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# Perceptual organization of moving stimuli modulates the relative position of a visual flash

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### Abstract

When a visual stimulus is flashed at a given location the moment a second moving stimulus arrives at the same location, observers report the flashed stimulus as lagging the moving stimulus, despite the fact that the flashed and moving stimuli are physically aligned at the instant of the flash. We investigated whether the global configuration (perceptual organization) of the moving stimulus influences the magnitude of this mislocalization of a visual flash relative to a moving stimulus. Our results indicate that a flash presented near the leading portion of a moving stimulus lags significantly more than a flash presented near its trailing portion. This result also holds for objects consisting of several elements which group to form a unitary percept of an 'object in motion'. The present study demonstrates a novel interaction between the global configuration of moving objects and the representation of their spatial position. Our observations may provide a new and useful tool for the study of perceptual organization.

Perceptual organization of moving stimuli modulates  
the relative position of a visual flash

One of the main tasks of the visual system is to represent spatial relationships among visual objects. In everyday life, we perceive and act on the basis of relative position information, and from the behaviors typically observed it would seem that our perceptions are virtually flawless. However, under some conditions, mislocalizations do occur such that the relative position of a visual stimulus is perceived at a different position than its actual one. These illusory mislocalizations are informative sources of the underlying neural processes that typically yield an accurate perception of space (Gregory, 1997).

Consider the striking phenomenon that is observed when a visual stimulus is flashed at a given location the moment a second moving stimulus arrives at the same location. Despite the fact that the flashed and moving stimuli are physically aligned, observers report the flashed stimulus as lagging the moving stimulus -- the 'flash-lag' effect (Nijhawan, 1994). The first report of a similar phenomenon involving saccadic eye movements can be traced back to Ernst Mach (1897; pp. 61). Later, Mackay (1958) came across this phenomenon, which led to more systematic studies (see e.g., Mateeff, Mitrani & Stojanova, 1982). Recently, the flash-lag effect (FLE) has been revisited by Nijhawan (1994), leading to renewed interest in the phenomenon.

Multiple accounts of the flash-lag effect have been forwarded. Mach (1897) suggested that the effect was due to visible persistence of the flash. This account was also proposed by Nijhawan (1992) and significantly extended by Lappe and Krekelberg (1998) and Krekelberg and Lappe (1999, 2000). However, it has been reported that if the persistence of the flash is reduced by a masking stimulus, the FLE occurs undiminished (Whitney, Murakami & Cavanagh, 2000). Thus, persistence of the flash is an unlikely explanation of the FLE.

Metzger (1932) posited a difference in the visual latencies of moving versus flashed items to account for the mislocalization of the flash. Recently, two findings revived the

appeal of such an account. Firstly, when a moving object abruptly reverses direction at the moment of the flash, the moving object does not appear to overshoot the reversal point (Whitney & Murakami, 1998). Secondly, when the contrast of the moving and the flashed items is manipulated, the FLE is found to decrease with increased contrast of the flash, and decreased contrast of the moving item (Purushothaman, Patel, Bedell, & Ogmen, 1998). Both sets of observations are handled by postulating differential processing delays between moving versus flashed items.

Nijhawan (1994, 1997) pointed out that significant transit delays of neural signals between the photoreceptors and higher cortical areas in the primate visual system should result in the retinal image location of a moving object leading the object's neural representation in higher, retinotopically organized, cortical areas. He hypothesized, however, that an early visual operation, computationally akin to extrapolation, corrects the cortical lag and maintains position correspondence between different processing levels for predictably moving objects (Nijhawan, 1994, 1997; Nijhawan & Khurana, 2000). On this view, the FLE occurs because of the 'extrapolation' of the moving item and the delay in the visibility of the flashed item, which cannot be corrected.

Baldo and Klein (1995) argued that the perceived lag of a flashed object relative to a moving one is the consequence of the delayed allocation of attention to the flashed object. This view must assume that a moving object solicits and sustains attentional deployment (e.g., Pylyshyn, 1989, 1994; Watanabe & Shimojo, 1998) prior to the onset of the flashed object. Time delays result from either stimulus-driven attentional capture by the flashed object (Yantis & Jonides, 1984; Nakayama & Mackeben, 1989; Yantis & Jonides 1990; Hillstrom & Yantis, 1994; Yantis and Hillstrom, 1994; Jonides & Yantis, 1998), or attentional shifts from the moving to the flashed locations (Tsal, 1983; Weichselgartner & Sperling, 1987). Thus, the FLE is due to some time consuming process that shifts visual attention, the latency of which increases as a function of eccentricity (Baldo & Klein, 1995; Tsal, 1983; but see Nakayama & Mackeben, 1989). By the time the flashed object is fully

registered the moving object has moved on and the flashed object is incorrectly perceived to spatially lag the moving one. However, recent experiments show that the differential deployment of attention does not impact the FLE (Khurana & Nijhawan, 1995; Khurana, Watanabe & Nijhawan, 2000).

The precise mechanism(s) responsible for the FLE is still under intensive debate (Baldo & Klein, 1995; Eagleman & Sejnowski, 2000; Khurana & Nijhawan, 1995; Khurana et al., 2000; Krekelberg & Lappe 1999; 2000; Purushothaman et al., 1998; Whitney & Murakami, 1998; Whitney et al., 2000). However, until now most explanations of the FLE have focused on the basic data of the flash mislocalization. There are additional notable observations that accompany the basic FLE, and these observations will no doubt constrain the explanation of the phenomenon. While exploring the flash-lag phenomena, we encountered an interesting observation which provided the basis for the present set of experiments. A black ring translated on a circular path on a gray background. A white disk was briefly flashed such that it physically filled the center of the black ring (Figure 1). As expected observers perceived the flashed disk to lag the moving ring (Nijhawan, under review). However, the appearance of the disk close to the leading edge of the ring differed significantly from that close to its trailing edge. The disk appeared to be compressed along the path of motion (thus it appeared elliptical rather than circular) and to be "cut off" by the ring's trailing edge .

We initially reasoned that if the FLE is greater around the leading portion of the ring than the trailing portion then the apparent shape distortion of the flashed disk would result. Thus, our working hypothesis was that different portions of an extended flashed stimulus suffer different lags, and that the extent of the lag is influenced by the global configuration of the moving stimulus. In order to investigate the problem we simplified the experimental paradigm and employed a small flashed disk so that the shape distortion would not be an issue. We conducted eleven psychophysical experiments to explore (a) whether the FLE magnitude is different around the leading versus the trailing portions of a moving stimulus, and (b) under what conditions does such an asymmetrical FLE occur. To anticipate the

results: When moving stimuli were perceived as forming a unitary object, such that the object could be said to consist of a leading and a trailing portion, the leading portion of the moving stimulus produced a greater FLE than the trailing portion. This asymmetrical effect, where the global configuration of the moving stimulus influences the perceived position of a visual flash, not only constrains the type of explanation for the FLE, but also provides a new and useful tool in the study of perceptual organization.

### General Method

Unless otherwise stated, the following conditions hold true for all the experiments.

All visual stimuli were displayed on a color monitor (48° high, 60° wide, in visual angle), controlled by a Silicon Graphics Iris work station, in a dimly lit room (about 0.5 lux). The edge of the monitor was visible. The frame rate of the monitor was 75 Hz. A black fixation cross (0.02 cd/m<sup>2</sup>, 0.48° in visual angle) was displayed throughout each session. The background was gray with a luminance value of 8.2 cd/m<sup>2</sup>. At the beginning of each trial, a stimulus (moving item; MI) appeared randomly at either the left or right side of the screen. Each MI was composed of straight bars with a thickness of 0.168°, except for that in Experiment 10. The center of MI was initially placed 2.88° above and 4.8° to the left or to the right of the fixation cross (Figure 2). Immediately after its appearance, the MI moved laterally toward the opposite side of the screen. The frame-to-frame spatial offset of the MI was 0.096°, which resulted in a constant speed of 7.2°/s. A small white disk (61.0 cd/m<sup>2</sup>) was flashed 2.88° above the fixation cross for 1 frame (approximately 13.3 ms) at various timings. The diameter of the disk was 0.168°, which was equal to the MI bar thickness. Since the disk was flashed at various timings, it appeared at various positions relative to the MI. The shape, luminance, and color of MI differed for each experiment (see Figure 3), and all observers agreed in that they perceived the MIs being well grouped because those components moved at the same velocity.

Observers viewed the stimulus display binocularly from a distance of 57 cm while fixating at the black cross throughout each trial. After viewing the stimulus sequence, they reported where the flash appeared relative to the MI by pressing appropriate keys (two-, three-, or five-alternative forced-choice; not speeded). If they perceived the flash directly on top of a moving bar, they were to make an arbitrary choice. But, as the bar thickness and the size of the flash disk were identical, this percept would be highly unlikely and it was confirmed by the post-experiment interview. Immediately after the observer's response, the next trial began. For each different timing of the flash presentation (i.e., different distance of the flash from the MI center), 20 trials were repeated randomly using the method of constant stimuli.

When the disk was flashed directly on top of the vertical bar element of the MI, according to the FLE, the disk should be perceived to lag behind the bar. We estimated how long before (or how far ahead) the disk had to be flashed in order for observers to perceive the flash and the vertical bar of the MI to be at the same location. For each observer, we linearly interpolated data and found the crossing point of the categorical responses for each corresponding vertical bar (i.e., the point of subjective equality where the observer was equally likely to say that the disk appeared 'ahead' of or 'behind' a given vertical bar of the MI). This corresponds to the magnitude of the FLE for an individual observer for a given vertical bar. For MIs which had more than one vertical bar, such as a square, we repeated this procedure for each vertical bar. All the data in the current study, except for Experiment 11, are presented as both (a) the mean percentage of each categorical response against the position of the flash relative to the center of the MI (which summarize raw data), and (b) the magnitude of the FLE, calculated as above and then averaged across observers (which is subject to statistical analysis).

### Experiment 1: One Square

The initial observation was that, when a disk was flashed to fill a moving ring, the disk appeared to lag the leading edge of the ring and to be compressed at its trailing edge (Figure

1). This observation leads to the prediction that a flash presented near the leading portion of a MI would be perceived to lag more than a flash presented near the trailing portion. As a starting point, we used a square as the MI in Experiment 1.

### Method

Observers. Seven observers participated in each experiment (O.S., M.W., J.W., B.S., E.B., K.W., and S.S.; two of whom, K.W. and S. S. were authors). Except for the authors, all other observers were naive as to the purpose of the study. Observers' ages ranged from 20 to 43 years. They all had normal or corrected-to-normal vision and reported no difficulty with the tasks.

Stimuli. The MI was a black open square ( $0.02 \text{ cd/m}^2$ ), composed of four bars ( $0.168^\circ$  thick;  $1.92^\circ$  long; Figure 3a). The direction of motion was randomized within a session. The white disk was flashed 0, 3, 6, 9, 12, 15, or 18 frames before or after (i.e., 0, 40, 80, 120, 160, 200, and 240 ms before or after) the moment the center of the square (MI center) passed the center of the screen. Therefore, the flash was presented  $0^\circ$ ,  $0.288^\circ$ ,  $0.576^\circ$ ,  $0.864^\circ$ ,  $1.152^\circ$ ,  $1.44^\circ$ , or  $1.728^\circ$  ahead of or behind the MI center. When the disk was flashed  $0.864^\circ$  ahead of (or behind) the center of the square, it was physically on top of the leading (or trailing) bar of the square.

Procedure. Each observer was instructed to fixate the fixation cross throughout a trial and to report whether the flashed disk appeared to the left, inside, or to the right of the square (three-alternative forced-choice). A session consisted of 260 trials: 20 repetitions of 13 flash positions. Each session took approximately 15 minutes.

### Results and Discussion

The results of Experiment 1 are presented in Figure 4. In the top panel, the horizontal axis shows the physical distance of the flash from the center of the square. A larger negative (or positive) value means that the flash was presented far ahead of (or behind) the center of the square. The vertical axis is the percentage of each categorical report, averaged for all the

seven observers, with vertical lines indicating standard error (between-observer variability). The gray regions represent the position of the square. The precision of localization can be inferred by inspecting the slope of the line which cross over the other line. In Experiment 1, the slope for the leading bar was 3.64 %/min and that for the trailing bar was 4.09 %/min (see Appendix for details).

The bottom panel shows the estimated magnitude of the FLE in visual angle ( $^{\circ}$ ). A larger positive value suggests that, in order for the flash to appear aligned with a given vertical bar of the MI, it had to be presented more ahead of the bar. An ANOVA with repeated measures showed that the FLE magnitude was greater for the leading bar ( $\bar{M} = 0.415^{\circ}$ ) than for the trailing bar ( $\bar{M} = 0.154^{\circ}$ ) ( $F(1,6) = 30.81, p < 0.001$ ).

Does the asymmetrical FLE really reflect the observer's perception? Or, it is an unknown response-bias for observers to somehow report 'ahead' more often than 'inside' under this specific stimulus configuration? There are two pieces of evidence against the response-bias hypothesis. First, all the observers expressed their high confidence in the post-experiment interview. Secondly, we know that the FLE vanishes when an observer tracks the moving stimulus with the eyes (**XX: REF**). If an unascertained response-bias, which is independent of the FLE, was the main cause of the asymmetrical effect, it should have survived the tracking manipulation. But, an informal observation clearly showed that this was not the case. When the MI was tracked with the eyes, the FLE totally disappeared, so did the asymmetry of it.

The results of Experiment 1 confirm our hypothesis based on the phenomenology of the ring-disk observation. The apparent shape distortion of the flashed disk inside the ring may be explained by the asymmetry of the FLE, in that the magnitude of the FLE is greater for the leading edge of the ring than for the trailing edge. It is hard, however, to draw a general conclusion of the FLE asymmetry from the results of Experiment 1 because there remains the possibility that the results are specific to the particular (closed or bounded) shape configurations of squares or rings. Therefore in further experiments we attempted to narrow

down the critical conditions under which the asymmetrical FLE is observed. In the next experiment, we examined whether closure of the MI is necessary to produce the FLE asymmetry.

### Experiment 2: Leading and Trailing Bars

In Experiment 2, two vertical bars were used as the MI. We simply removed the horizontal bar components from the square used in Experiment 1, which destroyed the property of closure of the MI. We chose this change because (1) closure was one of the properties of the configurations present in both the ring in the initial observation and the square in Experiment 1, and (2) this would retain the reference stimuli (vertical bars) for measuring the FLE. If closure of the MI is critical for the asymmetrical FLE, we would observe a different pattern of results in Experiment 2. If not, the two vertical bars should produce the same results as the complete square used in Experiment 1.

#### Method

Observers. The same seven observers participated in Experiment 2 as in Experiment 1.

Stimuli. The MI was two black vertical bars, made by removing the horizontal bars from the square used in Experiment 1 (Figure 3b). The other stimulus conditions were identical to those of Experiment 1.

Procedure. Each observer reported whether the flashed disk appeared to the left, between, or to the right of the two bars. Otherwise, the procedure was the same as in Experiment 1.

#### Results and Discussion

Figure 5 shows the results of Experiment 2 in the same manner as in Experiment 1. Again, we found a significantly larger FLE for the leading bar ( $\underline{M} = 0.427^\circ$ ), compared with the trailing bar ( $\underline{M} = 0.144^\circ$ ) (ANOVA with repeated measures;  $F(1,6) = 24.78$ ,  $p < 0.001$ ). Planned comparisons between Experiment 1 and Experiment 2 for each bar position indicated that there was no statistical difference in FLE magnitude between the square and

the two-bar conditions (leading bars,  $F(1,6) = 0.058$ ,  $p = 0.814$ ; trailing bars,  $F(1,6) = 0.034$ ,  $p = 0.856$ ).

The results of Experiment 2, together with those of Experiment 1, show that the asymmetry of the FLE is not specific to closed shapes such as rings and squares, and that it is a general phenomenon which occurs when the leading/trailing relationship is perceived to be exist in a moving stimulus.

When two parallel bars move perpendicular to bar orientation, the leading bar produces a larger FLE than the trailing bar. An obvious and important next question is: What would happen if there is only one moving bar? Is the asymmetry of the FLE due to the reduction of the FLE for the trailing bar, or to the enhancement of the FLE for the leading bar? We addressed this question in the next experiment.

### Experiment 3: One Vertical Bar

In Experiment 3, only one vertical bar was presented as the MI. The purpose of Experiment 3 was to determine the baseline FLE for the single bar component. If the magnitude of the FLE for this one-bar configuration is similar to that for the leading bar, it would suggest that the asymmetry of the FLE occurs because the FLE for the trailing bar is reduced. In contrast, if the FLE for the single bar is comparable to that for the trailing bar, it would suggest that the asymmetrical FLE occurs because the FLE for the leading bar is enhanced.

#### Method

Observers. With the exception of E.B., 6 observers from the previous experiments participated.

Stimuli. The MI was one black vertical bar, identical to one of the two bars in Experiment 2 (Figure 3c). The white disk was flashed 0, 3, 6, or 9 frames before or after (i.e., 0, 40, 80, or 120 ms before or after) the moment the bar passed the center of the screen. Accordingly, the flash was presented about  $0^\circ$ ,  $0.288^\circ$ ,  $0.576^\circ$ , or  $0.864^\circ$  ahead of or behind the bar. The other stimulus conditions were identical to those in the previous experiments.

Procedure. Each observer reported whether the flashed disk appeared to the left or to the right of the bar in a two-alternative forced-choice procedure. A session consisted of 140 trials: 20 repetitions of 7 flash positions. Otherwise, the procedural details were the same as in the previous experiments.

### Results and Discussion

Figure 6 shows the results of Experiment 3. Intriguingly, the magnitude of the FLE of the single bar ( $\bar{M} = 0.144^\circ$ ) was similar to that of the trailing bar in Experiment 1 and Experiment 2. Since one observer (E.B.) did not participate in Experiment 3, the following statistical analysis was performed with the data of observer E.B. excluded. A one-way ANOVA revealed that there was no significant difference in the magnitude of the FLE among the single bar in Experiment 3, the trailing bar element in Experiment 1, and the trailing bar in Experiment 2 ( $F(2,10) = 0.021$ ;  $p = 0.979$ ). Therefore, the asymmetry of the FLE between the leading and the trailing bars seems to be due to the enhancement of the FLE for the leading bar.

The results of Experiment 2 and Experiment 3 can be described as follows: When a single bar (B1) moves and a flash appears around the bar, a small magnitude FLE is observed. If another bar (B2) leads B1 (i.e., B1 is now the trailing bar), there is no change in the effect measured relative to B1. If, however, B2 follows B1 (B1 now serves as the leading bar), the magnitude of the FLE relative to B1 increases almost four-fold.

From a simple view of a strictly retinotopic representation this is rather paradoxical. When two bars sweep across the retina, or any other retinotopic map, the leading bar should stimulate a given retinotopic location first, and the trailing bar should reach that location later (about 240 ms after the leading bar passes in Experiment 2). So, if one considers only local interactions, it is logical for the leading bar to have an effect on the trailing bar, whereas the trailing bar could not affect the leading bar. This suggests that some form of spatial interaction between the two bars is involved in the production of the asymmetrical FLE.

Since the two bars of Experiment 2 produced similar results to the square of Experiment 1, we hypothesized that the postulated spatial-interaction acts somehow to group visual elements into a single moving 'unit'. Thus, when moving visual elements are perceived as a unitary object, the asymmetry of the FLE manifests itself such that the flash presented around a leading portion of the 'unit' lags more than the flash presented at the other portions of the 'unit', particularly that presented around its trailing portion. We will call this the grouping hypothesis. In the following experiments, we attempted to test the grouping hypothesis in order to obtain a more detailed picture of interaction between perceptual grouping and the FLE asymmetry.

#### Experiment 4: Four Vertical Bars

Experiment 4 was basically a variant of Experiment 2. Instead of the two vertical bars, four equally-spaced bars were used as the MI. The four bars appeared to be grouped and perceived as a unitary moving object, due to the law of 'common fate' (e.g., Gibson, Gibson, Smith, & Flock, 1959; Johansson, 1950, 1973; Koffka, 1935; Köhler, 1928; Wertheimer, 1923). The grouping hypothesis predicts that the FLE would be most prominent at the first (leading) bar of the four bars and be least at the fourth (trailing) bar.

#### Method

Observers. The same six observers as in Experiment 3 participated.

Stimuli. The MI was four black vertical bars (Figure 3d). We made this MI by adding one vertical bar to the left and one to the right of the MI used in Experiment 2. The bar separations were equal to the distance between the bars used in Experiment 2 (i.e., bar length ( $1.92^\circ$ ) - bar thickness ( $0.168^\circ$ )  $\times 2 = 1.584^\circ$ ). The bars were numbered as the leading bar being the first bar and the trailing bar as being the fourth bar. The white disk was flashed 3, 6, 9, 12, 15, 21, 24, 27, 30, or 33 frames before or after, or 36 frames before (i.e., 40, 80, 120, 160, 200, 280, 320, 360, 400, or 440 ms before or after, or 480 ms before) the moment the MI center passed the center of the display. Thus, the flash appeared  $0.288^\circ$ ,  $0.576^\circ$ ,  $0.864^\circ$ ,  $1.152^\circ$ ,  $1.44^\circ$ ,  $2.016^\circ$ ,  $2.304^\circ$ ,  $2.592^\circ$ ,  $2.88^\circ$ , or  $3.168^\circ$  ahead of or behind, or  $3.456^\circ$  behind

the center of the four bars. When the disk flashed  $2.592^\circ$  ahead of,  $0.864^\circ$  ahead of,  $0.864^\circ$  behind, or  $2.592^\circ$  behind the MI center, it was physically on top of the first, second, third, or the fourth bar, respectively. The other stimulus conditions were identical to those in the previous experiments.

Procedure. Each observer reported, by pressing keys, where the disk flashed; to the left of the outer-left bar, between the outer-left and the inner-left bars, between the inner-left and the inner-right bars, between the inner-right and the outer-right bars, or to the right of the outer-right bar (five-alternative forced-choice). A session consisted of 420 trials (20 repetitions of 21 flash positions), and took approximately 25 minutes to complete. The other procedures were the same as in the previous experiments.

### Results and Discussion

Figure 7 shows the results of Experiment 4, graphed in the manner analogous to the previous experiments. A one-way ANOVA showed main effect of the bar position in the MI ( $F(3,15) = 8.069$ ;  $p < 0.002$ ). The first bar produced the greatest FLE (the first bar,  $\underline{M} = 0.5^\circ$ ; the second bar,  $\underline{M} = 0.16^\circ$ ; the third bar,  $\underline{M} = 0.085^\circ$ ; the fourth bar,  $\underline{M} = 0.049^\circ$ ). Application of Tukey's honestly significant difference (HSD) test showed that the FLE magnitude of the first bar was a significantly greater than the other bars ( $p < 0.05$ ). Thus, the results of Experiment 4 support the grouping hypothesis because the first bar behaved in the same way as the leading bar of the two bars in Experiment 2, and addition of multiple trailing bars did not further increase the FLE for the leading bar.

The primary grouping principle involved in Experiment 4 was the law of common-fate; things that move together are grouped together. Although common-fate is considered a very strong cue for grouping (Gibson et al., 1959; Johansson, 1950, 1973; Koffka, 1935; Köhler, 1928; Wertheimer, 1923), various other cues are available for visual grouping. In the following two experiments, keeping the basic configuration of the MI (four vertical bars) the same as in Experiment 4, we manipulated the appearance of the MI by adding other grouping cues so that the four bars would be perceived as two objects. According to the grouping

hypothesis the asymmetrical FLE occurs on the basis of the moving perceptual units. Therefore, if the four bars appear to form two moving objects, the FLE magnitude would be larger at the leading portion and smaller at the trailing portion of each perceived object.

#### Experiment 5: Four Bars or Two Squares?

In order to further investigate the grouping hypothesis, we took advantage of the four-bars configuration of Experiment 4. By simply connecting the two ends of the first and second bars, and those of the third and fourth bars, the four bars appear to be two squares (Figure 3e), due to closure (Wertheimer, 1923) and element connectedness (Palmer & Rock, 1994). Since the local features of the stimulus were unchanged, any difference in results between Experiment 4 and Experiment 5 should reflect the difference in the global configuration, namely, the difference in perceptual organization of the MI.

#### Method

Observers. The same six observers participated in the experiment.

Stimuli. The MI was two black outline squares (Figure 3e). We made this MI by adding the horizontal bars to the four vertical bars used in Experiment 4; between the outer-left and the inner-left bars, and between the outer-right and the inner-right bars. The other stimulus conditions were identical to those in Experiment 4.

Procedure. Each observer reported, by pressing the appropriate key, where they perceived the flashed disk; to the left of the left square, inside the left square, between the left and the right squares, inside the right square, or to the right of the right square (five-alternative forced-choice). The procedure was otherwise identical to that in Experiment 4.

#### Results and Discussion

Figure 8 shows the results of Experiment 5. Again, the first bar, which was the leading portion of the entire MI (the left square + the right square), showed a large FLE ( $\bar{M} = 0.386^\circ$ ). However, the third bar, which was the leading bar of the trailing square, also showed a large FLE ( $\bar{M} = 0.324^\circ$ ), comparable to the first bar. A one-way ANOVA showed main effect of the position of bar in the MI ( $F(3,15) = 9.079$ ;  $p < 0.001$ ). Post-hoc analyses

indicated that there were statistical differences in the magnitude of the FLE between the first and the third bars versus the second and the fourth bars (Tukey's HSD test,  $p < 0.05$ ).

A series of planned comparisons was performed between Experiment 4 and Experiment 5. The difference in the FLE magnitude for the third bar between Experiment 4 and Experiment 5 was significant ( $F(1,5) = 5.441$ ;  $p < 0.05$ ). The FLE on the other bars were not significantly different between the two experiments (first bars,  $F(1,5) = 1.424$ ;  $p = 0.260$ ; second bars,  $F(1,5) = 1.452$ ;  $p = 0.256$ ; fourth bars,  $F(1,5) = 0.053$ ;  $p = 0.823$ ).

The third bar was perceived as being an 'internal' part of the MI in Experiment 4, while the addition of the horizontal bars altered its perceived role in Experiment 5. By virtue of closure and uniform connectedness, the third bar in Experiment 5 was perceived as being the leading portion of the trailing square<sup>1</sup>. The dependence of the FLE magnitude on the global configuration of the MI, and on the perceptual role of each stimulus element, strongly endorses the grouping hypothesis. In the next experiment, we show that another grouping cue, similarity of color, is also effective in altering the role of the stimulus elements in the MI.

#### Experiment 6: Four Colored Bars

If the grouping hypothesis is correct, we can expect that other grouping cues would produce the same pattern of the results as closure did in Experiment 5. Grouping by color has been known to be an effective grouping factor (e.g., Carrasco & Chang, 1995; Gorea & Papathomas, 1991; Koffka, 1935; Köhler, 1928; Kramer & Jacobson, 1991; Wertheimer, 1923). Therefore we tested whether perceptual grouping by similarity of color would cause the asymmetrical FLE.

#### Method

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<sup>1</sup> One may wonder why the horizontal bars in Experiment 1 did not matter at all but those in Experiment 5 did. The difference between Experiment 4 and Experiment 5 was whether the stimuli were grouped into one object or two objects, not whether grouped or not grouped. In other words, the role of the horizontal bars in Experiment 5 was to segregate the left two bars and the right two bars. On the other hand, the two vertical bars in Experiment 2 were already well grouped because of the common-fate law. The role of the horizontal bars in Experiment 2 is to add another grouping cue for two vertical bars. Thusly the consequences of the horizontal bars in Experiment 1 and Experiment 5 were supposed to be different.

Observers. The same six observers participated in Experiment 6.

Stimuli. The stimulus conditions were almost identical to those in Experiment 4. However, the outer and inner left-bars were perceptually distinct from the outer and inner right-bars because of their color (Figure 3f). One pair of bars was colored red and the other green. Color of bars was randomized between the two left and right bars. The bar luminance was  $1.5 \text{ cd/m}^2$ , irrespective of their color.

Procedure. The procedure was identical to that in Experiment 4.

### Results and Discussion

The results of Experiment 6 are shown in Figure 9. Grouping by color in Experiment 6 produced the same pattern of results as grouping by closure and connectedness in Experiment 5. The magnitude of the FLE was larger for the first and the third bars (i.e., the leading portions of each color-pair of bars) than for the second and the fourth bars (i.e., the trailing portions). A one-way ANOVA showed a significant main effect of bar position in the MI ( $F(3,15) = 4.93, p < 0.05$ ). A Tukey's HSD test showed statistical differences between the first and the third bars versus the second and the fourth bars ( $p < 0.05$ ). Thus grouping by color was as effective as grouping by closure in biasing the perception of the MI such that two, as opposed to one, moving objects were perceived. This perception was reflected, in turn, in the measured asymmetry of the FLE.

The main implication of the grouping hypothesis is that, as long as the moving stimuli are grouped into and perceived as units, the FLE asymmetry is observed in each perceived unit. To further generalize the grouping hypothesis, we conducted four additional experiments (Experiment 7-10). In these experiments, the possibility that various low-level features might be responsible for the asymmetrical FLE was examined.

#### Experiment 7: Two White Bars

The question addressed in Experiment 7 was: Would the same asymmetry of the FLE be observed when the polarity of the MI was reversed? If results where the MI was composed of white bars were different from results where the MI was composed of black bars, then it

might imply that the asymmetrical FLE is due to some low-level processing in the visual system. In contrast, if the pattern of results is not altered, the grouping hypothesis would be further strengthened.

### Method

Observers. The same six observers participated in Experiment 7.

Stimuli. The stimuli were identical to those used in Experiment 2, except that their luminance was  $16.4 \text{ cd/m}^2$  (Figure 3g). The luminance of the disk flash was not changed ( $= 61.0 \text{ cd/m}^2$ ). The background luminance was gray ( $8.2 \text{ cd/m}^2$ ) as before.

Procedure. The procedure was the same as that in Experiment 2.

### Results and Discussion

The pattern of the results in Experiment 2 was replicated in Experiment 7 (Figure 10). That is, there was a significantly larger FLE for the leading bar ( $\underline{M} = 0.391^\circ$ ), compared with the trailing bar ( $\underline{M} = 0.072^\circ$ ) ( $\underline{F}(1,5) = 8.76, p < 0.05$ ). Since the contrast polarity of the MI did not affect the asymmetrical pattern of the FLE, it can be inferred that the mechanisms responsible for the asymmetry of the FLE are not specific to low-level interactions among luminance-based processes in early vision.

#### Experiment 8: Non-aligned Vertical Bars

The grouping hypothesis stresses the importance of the perceived unity of a moving stimulus. According to this hypothesis, therefore, it should not matter whether or not the vertical bars pass over the same retinotopic location as long as the bars are perceived to form a moving unit. In order to test this possibility, we changed the relative position of the two vertical bars such that the two bars would not move over the same area of the retina. In Experiment 8, the left bar was shifted up and the right bar shifted down by half their length, or the other way around (Figure 3h). Even with this configuration, observers reported that they perceived the two bars being a unitary moving object. The question was: Would the FLE asymmetry persist with this non-aligned configuration?

### Method

Observers. The same six observers participated in Experiment 8.

Stimuli. The MI was two black vertical bars (Figure 3h). One bar was shifted up by half of the bar length, and the other shifted down by the same distance. The shift direction (left-up/right-down or right-up/left-down) was randomized among observers. The white disk was flashed at various timings as in Experiment 2 (see Figure 11). Note that the positions in which the flashed disk could be presented was determined by the oblique imaginary line joining the centers of the bars. Accordingly when the disk was flashed  $0.864^\circ$  ahead of (or behind) the center between the two bars, it was physically located on the center of each bar. For this timing the spatial position of the flashed disk relative to the moving bar was identical to that in the previous experiments.

Procedure. The procedure was identical to that in Experiment 7.

### Results and Discussion

The results of Experiment 8 (Figure 12) were similar to those of Experiment 2. In order for the flashed disk to be perceived directly on top of the bars, the flash had to be presented more ahead of the leading bar ( $\underline{M} = 0.411^\circ$ ), compared with the trailing bar ( $\underline{M} = 0.054^\circ$ ) ( $F(1,5) = 12.51, p < 0.01$ ). Therefore, for the asymmetrical FLE to occur, it is not necessary that the bars traverse over the same retinal locations. This result clearly makes a simple low-level account of the asymmetrical FLE based on visible persistence or energy summation of two bar elements untenable.

### Experiment 9: Illusory Object

In Experiment 9, we further tested the grouping hypothesis, by using illusory lines. When the stimulus configuration is appropriate, observers perceive an edge or an object in the absence of a corresponding physical stimulus (e.g., Kanizsa, 1976; Koffka, 1935; Meyer & Petry, 1987; Michotte, Thinés, & Crabbé, 1964; Schumann, 1904). For example, observers can readily tell whether a given location in Figure 3i is 'inside' or 'outside' the figure, as the two 'brackets' can be grouped together to form a subjective square. When these stimuli move together, due to common-fate, the impression of unity between them and the

illusory figure is even more compelling. We used this figure as the MI in Experiment 9. If results with this subjectively formed object are equivalent to those with luminance-defined square in Experiment 1, then it would suggest that even the presence of a physical bar is not necessary to produce the asymmetry of the FLE.

### Method

Observers. The same six observers participated in Experiment 9.

Stimuli. Figure 3i depicts the MI used in Experiment 9. We made this MI by removing the middle portion ( $= 0.96^\circ$ ) of the vertical bars of the square used in Experiment 1. The other stimulus conditions were the same as in Experiment 7.

Procedure. The procedure was identical to that in Experiment 7.

### Results and Discussion

In Experiment 9, we obtained results (Figure 13) comparable to those of Experiment 1. The leading portion of the subjective square exhibited a greater FLE ( $\underline{M} = 0.507^\circ$ ) than the trailing portion ( $\underline{M} = 0.194^\circ$ ) ( $F(1,5) = 7.451$ ,  $p < 0.05$ ). Since the illusory edges of the MI in Experiment 9 produced the same pattern of results as the luminance-defined edges in Experiment 1, we conclude that the asymmetry of the FLE in the moving stimuli is in fact the asymmetry of the FLE measured relative to the perceived moving object.

#### Experiment 10: One filled square

All the experiments so far used MIs composed of straight bars. The purpose of Experiment 10 was to reject the possibility that the peculiarity of this stimulus composition might be the cause of the asymmetrical FLE. The MI was a black filled square.

### Method

Observers. The same six observers participated.

Stimuli. The MI was a black filled-square (Figure 3j), which was made by filling up the inside of the square used in Experiment 1. The other stimulus conditions were the same as in Experiment 7.

Procedure. Each observer was instructed to report whether the flashed disk appeared to the left, inside, or to the right of the filled square. If observers perceived the disk be on the edge, they judged the relative position between the edge and the center of the disk.

Otherwise, the procedure was the same as in Experiment 7.

### Results and Discussion

In Experiment 10, there was a significantly large FLE in the leading edge ( $M = 0.314^\circ$ ) compared with the trailing edge ( $M = -0.163^\circ$ ) (Figure 14;  $F(1,5) = 26.66$ ,  $p < 0.001$ ). The FLE magnitude for the trailing edge had a negative value probably because the instruction was different in Experiment 10 from the other previous experiments. In Experiment 10 the observers judged the position of the center of the flashed disk relative to the edges of the filled square, which corresponded to the outer edge of the vertical bar components of the open square in Experiment 1. In any case, the pattern of the results was basically the same as that in Experiment 1. So the results of Experiment 10 add further evidence for generality of the phenomenon, namely, evidence that the asymmetrical FLE is not restricted to the figures composed of straight bars.

#### Experiment 11: Shape Distortion of Moving Item or Mislocalization of Flash?

All the results thus far strongly support the grouping hypothesis and show that various cues could be used for grouping moving stimuli into perceptual units. It is clear that a visual flash presented around the leading portion of a perceived moving object lags farther behind than that presented around the other portions, particularly the trailing edge.

There are at least two conceivable explanations for this FLE asymmetry. When a visual stimulus moves, the relative position of the leading portion might be shifted more ahead, compared with that of the trailing portion. If this were the case, we should expect the shape of a moving stimulus to be elongated along the path of motion by a magnitude equal to the difference in the FLE magnitude between the leading and trailing edges. In Experiment 11, we compared the perceived shape of a moving square with that of a stationary square. If the moving square was elongated along the path of motion by the same magnitude as the FLE

asymmetry observed in Experiment 1, it would imply that the asymmetry of the FLE occurs because the leading part of the square might be perceived more ahead than its trailing part (shape distortion hypothesis). Alternatively, the flash may be mislocalized relative to the moving square, more for the leading than the trailing edge of the square, despite the shape of the square being veridically perceived (mislocalization hypothesis).

### Method

Observers. The same six observers participated in the experiment.

Stimuli. A rectangle, composed of bars with a thickness of  $0.168^\circ$ , was presented in Experiment 11. The height of the rectangle was fixed at  $1.92^\circ$ , which is equal to the height (and width) of the square used in Experiment 1. The width of the rectangle randomly varied from  $1.632^\circ$  to  $2.112^\circ$  in  $0.048^\circ$  steps. In the Stationary condition, the rectangle was placed  $2.88^\circ$  above the fixation cross. In the Moving condition, the rectangle traveled horizontally at a speed of  $7.2^\circ/\text{s}$  as in the previous experiments. The direction of movement was randomized. Both the stationary and the moving rectangles were presented for about 1.33 s, which was also the stimulus duration of the MIs in the previous experiments.

Procedure. The Stationary and the Moving conditions were tested in separate sessions. The order of the sessions was randomized among observers. Each observer was asked to look at the fixation cross throughout a trial and to report whether the rectangle was elongated vertically (Thin) or horizontally (Fat). A session consisted of 220 trials: 20 repetitions of 11 rectangle widths. Each session lasted for approximately 15 minutes.

### Results and Discussion

Figure 15 shows the results of Experiment 11. The mean percentages of 'Fat' responses are plotted against the physical elongation of the rectangle. On average, when the width of the stationary rectangle was equal to the height, the observers seemed not to show any significant bias with our display. When the rectangle was in motion, however, it was

perceived to be slightly wider than when it was stationary (as indicated by the leftward shift of the psychometric function in Figure 15).

We performed statistical analysis after fitting the data with a logistic function (Finney, 1971) and calculating the point of subjective equality (PSE) for each observer. The PSE is the horizontal elongation of the rectangle at which each observer perceived it to be a square. A negative value indicates that an observer saw the MI as a square even when it was shrunk horizontally. The mean PSE for the Stationary condition was  $-0.006^\circ$  ( $SD = 0.0251$ ). The mean PSE for the Moving condition was  $-0.073^\circ$  ( $SD = 0.0669$ ). There was a significant difference between these conditions ( $F(1,5) = 5.369$ ;  $p < 0.05$ ). However, the averaged difference was only about  $0.068^\circ$  and therefore cannot explain the large difference in the FLE magnitude between the leading and the trailing portions of the square in Experiment 1 (approximately  $0.261^\circ$ ). So, it is rather difficult to attribute the large FLE asymmetry solely to the shape distortion of the moving stimulus. The main cause of the asymmetric FLE, therefore, must then be the asymmetric mislocalization of the flash relative to the moving item.

### General Discussion

The present study reports a novel case of the dynamic representation of relative positions of objects, that is, the influence of the perceptual organization of moving objects on the relative localization of another visual object. In summary: (1) When a small visual stimulus is flashed around the leading edge of a moving object, the flash appears to lag more than when it is flashed close to the other parts of the object, in particular its trailing edge. (2) This asymmetry of the FLE is observed as a function of the moving stimuli being perceived as a unit, even when the leading and trailing edges of the stimuli are otherwise identical. (3) Various grouping cues used to establish the unity of the moving stimuli give rise to the FLE asymmetry. (4) The asymmetrical FLE is due to a difference in relative mislocalization of the flash, rather than to a shape distortion of the moving stimulus. In the context of our current findings, we (a) discuss other phenomena of mislocalization of a briefly presented stimulus,

(b) speculate on a possible functional role of the FLE asymmetry, (c) suggest the applicability of the current paradigm for investigation of object perception, and (d) briefly outline the implications of the FLE asymmetry for current theories of the FLE.

#### Dynamical representation of the relative position of visual objects

There are numerous examples of errors in the dynamic representation of the relative position between visual objects. When a small visual stimulus is flashed in the dark up to 100 ms before a saccadic eye movement, its absolute position (relative to the observer's head and/or body) is perceived to be shifted in the direction of the saccade (Dassonville, Schlag, & Schlag-Rey, 1992; Honda, 1990, 1991, 1997; Matin, 1976; Matin, Matin, & Pearce, 1969; Matin, Matin, & Pola, 1970; Schlag & Schlag-Rey, 1995). This mislocalization also occurs, though its magnitude is reduced, when the flash is presented on a visible background (Bischof & Kramer, 1968; Honda, 1993; Mateeff, 1978; O'Regan, 1984), and also when observers are asked to judge its position relative to other continuously visible stimuli (Cai, Pouget, Schlag-Rey, & Schlag, 1997; Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). Further examples of dynamic-context modulating relative position of objects comes from the experiments on 'movement-based positional bias' (Anstis, 1989; DeValois & DeValois, 1991; Nishida & Johnston, 1999; Ramachandran & Anstis, 1990; Snowden, 1998). For instance, DeValois and DeValois (1991) showed observers three Gabor patches aligned on the same vertical axis. The envelopes of the Gabor patches were stationary, but within those envelopes sinusoidal gratings drifted either leftward or rightward. The gratings in the top and bottom patch drifted in one direction while the grating in the middle patch drifted in the opposite direction. Observers misperceived the position of the stationary Gabor patches to be shifted in the direction of the moving gratings such that the three patches no longer appeared on the same vertical axis. Thus, the relative position of a visual stimulus can be affected by motion signals contained within the stimulus. These mislocalization effects, altering the relative position of visual stimuli, suggest that our perception of object positions can be dynamically modulated by eye movements and/or motion signals. In our experiments,

however, no eye movements were involved and all the visual elements of the MIs moved at the same speed in the same direction. Therefore, the mechanisms implicated in eye-movement-based and retinal-motion-based mislocalizations cannot account for the present findings, that is the asymmetrical mislocalization of a flash.

Why should perceptual organization affect the relative localization?

What could this asymmetrical flash localization based on the perception of moving objects signify? When a stimulus (e.g., a small disk) is inside a perceived object (e.g., square), the visual system tends to process the two visual stimuli as parts of a single object. In contrast, when the disk is placed outside the square, the two are perceived as two separate objects. This may be true even when the disk is flashed and the square is continuously visible and in motion. We speculate that the FLE asymmetry reflects a perceptual strategy of the visual system in evaluating the spatial relationship between a moving object and a flash.

A brief flash may be regarded as informationally weak (e.g. see Mackay, 1958) for the visual system to extract its absolute location and/or motion information with precision. Under such circumstances the perceived position of the flash may be influenced by visual contexts in which the flash appears. When the position of the flash physically overlaps that of the moving object, it may be treated as a part of the moving object. The visual system might interpret such an event as something that occurred on the moving object, rather than an event that happened to occur just when the moving object passed a certain spatial position. Thus, the flash is not registered as accidentally appearing at the same location as the moving object. When this occurs the flashed object appears to be dragged by the moving object (Hill, 1998; Cai, Schlag-Rey, & Schlag, 1999), which would typically help in perceiving the veridical position of the flash (i.e., on the moving object). This in turn is reflected as a reduced FLE for a flash presented inside MIs. Consider, on the other hand, a flash presented outside the moving stimulus. This flash is more likely to be treated as an independent object which can, nonetheless, be perceived to overlap the moving object leading to a percept of

occlusion. Thus, a visual flash presented (physically and retinotopically) outside a moving object will give rise to a larger FLE. We suggest that the observed FLE asymmetry reflects the general asymmetry in nature where a part of an object is less likely to be spatially separated from the other parts, while two independent objects can spatially overlap. In brief, a large FLE occurs only when a moving stimulus and a flash are perceived to be separate objects and/or events. Thus, in order for the visual system to localize a visual flash, the perceptual organization (objectness) of each contextually present stimuli and its motion may play an important role.

#### Further investigations of object perception by using the asymmetrical FLE

We asked the observers to produce categorical responses (e.g., flash to the left of bar or flash to the right of bar). However, we did not ask them to report how large the spatial lag between a moving bar and a flash was. Therefore the present results cannot discern whether the FLE was greater when the flash appeared close to but behind the leading bar than when it appeared close to but ahead the trailing bar, namely, whether the FLE magnitude was homogenous inside a MI or decreased with the distance from the leading edge (although the results of Experiment 4 implies that the latter is more probable). Further investigations, which include an estimation of the perceived lag, are necessary to clarify this issue.

Whatever the functional role and the underlying mechanism of the asymmetrical FLE is, it is quite clear that the asymmetrical mislocalization of a visual flash occurs when moving stimuli are perceptually grouped into a single or multiple unitary object(s). Therefore, the asymmetrical FLE may be applied to investigate the visual grouping of moving stimuli.

Gestalt laws we employed in our displays worked for grouping moving stimuli which, in turn, was reflected in the asymmetrical FLE. The primary cue for grouping of moving stimuli is common-fate (Gibson et al., 1959; Johansson, 1950, 1973; Koffka, 1935; Köhler, 1928; Wertheimer, 1923). Additionally, similarity of color (Carrasco & Chang, 1995; Gorea & Papathomas, 1991; Koffka, 1935; Köhler, 1928; Kramer & Jacobson, 1991; Wertheimer, 1923), closure (Wertheimer, 1923) and uniform connectedness (Palmer & Rock, 1994) of the

moving stimuli, all impacted the magnitude of the FLE (Experiment 4, 5, and 6). However, we did not test proximity (things that are close together are grouped together; e.g., Kubovy & Wagemans, 1995; Wertheimer, 1923) as a grouping factor. This may be explored by changing the distance between two moving elements. A preliminary observation in our lab shows that proximity of moving elements has a moderate effect on the asymmetrical FLE. As separation between two moving stimuli is increased, the FLE asymmetry decreases. Also, note that we did not examine the effectiveness of the common-fate cue in and of itself. In future experiments, we intend to introduce a velocity difference between (among) moving stimuli, thereby manipulating the perceived unity of stimuli, and to study the effect on FLE magnitude. For example, one might employ two bars with one bar moving at double the speed of the other. If common-fate of moving stimuli (and grouping due to it) is a function of velocity similarity, the velocity difference between moving elements should modulate the FLE. In this manner, the asymmetrical mislocalization of a single visual flash can provide a new index of perceptual grouping.

#### Implication for current theories of the FLE

Finally, we would like to briefly discuss implications of the present findings for various accounts of the FLE. Although the present study was not designed to differentiate among the accounts, the results clearly show that a single low-level visual process cannot account for the various FLE phenomena. The shorter visual latency for motion signals (e.g., Purushothaman et al., 1998; Whitney & Murakami, 1998; Whitney, Murakami & Cavanagh, 2000), and/or the longer visible persistence for a flashed item, cannot explain the FLE asymmetry which is clearly based on global configuration of the moving stimuli. For instance, with a simple differential latency account, which assumes that moving stimuli have an advantage over flashed stimuli in terms of processing speed, one further assumption would be required; the visual latency for the leading edge of a perceived moving object has to be shorter than that for the trailing edge. Although this possibility cannot as yet be ruled out, it seems unlikely in light of the results of Experiment 11, which showed virtually no shape

distortion as the differential latency model would predict. In addition to this difference in the processing of leading and trailing edges, the differential latency would have to also suggest that the perceptual objectness of a moving stimulus affects its latency. This idea does not seem very plausible at the outset. The perceptual organization of the moving stimulus changing the visible persistence of the flash and, in turn, causing the FLE asymmetry, seems even more far fetched.

However, the current data are also not readily accounted for by mechanisms that rely on higher processes, such as motion extrapolation (Nijhawan, 1994), attention (Baldo & Klein, 1995), and 'postdiction' (Eagleman & Sejnowski, 2000). Until the nature of these high-level operations are specified, that is, what is extrapolated, what is affected by attention, and what is postdicted (e.g., absolute or relative location information of the retinal representation or perceived objects<sup>2</sup>), the high-level accounts remain equivocal with respect to the present findings.

In order to fully explain the findings involving the FLE asymmetry observed in the present study, the low-level accounts need to incorporate the effect of the global configuration of moving stimuli, while the high-level accounts have to become more explicit about the levels and representations of the high-level computations. The findings in the present study will undoubtedly provide further constraints on the choice of mechanism.

### Conclusion

We have demonstrated that the global configuration (perceptual organization) of moving stimuli modulates the relative position of a visual flash. This conclusion emerges because the perceptual grouping of moving stimuli strongly influences the magnitude of the FLE. A visual flash lags significantly more when it is presented around the leading portion of a perceived moving object than when it is presented close to its trailing portion. Thus the

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<sup>2</sup> Note that, in the present paper, we defined the FLE as a mislocalization of a visual flash relative to moving stimuli, as reflected our persistent use of "relative localization" and the use of the forced-choice procedure for relative position judgment (rather than an absolute localization procedure such as manual pointing). Whether the asymmetrical FLE can be observed even with an absolute localization procedure would be interesting to investigate.

visual system seems to not preserve accurate or precise information about spatial and temporal positions of stimuli defined by reference to a retinal coordinate frame. Rather, vision seems to preserve information about the field structure of images, somewhat as the Gestalt psychologists conceived of it. Since the asymmetrical mislocalization of visual flash is highly dependent on the objectness of moving stimuli, it may provide a novel tool for investigating perceptual grouping.

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## Appendix: Interaction between constant localization error and precision

The slope values of the psychometric curves were calculated by (1) taking the mean percentage of categorical responses just before and after the cross point in the upper panels in the result figures, and (2) linearly interpolate those two point. The unit of the slope is percent/min. We classified all the results into either the Large FLE group or the Small FLE group (Table 1). The number following immediately "E" donates the experiment number, and the number following "-" indicates the position of a bar in the MIs (e.g., E4-3 means the third bar from the leading edge of the MI in Experiment 4). There is a tendency that the large FLE might be accompanied with a slight loss of precision (one-tailed t-test,  $t(23) = 1.66$ ,  $p = 0.06$ ). This interaction between constant localization error (measured in the FLE magnitude) and localization precision (variability) may be interesting to examine. However, the effect size is small and this minimal difference in variability have little impact on our main result.

Table 1. Slope of psychometric functions of categorical responses.

Large FLE group		Small FLE group	
E1-1	3.64	E1-2	4.09
E2-1	3.27	E2-3	3.35
E4-1	2.65	E3-1	2.75
E5-1	3.09	E4-2	2.17
E5-3	2.70	E4-3	2.32
E6-1	2.32	E4-4	2.85
E6-3	1.59	E5-2	2.56
E7-1	1.72	E5-4	2.94
E8-1	2.51	E6-2	3.18
E9-1	2.56	E6-4	3.28
E10-1	2.79	E7-2	3.18
		E8-2	3.91
		E9-2	1.93
		E10-1	4.63
M	2.62	M	3.08
SD	0.60	SD	0.76
N	11	N	14

## Figure captions

Figure 1. The ring-disk observation.

While a black ring translates on a circular path, a white disk is briefly flashed such that it physically fills the ring (Left panel). The flashed disk appears to lag the leading edge, whereas the disk is perceived to be compressed along the path of the moving ring or to be cut off at the trailing edge.

Figure 2. Example of the stimulus display.

While the subjects kept fixating the center cross, a figure (moving item; MI) translated laterally at a constant speed of  $7.2^\circ/\text{s}$ . The MI composed of straight bars. A small white disk was flashed above the fixation cross for 1 frame at various timings so that it was placed various positions relative to the MI.

Figure 3. The moving items.

(a) A square in Experiment 1. (b) Two bars in Experiment 2. (c) One bar in Experiment 3. (d) Four bars in Experiment 4. (e) Two squares in Experiment 5. (f) Four colored bars in Experiment 6. Different filling patterns represent different colors. (g) Two white bars in Experiment 7. (h) Two non-aligned bars in Experiment 8. (i) Illusory object in Experiment 9. (j) Filled black square in Experiment 10.

Figure 4. Results of Experiment 1 (MI = a square; (a) in Figure 3).

Top panel: The horizontal axis shows the physical distance of the visual flash from the center of the square. The vertical axis is the averaged percentage of each categorical report with bars indicating one standard error (between-observer variability). The gray bars depict the position of the MI, schematically. Bottom panel: The estimated magnitude of the FLE,

averaged across all the subjects. The FLE was greater for the leading bar than for the trailing bar.

Figure 5. Results of Experiment 2 (MI = Two bars; (b) in Figure 3).

The results of Experiment 2 are shown in the same manner as in Figure 4. The results were similar to those of Experiment 1.

Figure 6. Results of Experiment 3 (MI = One bar; (c) in Figure 3).

The results of Experiment 3 are shown in the same manner as in Figure 4. The FLE magnitude with a single bar was small, resembling that of the trailing bars in Experiment 1 and Experiment 2.

Figure 7. Results of Experiment 4 (MI = Four bars; (d) in Figure 3).

The results of Experiment 4 are presented in the same way as in Figure 4. Note that there are five symbols in the top panel because the subjects performed a five-alternative forced choice task. The first bar produced a large FLE as the leading bar in the previous experiments. The other bars did not show a strong FLE.

Figure 8. Results of Experiment 5 (MI = Two squares; (e) in Figure 3).

The results of Experiment 5 are presented in the same way as in Figure 7. The FLE magnitude was large for the first bar (the leading portion of the leading square) and for the third bar (the leading portion of the trailing square).

Figure 9. Results of Experiment 6 (MI = Four colored bars; (f) in Figure 3).

The results of Experiment 6 are presented in the same way as in Figure 7. The FLE magnitude was large for the first bar and for the third bar. Grouping by color in Experiment 6 led to the same pattern of results as grouping by closure in Experiment 5 did.

Figure 10. Results of Experiment 7 (MI = Two white bars; (g) in Figure 3).

The results of Experiment 7 are presented in the same way as in Figure 4. The leading bar exhibited a greater FLE than the trailing bar.

Figure 11. Example of flash locations in Experiment 8.

In order for the flash presented  $0.864^\circ$  ahead of (behind) of the MI center (indicated by arrow) to be physically at the center of the bars, the vertical locations of the flash were moved as shown above.

Figure 12. Results of Experiment 8 (MI = Non-aligned bars; (h) in Figure 3).

The results of Experiment 8 are presented in the same way as in Figure 4. The leading bar showed a greater FLE than the trailing bar.

Figure 13. Results of Experiment 9. (MI = Illusory object; (i) in Figure 3).

The results of Experiment 9 are shown in the same way as in Figure 4. The leading portion of the moving item produced a larger FLE than the trailing portion, even when the bars were not defined by a visible feature.

Figure 14. Results of Experiment 10. (MI = Filled black square; (j) in Figure 3).

The results of Experiment 10 are shown in the same way as in Figure 4. The leading edge of the moving item produced a larger FLE than the trailing edge.

Figure 15. Results of Experiment 11.

The mean percentages of 'Fat' responses are plotted against the physical elongation of the rectangle. When the rectangle was stationary, there was no bias in terms of the perceptual elongation. When it was in motion, a significant but a small horizontal elongation was

observed. However, the averaged difference was only about  $0.068^\circ$ , and could not explain the large difference in the FLE magnitude.

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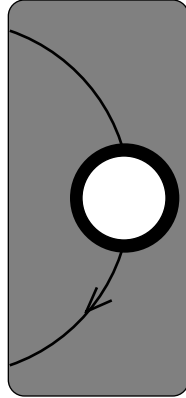
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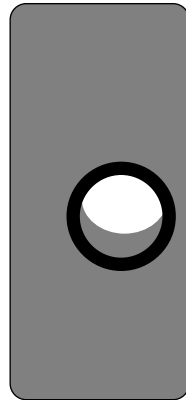
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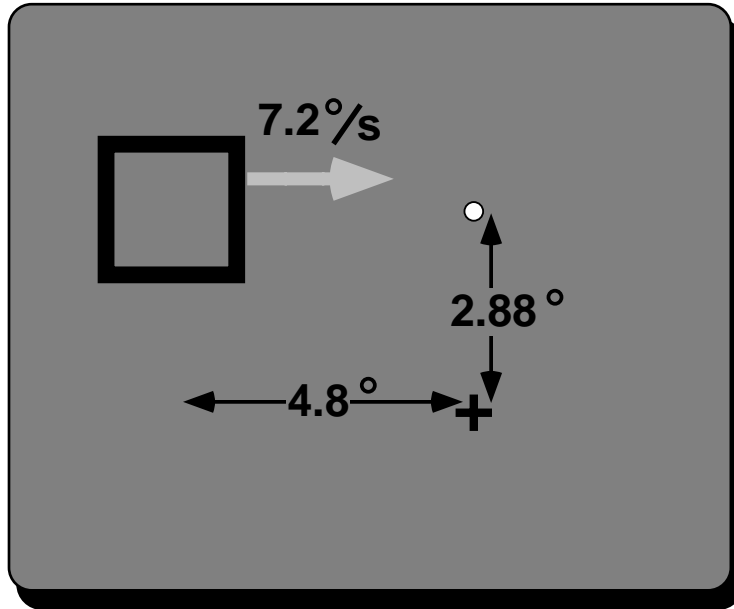
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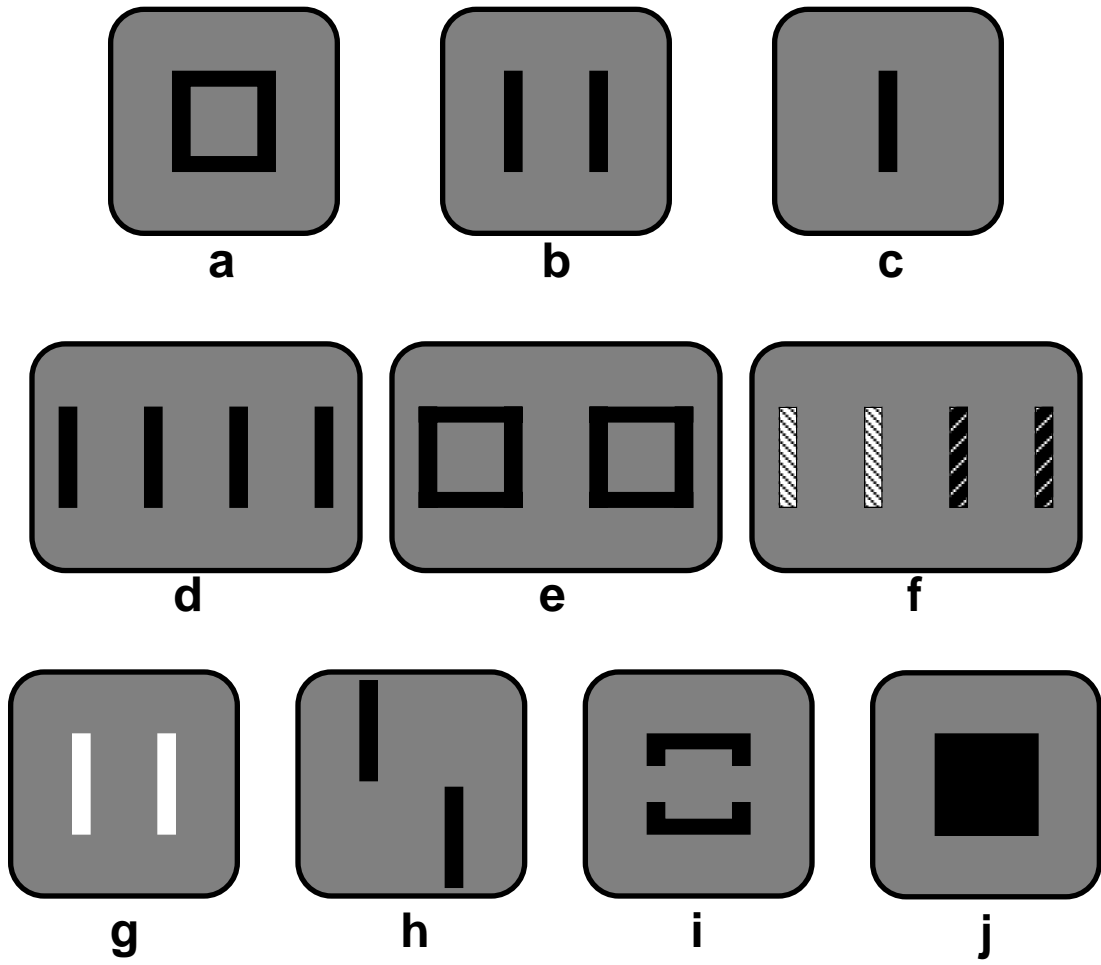
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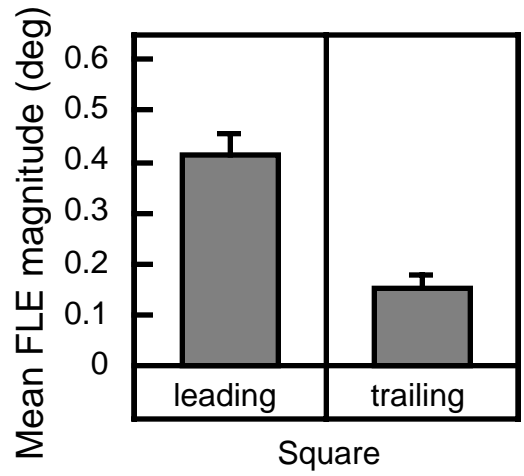
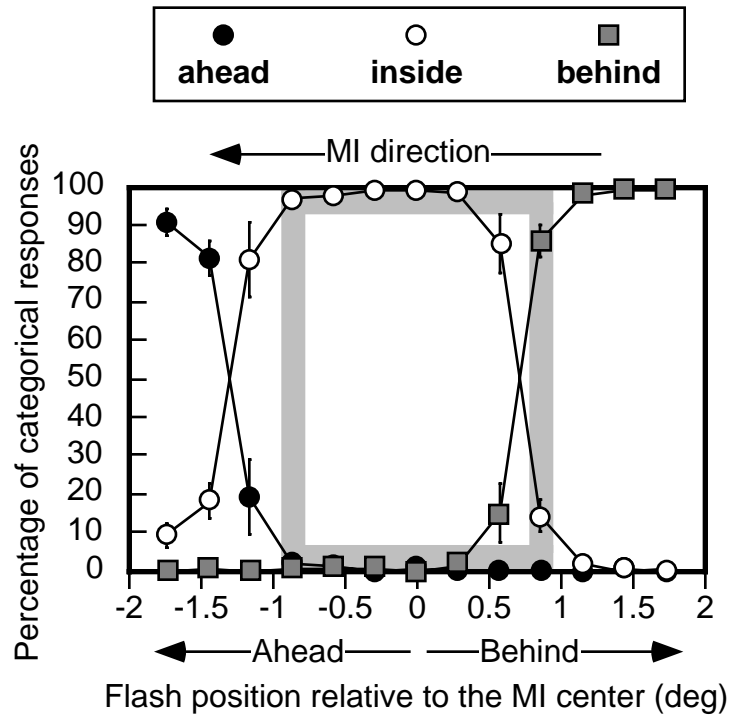
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**Figure 1**



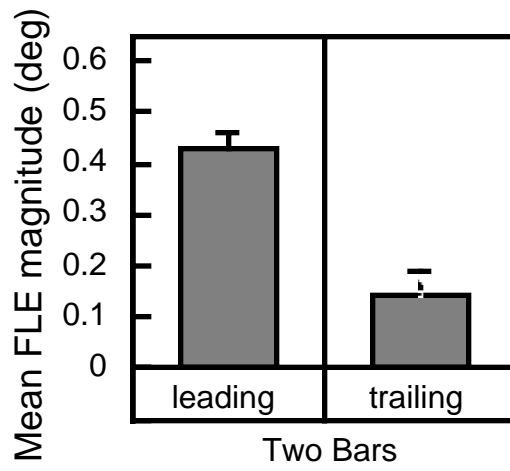
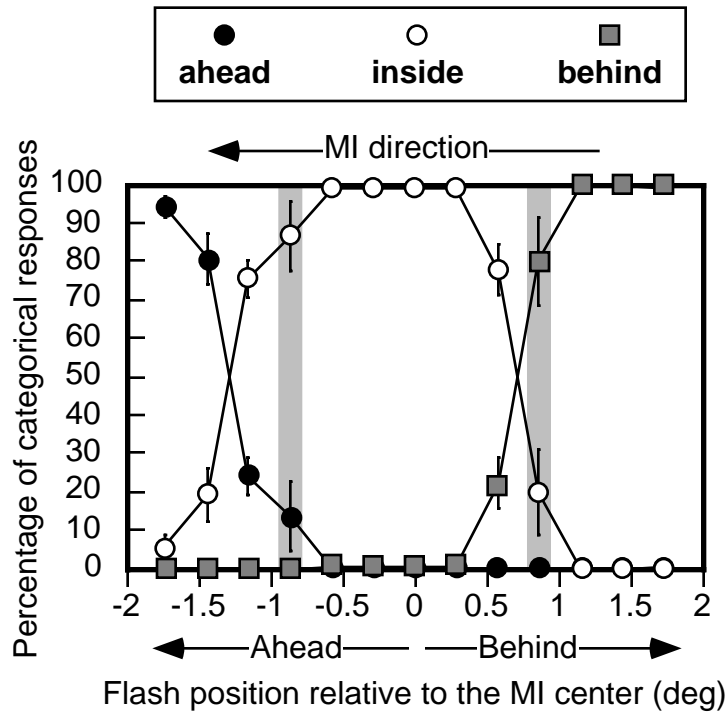
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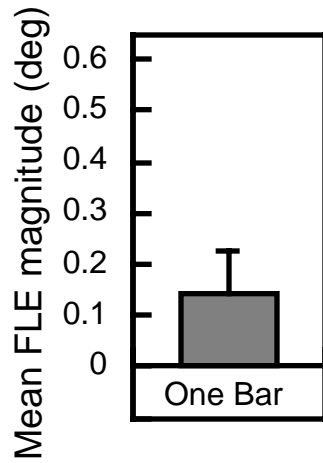
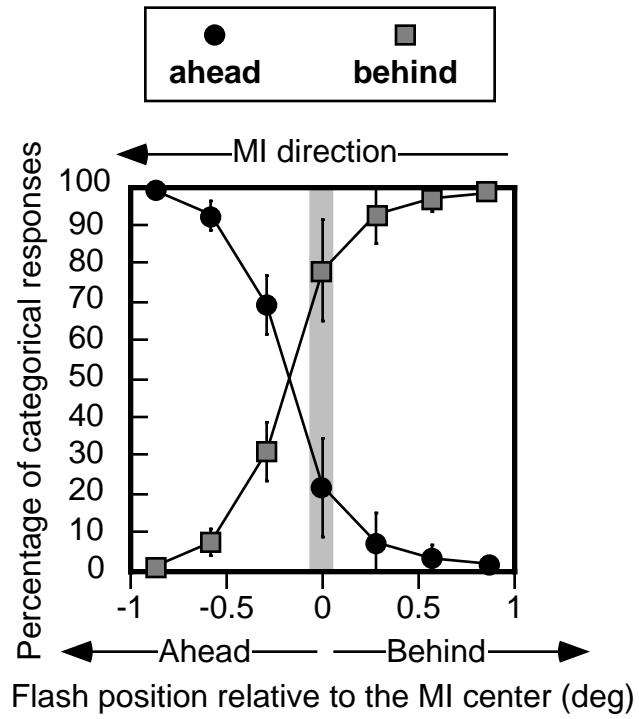
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Figure 3



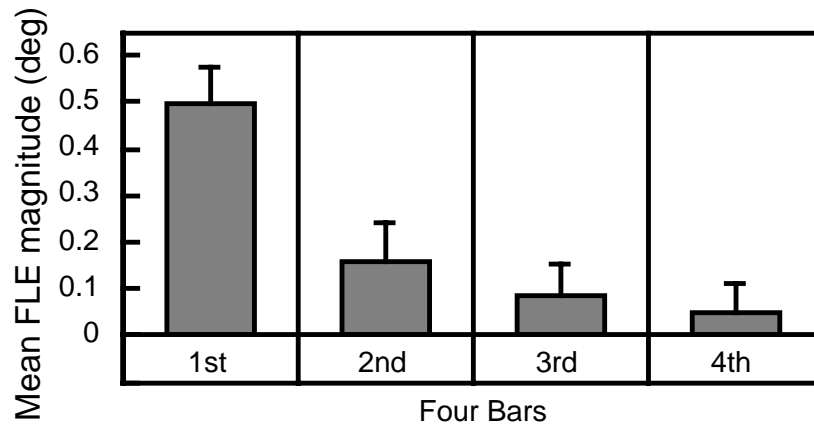
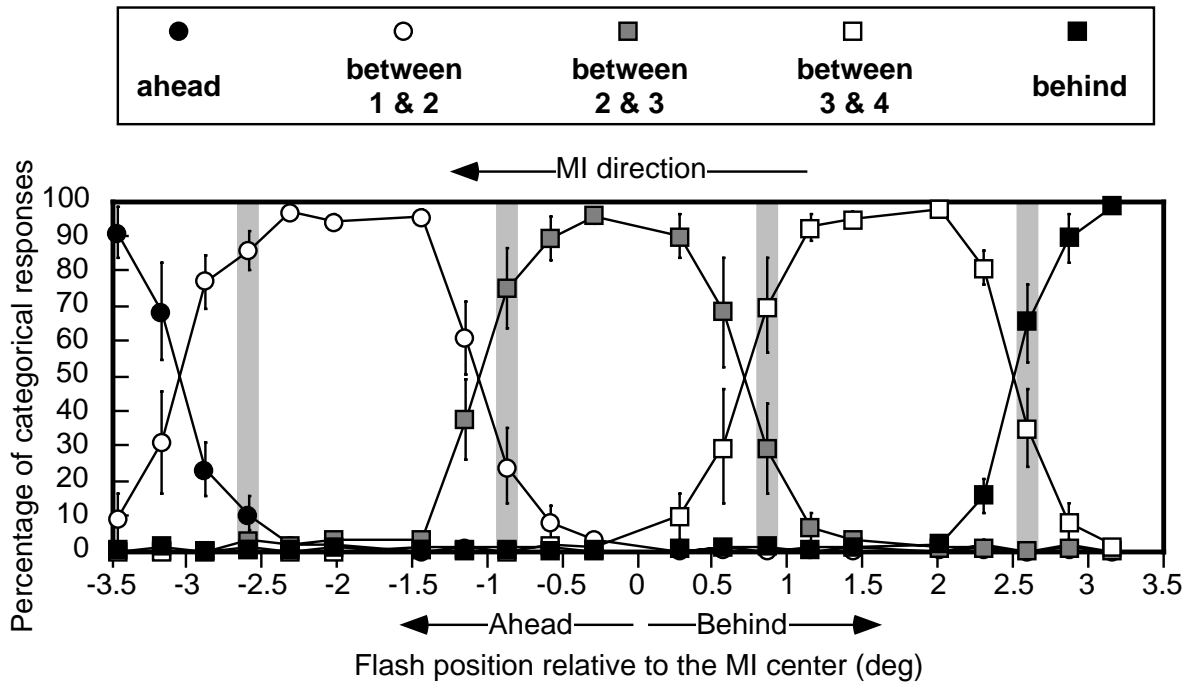
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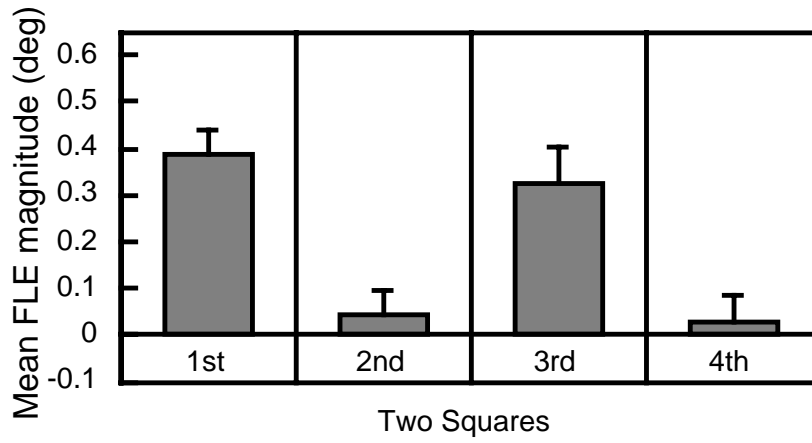
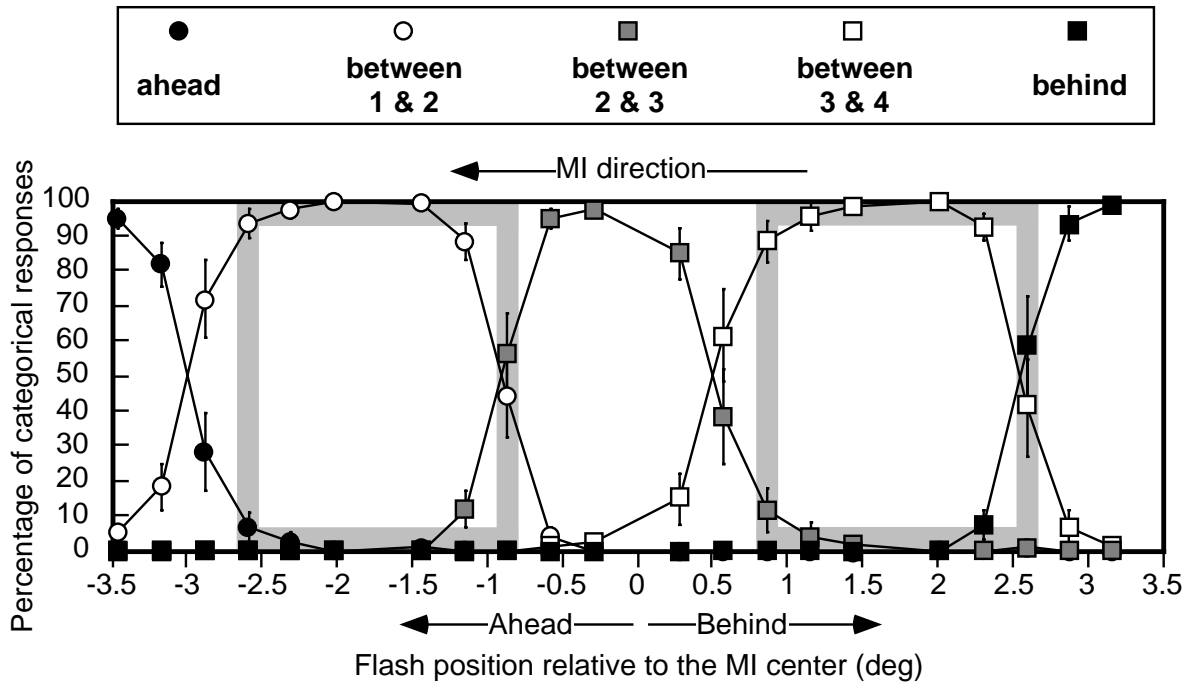
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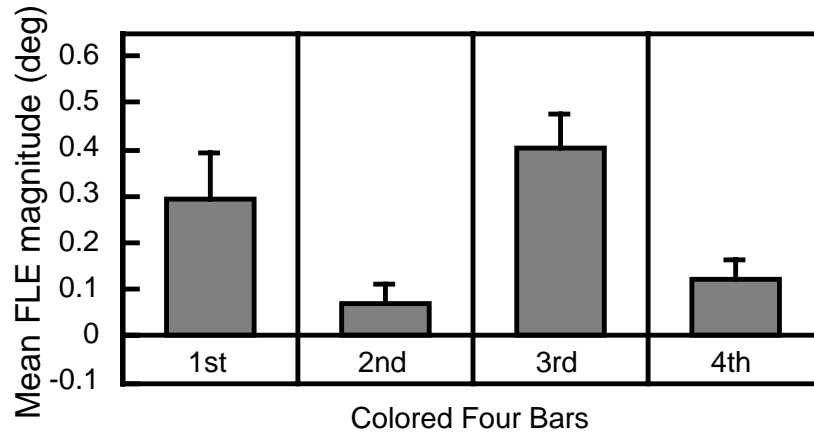
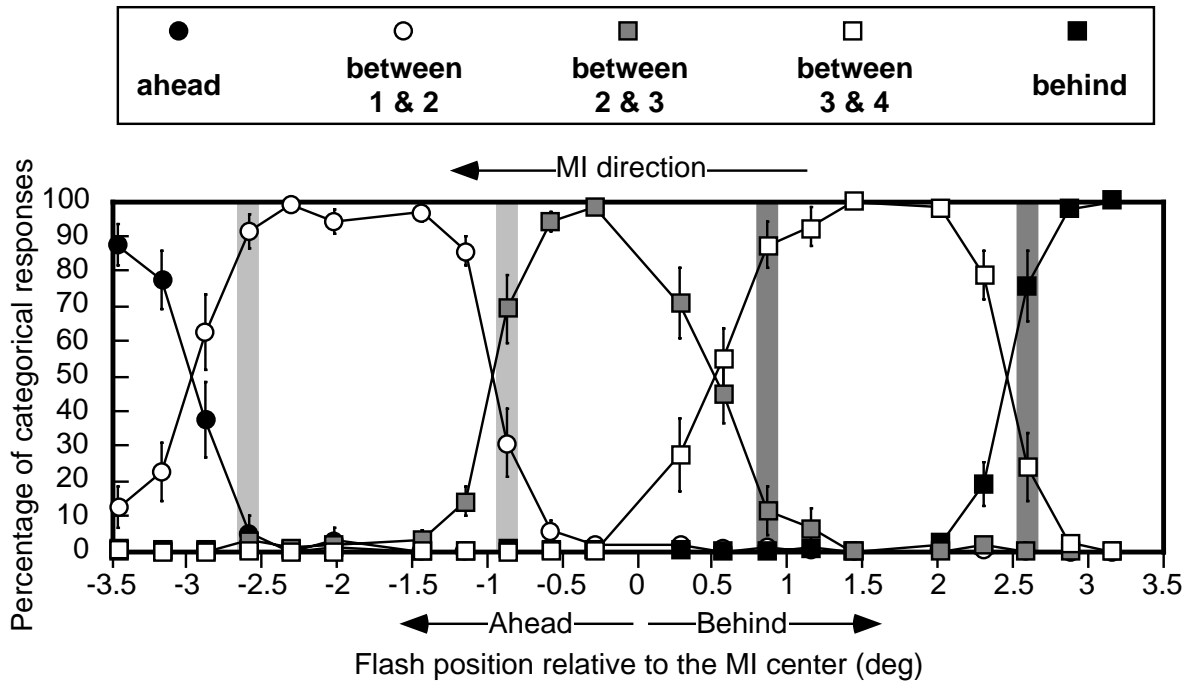
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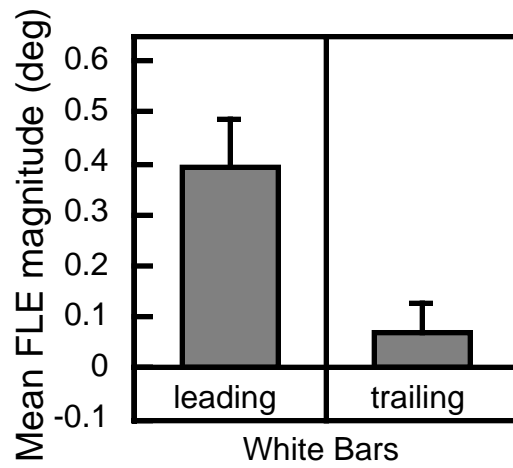
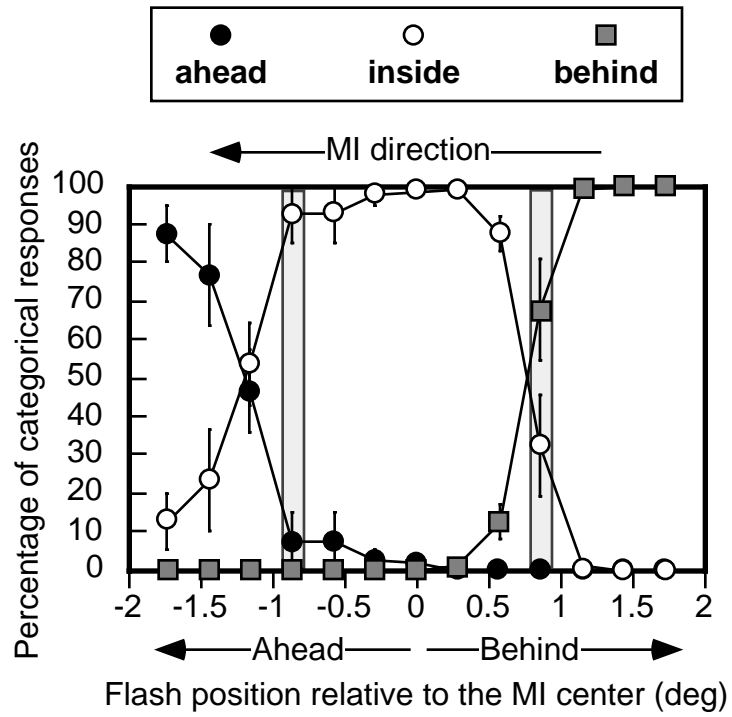
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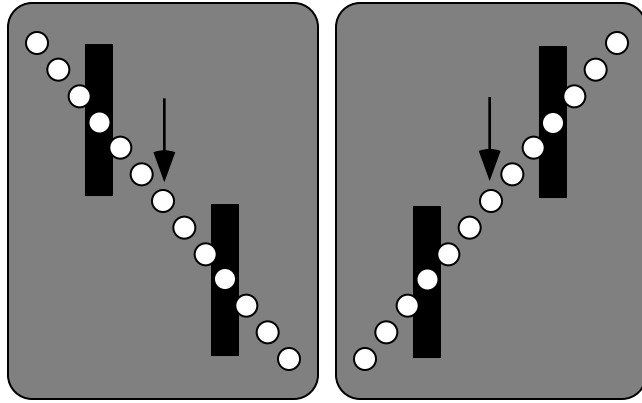
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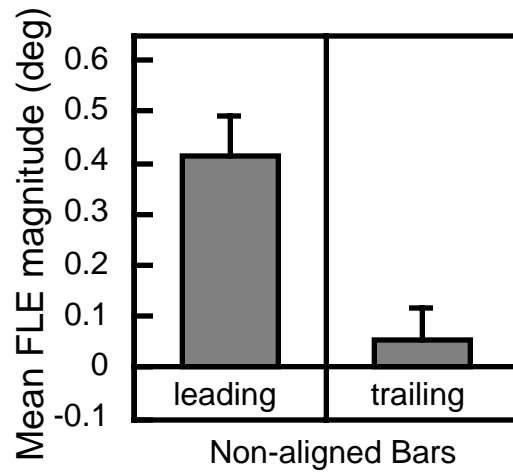
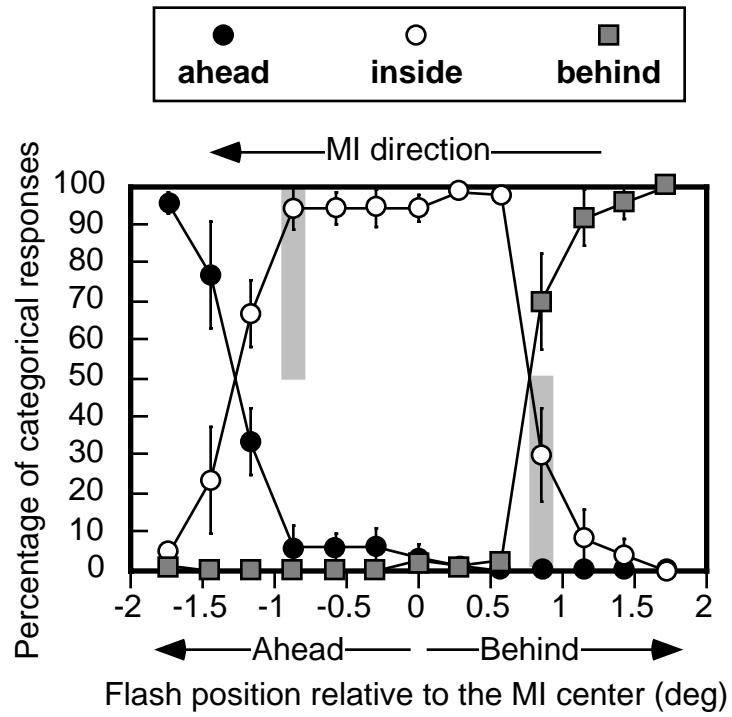
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Figure 9



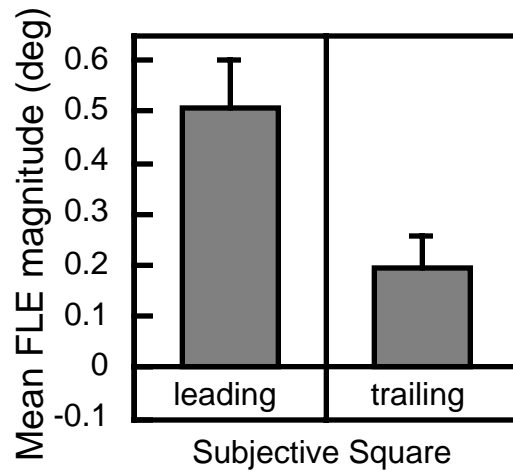
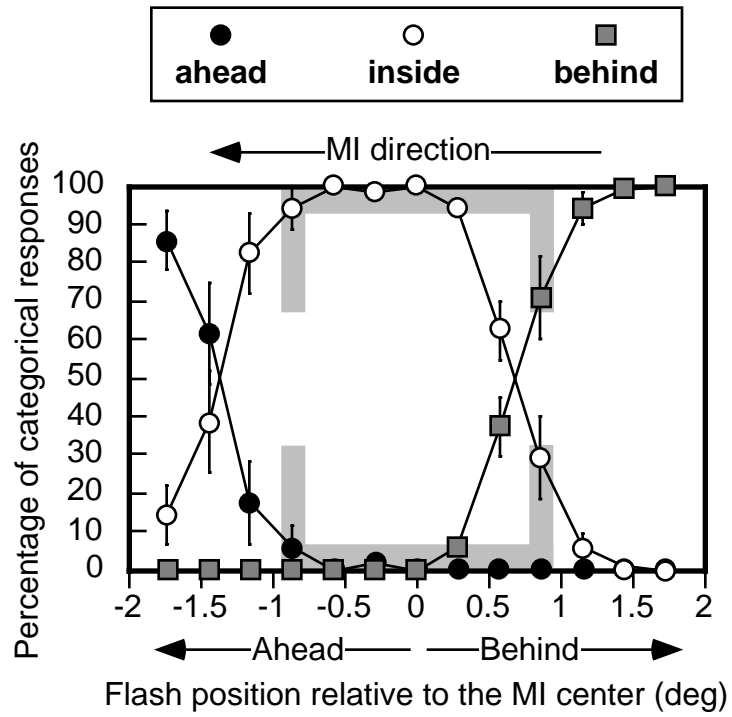
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**Figure 10**



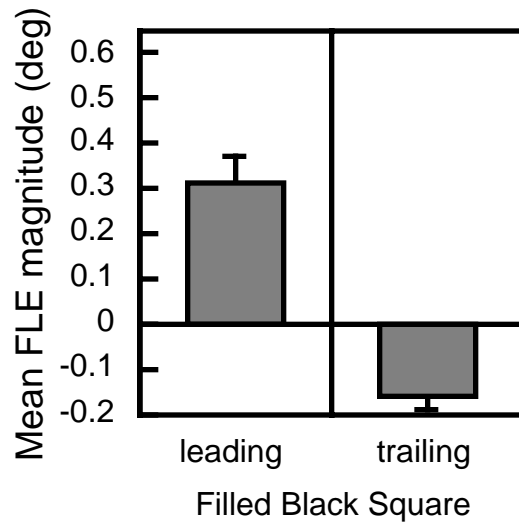
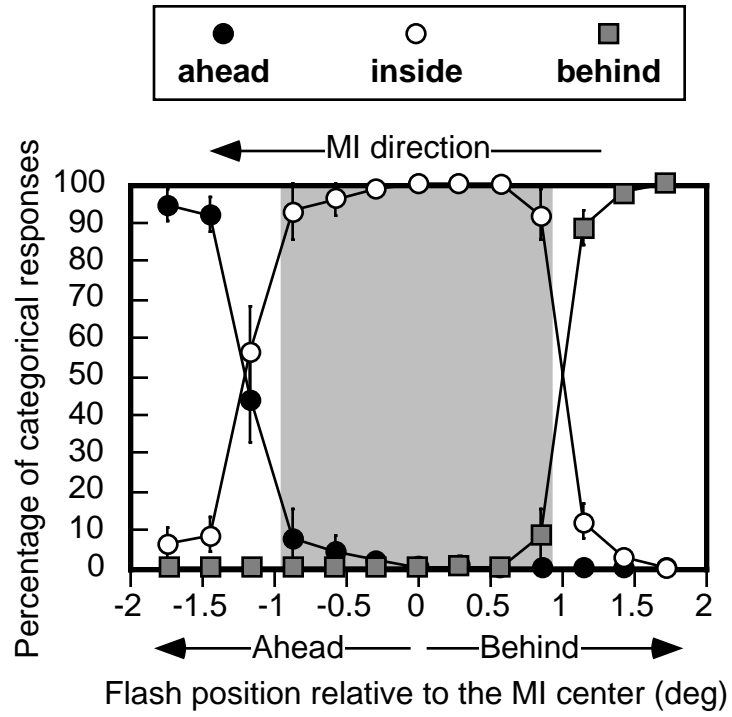
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**Figure 11**



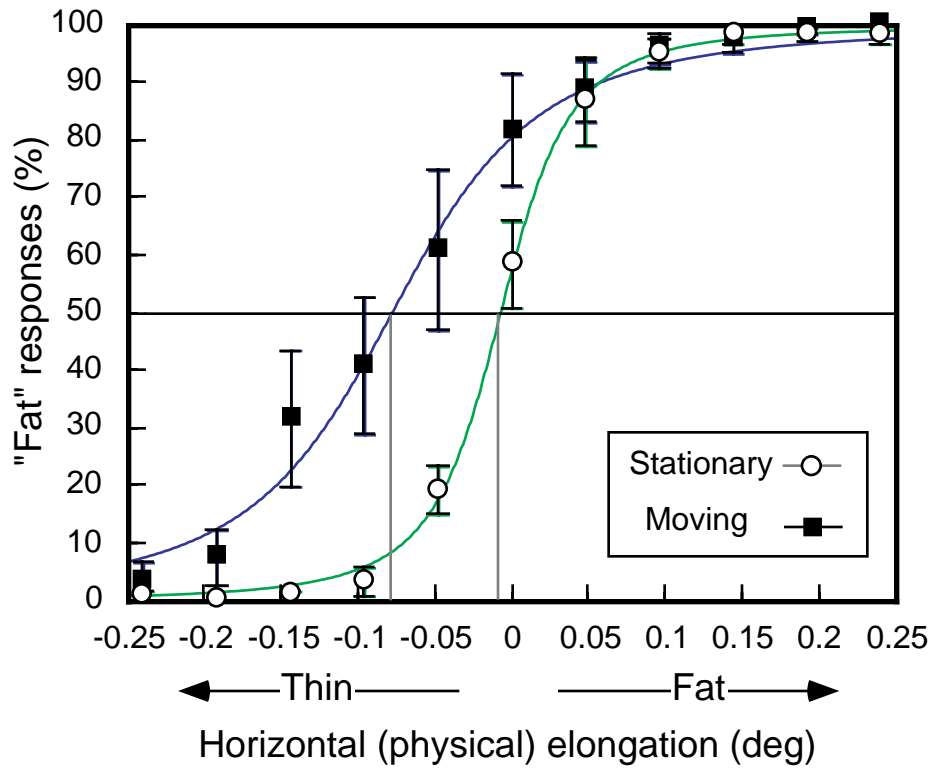
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**Figure 12**



**Watanabe et al.**  
**Figure 13**



**Watanabe et al.**  
**Figure 14**



**Watanabe et al.**  
**Figure 15**