

Fig. 2C and D depict data from the main experiment. Qualitatively speaking, several factors appear to contribute to the FLE in the FTC. (1) Eccentricity of the moving bar, (2) eccentricity of the flashed bar and (3) spatial separation between the moving and the flashed bars. We did a rigorous and quantitative analysis on the data shown in Figs. 2C and D using multiple linear regression.

Fig. 3 shows the simulated best-fit coefficients for moving bar eccentricity (C_m), flashed bar eccentricity (C_f) and spatial separation (C_{sep}). The estimated C_m was positive (4.48; 95% confidence interval $[4.03, 4.99]$; $P < 0.01$). This means that, as the moving bar's position became more peripheral, FLE magnitude increased. Our analysis revealed C_f to be negative (−2.25; 95% confidence interval $[-2.94, -1.61]$; $P < 0.01$), suggesting that as the flashed bar's position became more peripheral, FLE magnitude decreased. C_{sep} was positive (2.62; 95% confidence interval $[1.60, 3.80]$; $P < 0.01$). Therefore, as the distance between the moving and flashed bars increased, FLE magnitude increased. In sum, all three factors proved to be significant in modulating the FLE in the FTC ($P < 0.01$ for each). These factors can be understood as modulating uncertainty in the moving bar's position (with respect to the flashed bar's). For instance, if a moving bar is presented peripherally, its position is ambiguous, as peripheral objects are represented more coarsely in the visual system. If the spatial separation between the flashed and moving bars is increased, uncertainty in the moving bar's position with respect to that of the flashed bar's is enhanced (see Baldo & Klein, 1995 for an alternate attention-based interpretation).

A somewhat counterintuitive result was that the lag-effect increased as flash eccentricity decreased (see Baldo & Klein, 1995 for a different result in the CMC). The flashed and moving bars were both either above (UVF) or below (LVF) fixation on a given trial of the main experiment. Therefore, as flash position becomes more foveal, moving bar position becomes less so, which, in turn, increases the lag-effect (Figs. 2 and 3). Analogous to crowding (Toet & Levi, 1992), it is likely that the presentation of a near-foveal object has a disruptive effect on the localization of another object located farther out in the periphery. The auxiliary experiment tested the crowding analogy by comparing effects when the flashed and moving bars were placed on the (1) same (Fig. 4A), or (2) opposite (Fig. 4B) sides of fixation. Flash eccentricity was the same on each trial, as was moving bar eccentricity (Fig. 4A and B). Consistent with our crowding analogy, and though the spatial separation between the flashed and moving stimuli was larger in (2) than in (1), the effect was larger in (1) (13.91′, 95% confidence interval $[12.24, 15.64]$) than in (2) (9.39′, 95% confidence interval $[7.99, 10.77]$, Fig. 4C).

Curiously, the lag-effect was larger when the moving stimulus was in the UVF (13.89′, 95% confidence interval [12.17, 15.68]) than in the LVF (9.21′, 95% confidence interval [7.72, 10.74]). Visual processing has long been shown to be less reliable in the UVF (Van Essen, Newsome, & Maunsell, 1984). The larger lag-effect when the moving stimulus was in the UVF is consistent with the idea that uncertainty about the position of the moving stimulus is a key necessary component of the FLE. The lag-effect was no larger when the flash was in the UVF (11.73′, 95% confidence interval [10.13, 14.18]) than in the LVF (11.44′, 95% [9.94, 13.06]) which bolsters our point that it is the positional uncertainty of the moving, and not the flashed, stimulus that is key.

5. Experiment 3: Foveofugal versus foveopetal motion

In experiments so far, motion was directed toward the fovea. In general, flashed stimuli tend to be mislocalized toward the fovea (e.g. Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999; Sheth & Shimojo, 2001), a phenomenon known as foveal attraction or compression. Moving stimuli also tend to be mislocalized toward the fovea (Mateeff et al., 1991). If, for some reason, mislocalization toward the fovea is larger for moving than for flashed stimuli, this alone can explain the lag-effect in the FTC.

We examined the role of motion direction by measuring the lag-effects for the foveofugal (away from the fovea) versus the foveopetal (toward the fovea) motion directions. The terminal position of the moving bar was the same on both conditions. If the lag-effect was due to differential foveal attraction of the moving bar over the flash, there should not be a flash-lag effect in the foveofugal motion condition, but rather, a flash-*lead* effect.

5.1. Methods

Eight observers, including one of the authors (RK), participated. Three observers had not participated in any of our other experiments. The monitor resolution was 1280 × 1024 pixels and the refresh rate was 85 Hz. We tested four conditions: two directions of motion (foveopetal and foveofugal) in combination with two directions of motion (left or right; Fig. 5A and B). Each bar was 1.95° × 0.27° in size. The speed of the moving bar was 13.28°/s. It lasted for 424 ms, and disappeared after reaching the last frame of its motion. The last frame of the motion and the flash were synchronous. The vertical separation between the closest edges of the bars was 6.25°. The horizontal eccentricity of the last frame of the moving bar was a constant 5.86°. The position of the flashed bar was varied between 0′, ±9.38′, ±18.75′, ±28.13′, ±37.5′ relative to the last frame of the moving bar. For observers whose PSEs exceeded 30′, the experiment was repeated with a larger range of flashed bar positions (0′, ±18.75′, ±28.13′, ±37.5′, ±46.88′).

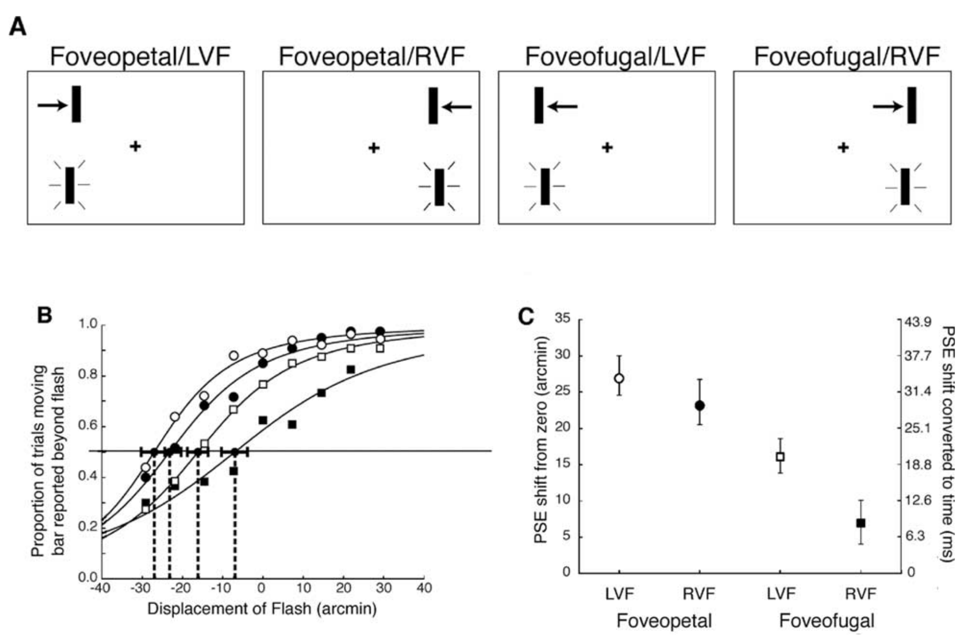

Fig. 5. Dependence of FLE on direction of movement with respect to fixation. (A) Four conditions are schematically illustrated. In the left two panels, the bar moves toward fixation (foveopetal conditions); in the right two panels, the bar move away from fixation (foveofugal conditions). In all four conditions, the last frame of the motion was presented at the same eccentricity. (B) Psychometric curves for the four conditions are shown ($n = 8$). The data points for foveopetal/LVF, foveopetal/RVF, foveofugal/LVF and foveofugal/RVF conditions are shown by open circles, filled circles, open squares, and filled squares, respectively. (C) FLE magnitude (PSE shift from 0) is shown for all four conditions. Error bars indicate 95% confidence intervals.

There were 15 trials for each condition for a total of 540 (15×9×4) trials per observer.

5.2. Results and discussion

The results, pooled over eight observers, are shown in Fig. 5B and C. On all four conditions, including, in particular, the two foveofugal ones, there was a significant overshoot of the perceived position of the moving bar beyond the (concurrent) flash in the direction of motion. The effect was smaller in the foveofugal condition than in the foveopetal condition, indicating that the mislocalization is determined, in small measure, by foveal attraction. Nonetheless, that a significant lag-effect was observed in the foveofugal motion condition indicates that differential foveal attraction is not the key factor determining the FLE in our experiments.

The lag-effect was larger in the left visual field (LVF) than in the right visual field (RVF). Rank-order correlation (Spearman) statistics showed a significant effect ($R_s = -0.6905$. $P < 0.001$), implying that the effect decreased monotonically in the order given in Fig. 5 (i.e. foveopetal/LVF > foveopetal/RVF > foveofugal/LVF > foveofugal/RVF). The cause of the asymmetric effect is unclear (representational momentum shows similar asymmetry, see White, Minor, Merrell, & Smith, 1993). It is known that the LVF is more vulnerable with regard to attentional processes: patients with parietal damage typically have hemineglect of the LVF (Brain, 1941; Costa, Vaughan, Horowitz, & Ritter, 1969; Heilman & Van Den Abell, 1980).

6. Experiment 4: Dependence on speed

In Fu et al. (2001), even though the spatial separation between the pair of visual targets was small (<1°), there was still perceptual overshoot after the cessation of motion so long as the targets were blurred and their speeds very slow: the effect peaked around 0.5°/s, and decreased drastically at higher speeds. In contrast, in our study, blurred stimuli were not required, but spatial separation between the stimuli and peripheral location was. It is natural to ask whether the FLE in our study shows a dependence on speed as in Fu et al. (2001).

6.1. Methods

Ten observers, including the four in the previous experiment, participated. Each bar was 1.95°×0.27° in size. We tested four values (3.32°/s, 6.64°/s, 13.28°/s and 26.56°/s), covering a wide range of biologically reasonable speeds (Nakayama, 1985). The moving bar drifted right for 424 ms, terminated on the vertical midline, and disappeared as soon as it stopped. The flashed bar was presented synchronously with the last frame of the moving bar and lasted for one frame only (11.8 ms duration). The nearest edge-to-edge spatial separation was 8.5°, as in previous experiments. The horizontal position of the flashed bar relative to the last frame of the moving bar was varied between 0′, ±9.375′, ±18.75′, ±28.125′ and ±37.5′. There were 720 trials (20×9×4) per observer. The conditions were randomly intermixed. The data were fitted with a saturation curve,

$$y = \frac{ax}{b + x}$$

x is the speed of the moving bar, and y is the PSE shift. a and b are free parameters. a represents the asymptotic value, and b the speed at which the PSE shift is half of the asymptotic value.

6.2. Results and discussion

As Fig. 6 shows, the FLE, measured in units of spatial distance, remained relatively unchanged with increasing speed; when converted to units of time, the

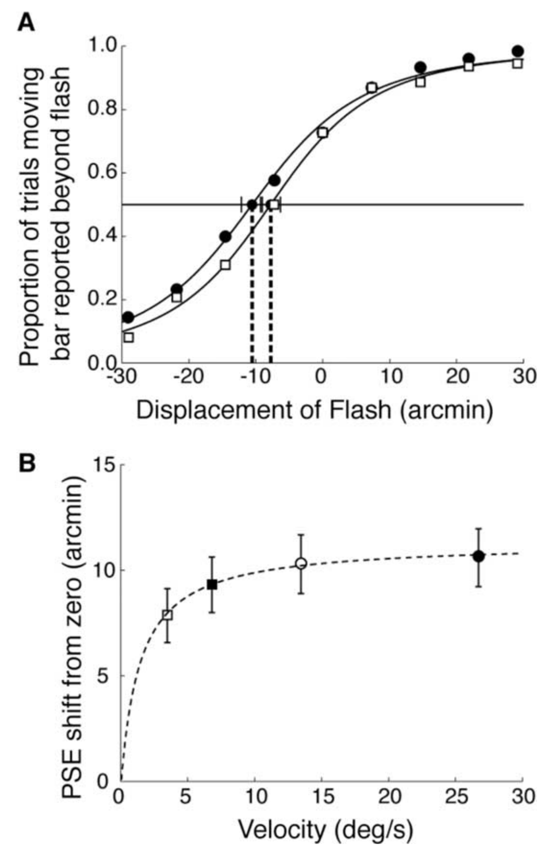

Fig. 6. Speed dependence of FLE in the FTC. (A) Psychometric curves for the different speeds are shown ($n = 10$). For the sake of clarity, only curves for the slowest (open squares) and fastest (filled circles) speeds are shown. Error bars indicate 95% confidence intervals. (B) FLE magnitude (PSE shift from 0) is plotted against speed. Error bars indicate 95% confidence intervals. The best fit to the non-linear saturation curve was achieved when a and b, the two free parameters, were 11.23 and 1.45, respectively (see text for details).

FLE actually decreased. Rank-order correlation analysis yielded a small, marginally significant correlation between speed and FLE magnitude ($r = 0.2538$, $P = 0.0565$). The FLE in the FTC was a bit larger at the faster speeds, in contrast to Fu et al. (2001). One might argue that the conditions in Fu et al. (2001)—blur and ultra-slow speeds—are too far removed from the conditions used in other studies, and, arguably, also from real-world conditions. The conditions—sharply defined stimuli traveling at reasonably fast speeds—under which we have observed a significant lag-effect are arguably more similar to the conditions used in other studies and perhaps, more realistic as well. Interestingly, our finding differs from reports on the CMC, in which the lag-effect, measured in spatial units, was found to vary in linear proportion with speed (Nijhawan, 1994, see Section 9 for a discussion about this).

7. Experiment 5: What if the moving stimulus disappears after it stops?

In our experiments, moving and flashed stimuli disappeared right after the motion stopped. The question in the present experiment is what happens to the lag-effect if either one or both remain on after the motion stops.

7.1. Methods

Four observers participated, including an author (RK). Stimuli and procedures were the same as in the previous experiment, with two exceptions. First, the speed of the moving bar was 13.28°/s. Second, we interleaved trials of three conditions (Fig. 7A). In one condition (both-off), both moving and reference bars disappeared as soon as the moving bar reached the last frame of its motion. In the second condition (motion-off), the moving bar disappeared, but the reference bar remained visible until the observer's response. In the third condition (motion-on), the reference bar disappeared after one frame (11.8 ms duration), but the second bar remained on after it stopped moving, until the observer's response. These three conditions were randomly interleaved in a single session. There were 20 trials/condition, for a total of 540 ($20 \times 3 \times 9$) trials/observer.

7.2. Results and discussion

The results are shown in Fig. 7B and C. A significant lag-effect was observed in the both-off and the motion-off conditions, but none in the motion-on condition. There was no difference in the magnitude of the effect in the both-off and motion-off conditions. The results lead

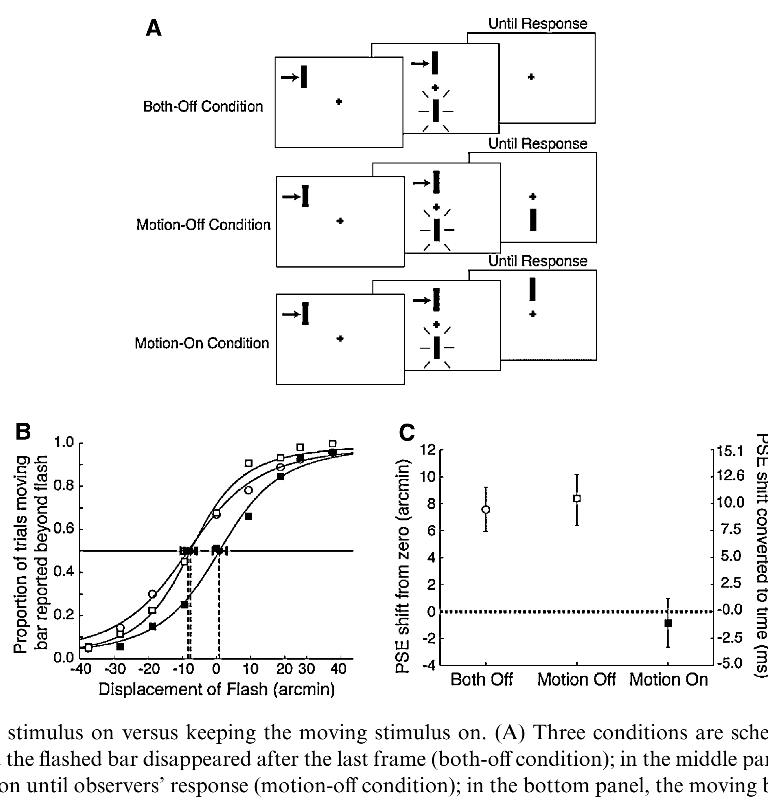

Fig. 7. Keeping the stationary stimulus on versus keeping the moving stimulus on. (A) Three conditions are schematically illustrated. In the top panel, both the moving bar and the flashed bar disappeared after the last frame (both-off condition); in the middle panel, the moving bar disappeared, whereas the flashed bar stayed on until observers' response (motion-off condition); in the bottom panel, the moving bar stayed on when it reached its final position, whereas the flashed bar disappeared after its presentation. (B) Psychometric curves for the three conditions are shown ($n = 4$). The data points for both-off, motion-off and motion-on conditions are shown by open circles, filled circles and filled squares, respectively. (C) FLE magnitude (PSE shift from 0) is shown for all three conditions. Error bars indicate 95% confidence intervals.

us to reason that differences in experimental conditions between the motion-on trials on the one hand, and the motion-off and both-off trials on the other, must underlie the difference in their lag-effects, whereas differences between the motion-off trials and the both-off trials must not. In the motion-on condition, the moving bar remained on after it stopped, whereas in the remaining two conditions, it was extinguished. By our reasoning above, this difference in experimental condition must be critical to the FLE in the FTC. In the motion-off condition, the stationary reference bar remained on for several seconds after the other bar had stopped moving, whereas in the both-off condition, the reference bar was extinguished the instant after it flashed on. By our reasoning, this difference in experimental condition must not be critical. Thus, it was the reliability of the positional signal because the bar remained on after it stopped moving that eliminated the FLE in the motion-on condition, and conversely, the unreliability of the positional signal because the bar was extinguished after it stopped moving that enhanced the FLE in the motion-off and both-off conditions. In other words, the size of the overshoot, namely the lag-effect, is dependent on perceptual uncertainty about the final position of the moving stimulus, and not the (presumably veridically) perceived location of the reference, usually flashed, stimulus.

8. Experiment 6: Dependence on contrast

One way to enhance uncertainty about the location in space of a stimulus is to enhance uncertainty about the stimulus itself. One way is to reduce its contrast with respect to the background. Below a certain contrast level, the lower the contrast of a stimulus, the less detectable it is from the background, and less certain one is of its location in space. In neural jargon, more similar the neural signals corresponding to a stimulus and the background are, less well defined is the neural representation of stimulus position. Indeed, the extent of spatial summation in macaque V1 neurons is significantly greater at low stimulus contrasts (Sceniak, Ringach, Hawken, & Shapley, 1999). Thus, we predict that the lag-effect should increase with decreasing contrast of the moving stimulus.

8.1. Methods

Four observers, including one of the authors (RK), participated. The procedure was essentially identical to previous experiments. A bar moved right from the LVF to just above or below the FP. A second bar was flashed respectively below or above the FP. Both bars had a higher luminance than the gray background. The luminance contrast was varied across trials (Michelson contrasts: 0.043, 0.35, 0.56 and 0.64). Both stimuli were close to the fovea, with the spatial separation between them a small 2.2°. The speed of the moving bar was 18.9°/s. As in previous experiments, the position of the flashed bar relative to the final frame of motion was varied across trials. Observers responded whether the final position of the top or bottom bar was farther right at the time of the flash. Because a low-contrast bar presented just briefly turned out to be difficult to detect, we kept the reference bar on until the observer response. Experiment 5 (see Fig. 7) demonstrated that this manipulation has negligible impact on the FLE in the FTC.

8.2. Results and discussion

The results are illustrated in Fig. 8. As the shallower slope in the low-contrast condition in Fig. 8A attests, observers performed worse at the lowest than at the highest contrast, supporting the notion that reducing

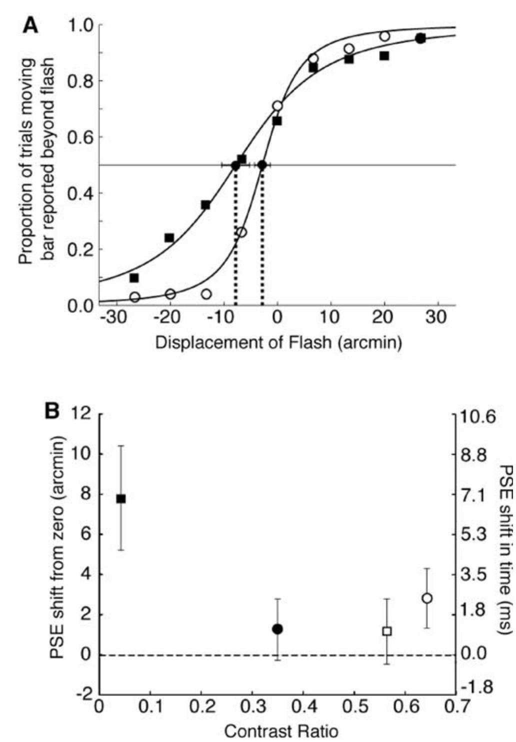

Fig. 8. Contrast dependence of FLE in FTC. (A) Psychometric curves ($n = 4$) are shown with respect to luminance contrast of moving and flashed stimuli relative to the background. Moving and flashed stimuli were of identical contrast for a given contrast ratio depicted in the figure. For the sake of clarity, only curves for the lowest (circles) and highest contrasts (squares) are shown. Error bars indicate 95% confidence intervals. (B) FLE magnitude (PSE shift from 0) versus contrast is plotted. The pooled data for four different Michelson contrasts, 0.043, 0.35, 0.56 and 0.64, are given by filled square, filled circle, open square and open circle, respectively. Do note that the psychometric curve at low stimulus contrast was less sensitive than the psychometric curve at high stimulus contrast.

stimulus contrast enhances spatial uncertainty. Over and above, as Fig. 8B illustrates, the largest lag-effect was obtained at the lowest stimulus contrast. The magnitude of the effect in the low-contrast condition was significant, and was significantly larger than that obtained using higher contrasts. In sum, reducing contrast enhances spatial uncertainty, which, in turn, is necessary for the generation of a FLE in the FTC.

In general, uncertainty about the position of the moving bar is necessary to get a FLE. All of our experiments on the FTC in which we observed a lag-effect worked by enhancing uncertainty of the moving bar's position. Peripheral location of the moving bar, large spatial separation between the moving bar and the reference (flashed) bar, crowding, presentation of the moving bar in the less reliable UVF or LVF, extinction of the moving bar after the cessation of motion, reduction of contrast of the moving bar—all are ways to enhance spatial uncertainty. We argue the same concept underlies Fu et al. (2001). [1] We further argue that spatial uncertainty of the moving stimulus is necessary for all forms of the lag-effect: in the CMC, uncertainty is built-in, as one has to perceptually isolate in time and space an intermediate, non-terminal position of a moving stimulus (general discussion below).

9. General discussion

Our experiments yield the following outcome: under select stimulus conditions, there was a significant lag-effect in the FTC; in other conditions, there was not.

9.1. Spatial uncertainty in positional percept: the common thread

What is common to the apparently diverse manipulations that yielded significant flash-lag effects? A key necessary component common to our manipulations was a high degree of perceptual uncertainty regarding the terminal position of the moving stimulus. There is a correlation, at least in a qualitative sense, between the degree of spatial uncertainty and the magnitude of the flash-lag. For instance, a peripherally presented moving stimulus, as compared to a foveally presented one, is less localizable, namely, its perceived position space is relatively less certain. Consequently, the lag-effect was larger for peripheral than foveal stimuli (Figs. 1–3). A flashed stimulus, if placed between the moving stimulus and fixation, causes crowding (Levi, Klein, & Aitsebaomo, 1985), which degrades perception of the moving stimulus, enhances uncertainty about its position, and thereby enhances the lag-effect (Fig. 4). Detecting an extremely low contrast stimulus is difficult, and therefore, estimating reliably its position in space is also difficult, which causes a larger lag-effect at lower contrasts (Fig. 8). We posit, therefore, that there is a large flash-lag in the FTC only if there is a high degree of perceptual uncertainty about the final position of the moving stimulus.

It is important to note that uncertainty about the position of the moving stimulus is a necessary, but not sufficient, factor in flash-lag. An increase in uncertainty is an increase in the variance of the probability distribution of positional estimates; variance is an unbiased, *non-directional* measure. Positional uncertainty enhances susceptibility to effects like flash-lag, but does not by itself cause the *directional* bias in position: if the distribution is wider, the potential impact of factors that skew distributions in one or another direction is larger. Positional uncertainty per se cannot skew distributions, and therefore cannot, by itself, explain flash-lag, which is a directional bias in positional percept.

9.2. The asymmetric spread account

We propose a schematic account of the directional bias, i.e. the FLE (see Sheth et al., 2000 for sketches of a similar account). Our account's claim to novelty does not lie in the proposition of novel mechanisms, but rather, in being the first to weave together seemingly mutually contradictory aspects of past various models into a single whole; furthermore, it does so with a biologically plausible thread. A significant chunk of the account hinges on the established neurophysiological fact that strong excitation of a cortical cell excites weakly excited cells (such as those in the future path of the moving stimulus M, see Fig. 9), but inhibits strongly excited ones (such as those in the immediate past path; Henry, Goodwin, & Bishop, 1978; Levitt & Lund, 1997; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Sengpiel, Sen, & Blakemore, 1997; Somers et al., 1998; Stemmler, Usher, & Niebur, 1995). First, we will look at what happens across time in a single cell as M traverses space (left → right), and then at a time-frozen snapshot of the network.

Even before the moving stimulus M arrives at a location in space corresponding to the receptive field

[1] Object blur in Fu et al. (2001) can be thought of as an indirect means to achieve low contrast. Each segment of the stimulus differs slightly in contrast from its neighboring segment, as do the stimulus ends from the adjoining background. As the stimulus slowly moves, it remains at each location long enough for light or contrast adaptation to occurs all along its path (Fu et al. themselves acknowledge this as a possibility). This causes the path traversed to appear slightly darker than the untraversed region of same physical contrast. The adaptation is enough for a blurred, low-contrast stimulus to be perceived as being shifted beyond its actual position along the adapted path, giving rise to a FLE. In contrast to Fu et al. (2001), our experiments used sharp-edged stimuli moving at fast velocities, so contrast adaptation cannot account for our findings.

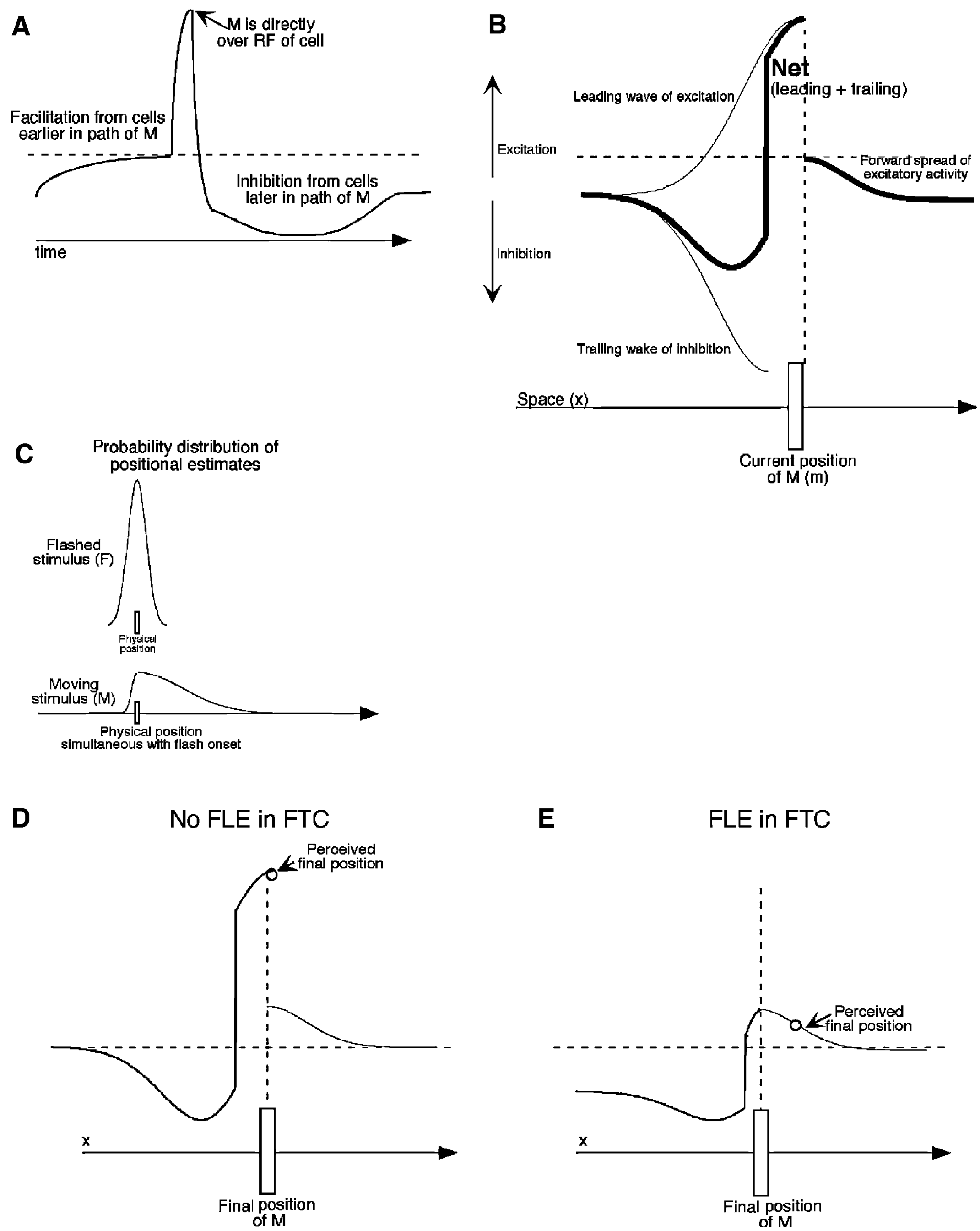

Fig. 9. The asymmetric spread account. (A) The evolution of activity over time in a single cell. The abscissa represents time, and the ordinate represents activity. (B) A snapshot of the network. The abscissa represents space, and the ordinate represents activity. The moving stimulus M moves from left to right. The summed spatial effect of the leading excitatory wavefront and trailing inhibitory wake is depicted in bold. The asymmetry in spread impacts the probability distribution from which positional estimates will be obtained. (C) The probability distribution of position locations from which the perceived positions of the flashed (top) and moving (bottom) stimuli will be chosen. (D,E) The importance of spatial uncertainty in the FLE. (D) If the spatial signal is strong and positional information at position m is good, the neural basis of the positional percept is dominated by the position signal corresponding to m. (E) If the positional information at motion offset is poor, the neural basis of the positional percept is no longer dominated by the position signal corresponding to m.

(RF) center of a cell, it has already begun to excite (Fig. 9A; referred to as priming in Sheth et al., 2000; see Sillito, Jones, Gerstein, & West, 1999 who showed lower thresholds of LGN cells in the expected path of future motion) the given cell via lateral connections from nearby cells (Gilbert, 1998) that were in the path of M earlier. As M moves into the cell's RF center, its activity increases sharply. Soon after M passes the cell's RF center, its activity subsides sharply to below baseline levels owing to two factors: the cell's refractory period, and inhibition from cells later in M's path. Correspondingly, a stationary snapshot of the network across space consists of an excitatory wave of population activity with its crest located at the present location of M, a smaller peak in unstimulated regions including the future positions of M, and a trailing inhibitory wake corresponding to positions of M previously occupied during its motion (Fig. 9B; the suppression was referred to as backward masking in Sheth et al., 2000). Thus, unlike in the case of a stationary flashed stimulus, the spread of activity corresponding to a moving stimulus is asymmetric, which, in turn, contributes to the asymmetry—specifically, the forward bias—in estimates of its position (Fig. 9C). Inhibition, which is in the wake of the large excitatory wavefront, sharpens the representation leading to the crisp percept of the moving stimulus that is seen in the FLE.

Uncertainty in the perceived position of the moving stimulus, that is to say the strength of its positional signal in the brain, is a factor as well. If the terminal position of the moving stimulus is relatively certain, the distribution of possible positions is narrow, namely the activity peak is sharply defined, and the peak dominates the spatial average; consequently, the perceived position is negligibly distant from the actual position M, and is not biased forward (Fig. 9D). On the other hand, if the positional signal is relatively imprecise, the peak does not dominate the spatial average, and the tiny hump beyond and the inhibition behind contribute as well; consequently, the perceived position is biased forward (Fig. 9E). Alternately, and equivalently, the perceiver may resort to a dual-mode "mode or mean" approach to estimate stimulus position (see Sheth & Shimojo, 2003 for a similar account of a different perceptual mislocalization effect). In the case of a narrow activity spread or probability distribution of position, the perceiver chooses the mode or peak; in the case of a broader, more diffuse spread or distribution, the perceiver monitors over time and space to obtain an estimate.

Perceptual uncertainty is a key factor in yet other ways. Flash-lag, we contend, results from a tug-of-war between the need to continually monitor the motion signal over time in order to reduce spatial uncertainty on the one hand, and the requirement to perceive it in the same moment as the flash on the other. Isolating a single snapshot of a moving stimulus is difficult (see e.g. http://www.klab.caltech.edu/~farshadm/demo/). To reduce the uncertainty, the moving stimulus is monitored over time until an internal criterion of certainty is crossed, or the percept of the present times out. Several "snapshots" are taken, with each successive snapshot replacing the previous one and biasing the percept further forward (this is loosely related to temporal pooling, see Krekelberg & Lappe, 1999, 2000a, 2000b; although in our account, snapshots are replaced, and suppression deblurs the smear). Uncertainty about moving stimulus position prolongs the monitoring, which, in turn, enhances the flash-lag (our concept of uncertainty is related to low signal-to-noise ratio in Eagleman & Sejnowski, 2000, but is more specific: it is limited to position, and only that of the moving stimulus). The monitoring cannot go on for too long, as the judged position of the moving stimulus must be perceived within the perceived moment of flash perception. Therefore, the monitoring must stop once this perceived moment times out. The perceived "moment" is not momentary, however, but protracts if the observer has to perform a demanding task. Once the flash is detected, its image (masking it later as in Whitney et al., 2000 disrupts the processing of sensory features of the flash, but not its detection or token individuation) lingers in post-sensory buffers for around 100–300 ms (Parks, 1965; cf. Palmer, 1999; this idea has ties to persistence based accounts of the FLE), which makes the protraction possible. Faced with the difficult task [2] of having to *compare* the *instantaneous* positions of *two* stimuli, one of which is moving, observers' perception of the perceived present is dilated. During this dilated perceived present, the snapshot spatially and temporally coincident with the flash is irretrievably replaced by later ones. Attention grabbed by the flash and away from the moving stimulus, delays the onset of monitoring (Sheth et al., 2000), further enhancing the flash-lag (Baldo, Kihara, Namba, & Klein, 2002; Baldo & Klein, 1995). Naturally, varying flash stimulus parameters (Purushothaman et al., 1998) will change the duration of the perceived moment, and thus alter the flash-lag. [3,4]

9.3. FTC versus the CMC

We briefly discuss differences between the CMC and the FTC. In the CMC, the moving bar continues moving after the occurrence of the flash; hence, the observer is inherently uncertain about the moving bar's position at the moment of flash perception. Because baseline uncertainty is high, experimental manipulations can only rarely enhance uncertainty any higher, whereas reducing uncertainty to below baseline levels is easier. In

[2] Only in the absence of a demanding task are observers' temporal order judgements of the times of the flash and the final (RK and BRS, unpublished observations) or initial (Eagleman & Sejnowski, 2000) position of the moving bar precise.

[3] Increased uncertainty will prolong the monitoring process but at the expense of gradually decreasing certainty that the moving stimulus position is perceived in the perceived present.

[4] Our notion of the perceived moment (a dilated timestamp) obviates the need to postdict or timestamp perception, namely to retrospectively attribute an interpretation to events in the past (Eagleman & Sejnowski, 2000).

the FTC, the moving bar stops after the flash; hence, the observer is far more certain about the moving bar's position at the moment of flash perception. It is possible, therefore, for experimental manipulations, such as those in our study, to be able to increase the uncertainty in the FTC from this low baseline level. The difference in baseline uncertainty regarding moving stimulus position between the CMC and the FTC is consistent with the finding that decrease in the luminance of the moving stimulus decreases or leaves unchanged the FLE in the CMC (Purushothaman et al., 1998), but enhances the FLE in the FTC. The difference is also consistent with the finding that increase in moving stimulus eccentricity enhances the lag-effect in the FTC, but has little effect in the CMC (Baldo & Klein, 1995), and with the finding that, in the CMC, increase in speed leaves the FLE, measured in units of time, unchanged (Krekelberg & Lappe, 1999; Nijhawan, 1994). A second critical difference between the CMC and the FTC is that the perception of the flash is the lone temporal marker in the CMC, whereas, in the FTC, the perceived cessation of motion furnishes an additional marker. Therefore, the flash is a less crucial temporal marker in the FTC. Thus, delaying the perceived moment of flash perception by increasing flash eccentricity (Baldo & Klein, 1995), or dilating it by decreasing flash luminance (Purushothaman et al., 1998), increases the effect in the CMC, but not in the FTC.

We mention, in passing, that, owing to its biological plausibility and the incorporation and modification of aspects of past models in a single framework, other findings that were problematic for previous models (e.g. Eagleman & Sejnowski, 2000; Khurana & Nijhawan, 1995; Nijhawan, Watanabe, Khurana, & Shimojo, in press findings that were problematic for differential latency; Murakami, 2001a, 2001b for temporal pooling and compensation; Purushothaman et al., 1998 for postdiction) are less problematic for our account. Our account ties together seemingly disparate models of flash-lag—and other effects of perceptual mislocalization not discussed here—in a single web.

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References

Baldo, M. V., Kihara, A. H., Namba, J., & Klein, S. A. (2002). Evidence for an attentional component of the perceptual misalignment between moving and flashing stimuli. *Perception, 31*, 17–30.

Baldo, M. V. C., & Klein, S. A. (1995). Extrapolation or attention shift? *Nature, 378*, 565–566.

Berry, M. J., Brivanlou, I. H., Jordan, T. A., & Meister, M. (1999). Anticipation of moving stimuli by the retina. *Nature, 398*, 334–338.

Brain, W. R. (1941). Visual disorientation with special reference to leasions of the right cerebral hemisphere. *Brain, 64*, 224–272.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*, 433–436.

Brenner, E., & Smeets, J. B. J. (2000). Motion extrapolation is not responsible for the flash-lag effect. *Vision Research, 40*, 1645–1648.

Costa, L. D., Vaughan, H. G., Horowitz, M., & Ritter, W. (1969). Patterns of behavior deficit associated with visual spatial neglect. *Cortex, 5*, 242–263.

De Valois, R. L., & De Valois, K. K. (1991). Vernier acuity with stationary moving Gabors. *Vision Research, 31*, 1619–1626.

Eagleman, D. M., & Sejnowski, T. J. (2000). Motion integration and postdiction in visual awareness. *Science, 287*, 2036–2038.

Efron, B., & Tibshirani, R. J. (1993). *An introduction to the bootstrap*. New York: Chapman and Hall.

Foster, D. H., & Bischof, W. F. (1991). Thresholds from psychometric functions: Superiority of bootstrap to incremental and probit variance estimators. *Psychological Bulletin, 109*, 152–159.

Freyd, J. J., & Finke, R. A. (1984). Representational momentum. *Journal of Experimental Psychology—Learning Memory and Cognition, 10*, 126–132.

Fu, Y. X., Shen, Y., & Dan, Y. (2001). Motion-induced perceptual extrapolation of blurred visual targets. *Journal of Neuroscience, 21*(RC 172), 1–5.

Gilbert, C. D. (1998). Adult cortical dynamics. *Physiological Reviews, 78*, 467–485.

Heilman, K. M., & Van Den Abell, T. (1980). Right hemisphere dominance for attention: the mechanisms underlying hemispheric asymmetries of inattention (neglect). *Neurology, 30*, 327–330.

Henry, G. H., Goodwin, A. W., & Bishop, P. O. (1978). Spatial summation of responses in receptive fields of single cells in cat striate cortex. *Experimental Brain Research, 32*, 245–266.

Hill, N. J. (2001). *Testing hypotheses about psychometric functions—an investigation of some confidence interval methods, their validity, and their use in the evaluation of optimal sampling strategies*. D. Phil. thesis, University of Oxford, UK.

Khurana, B., & Nijhawan, R. (1995). Extrapolation or attention shift? Reply. *Nature, 378*, 566.

Krekelberg, B., & Lappe, M. (1999). Temporal recruitment along the trajectory of moving objects and the perception of position. *Vision Research, 39*, 2669–2679.

Krekelberg, B., & Lappe, M. (2000a). A model of the perceived relative positions of moving objects based upon a slow averaging process. *Vision Research, 40*, 201–215.

Krekelberg, B., & Lappe, M. (2000b). The position of moving objects. *Science, 289*, 1107.

Krekelberg, B., & Lappe, M. (2001). Neuronal latencies and the position of moving objects. *Trends in Neurosciences, 24*, 335–339.

Levi, D. M., Klein, S. A., & Aitsebaomo, A. P. (1985). Vernier acuity, crowding and cortical magnification. *Vision Research, 25*, 963–977.

Levitt, J. B., & Lund, J. S. (1997). Contrast dependence of contextual effects in primate visual cortex. *Nature, 387*, 73–76.

MacKay, D. M. (1958). Perceptual stability of a stroboscopically lit visual field containing self-luminous objects. *Nature, 181*, 507–508.

Mateeff, S., & Hohnsbein, T. (1988). Perceptual latencies are shorter for motion towards the fovea than for motion away. *Vision Research, 28*, 711–719.

Mateeff, S., Yakimoff, N., Hohnsbein, J., Ehrenstein, W., Bohdanecky, Z., & Radil, T. (1991). Selective directional sensitivity in visual motion perception. *Vision Research, 31*, 131–138.

McKee, S. P., Klein, S. A., & Teller, D. Y. (1985). Statistical properties of forced-choice psychometric functions: Implications of probit analysis. *Perception and Psychophysics, 37*, 286–298.

Montgomery, D. C. (2001). *Design and analysis of experiments*. New York: Wiley.

Murakami, I. (2001a). A flash-lag effect in random motion. *Vision Research, 41*, 3101–3119.

Murakami, I. (2001b). The flash-lag effect as a spatiotemporal correlation structure. *Journal of Vision, 1*, 126–136.

Müsseler, J., van der Heijden, A. H. C., Mahmud, S. H., Deubel, H., & Ertsey, S. (1999). Relative mislocalization of briefly presented stimuli in the retinal periphery. *Perception and Psychophysics, 61*, 1646–1661.

Nakayama, K. (1985). Biological image motion processing: A review. *Vision Research, 25*, 625–660.

Nijhawan, R. (1992). Misalignment of contours through the interaction of apparent and real motion systems. *IOVS, 33*(Suppl.), 1415.

Nijhawan, R. (1994). Motion extrapolation in catching. *Nature, 370*, 256–257.

Nijhawan, R. (2002). Neural delays, visual motion and the flash-lag effect. *Trends in Cognitive Sciences, 6*, 387–393.

Nijhawan, R., Watanabe, K., Khurana, B., & Shimojo, S. (in press). The compensation of neural delays in visual-motor tasks. *Visual Cognition*.

Palmer, S. E. (1999). *Vision science—photons to phenomenology*. Cambridge, MA: The MIT Press.

Parks, T. E. (1965). Post-retinal visual storage. *American Journal of Psychology, 78*, 145–147.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*, 437–442.

Polat, U., Mizobe, K., Pettet, M. W., Kasamatsu, T., & Norcia, A. M. (1998). Collinear stimuli regulate visual responses depending on cell's contrast threshold. *Nature, 391*, 580–584.

Purushothaman, G., Patel, S. S., Bedell, H. E., & Ogmen, H. (1998). Moving ahead through differential visual latency. *Nature, 396*, 424.

Ramachandran, V. S., & Anstis, S. (1990). Illusory displacement of equiluminous kinetic edges. *Perception, 19*, 611–616.

Sceniak, M. P., Ringach, D. L., Hawken, M. J., & Shapley, R. (1999). Contrast's effect on spatial summation by macaque V1 neurons. *Nature Neuroscience, 2*, 733–739.

Sengpiel, F., Sen, A., & Blakemore, C. (1997). Characteristics of surround inhibition in cat area 17. *Experimental Brain Research, 116*, 216–228.

Sheth, B. R., Nijhawan, R., & Shimojo, S. (2000). Changing objects lead briefly flashed ones. *Nature Neuroscience, 3*, 489–495.

Sheth, B. R., & Shimojo, S. (2001). Compression of space in visual memory. *Vision Research, 41*, 329–341.

Sheth, B. R., & Shimojo, S. (2003). Signal strength determines the nature of the relationship between perception and working memory. *Journal of Cognitive Neuroscience, 15*, 173–184.

Sillito, A. M., Jones, H. E., Gerstein, G. L., & West, D. C. (1999). Feature-linked synchronization of thalamic relay cell firing induced by feedback from the visual cortex. *Nature, 369*, 479–482.

Somers, D. C., Todorov, E. V., Siapas, A. G., Toth, L. J., Kim, D. S., & Sur, M. (1998). A local circuit approach to understanding long-range inputs in primary visual cortex. *Cerebral Cortex, 8*, 204–217.

Stemmler, M., Usher, M., & Niebur, E. (1995). Lateral interactions in primary visual cortex—A model bridging physiology and psychophysics. *Science, 269*, 1877–1880.

Toet, A., & Levi, D. M. (1992). The two-dimensional shape of spatial interaction zones in the parafovea. *Vision Research, 32*, 1349–1357.

Van Essen, D. C., Newsome, W. T., & Maunsell, J. H. R. (1984). The visual field representation in striate cortex of the macaque monkey: Asymmetries, anisotropies, and individual variability. *Vision Research, 24*, 429–448.

Whitaker, D., Pearson, S., McGraw, P. V., & Banford, M. (1998). Keeping a step ahead of moving objects. *IOVS, 39*(Suppl.), S1078.

White, H., Minor, S. W., Merrell, J., & Smith, T. (1993). Representational-momentum effects in the cerebral hemispheres. *Brain and Cognition, 22*, 161–170.

Whitney, D., & Murakami, I. (1998). Latency difference, not spatial extrapolation. *Nature Neuroscience, 1*, 656–657.

Whitney, D., Murakami, I., & Cavanagh, P. (2000). Illusory spatial offset of a flash relative to moving stimulus is caused by differential latencies for moving and flashed stimuli. *Vision Research, 40*, 137–149.