A flash-drag effect in random motion reveals involvement of preattentive motion processing

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The flash-drag (FDE) effect refers to the phenomenon in which the position of a stationary flashed object in one location appears shifted in the direction of nearby motion. Over the past decade, it has been debated how bottom-up and top-down processes contribute to this illusion. In this study, we demonstrate that randomly phase-shifting gratings can produce the FDE. In the random motion sequence we used, the FDE inducer (a sinusoidal grating) jumped to a random phase every 125 ms and stood still until the next jump. Because this random sequence could not be tracked attentively, it was impossible for the observer to discern the jump direction at the time of the flash. By sorting the data based on the flash's onset time relative to each jump time in the random motion sequence, we found that a large FDE with a broad temporal tuning occurred around 50 to 150 ms before the jump and that this effect was not correlated with any other jumps in the past or future. These results suggest that as few as two frames of unpredictable apparent motion can preattentively cause the FDE with a broad temporal tuning.

Keywords: motion, position perception, flash drag, binding

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Introduction

Localizing the positions of surrounding objects is vital: Precise position information is always required to make accurate reaching and eye movements toward any target. How does our visual system know the objects' positions? That the visual system is carrying out far more complicated computations than simply accessing retinal coordinates of each object at each instant is exemplified by many visual phenomena. Of particular interest is that the perceived position of an object can be influenced by visual motion and often deviates from the position predicted from the retinal coordinates of the object (De Valois & De Valois, 1991; Nijhawan, 1994; Ramachandran & Anstis, 1990; Whitney & Cavanagh, 2000; see also a review by Whitney, 2002). Therefore, it seems that the visual system takes into account the visual motion information in the scene when localizing objects, especially when these objects appear so brief or blurry that their retinal images yield only impoverished position signals. The flash-drag effect (FDE) is one of these phenomena. In the FDE, the position of a stationary flashed object in one location appears shifted in the direction of motion in another location in the visual field (Whitney & Cavanagh, 2000). Over the past decade, several researchers have investigated the motion processing responsible for the FDE and most of these studies have emphasized the contribution of high-level or top-down motion processing to the FDE. For example, Scarfe and Johnston (2010) showed that the FDE is caused by global motion that is detected at the stage where multiple local motion components are integrated. Watanabe (2005) found that the FDE does not occur when the motion information is suppressed by binocularly competing stimulus. Watanabe, Nijhawan, and Shimojo (2002) showed that when an object moves horizontally behind a slit from which subjects can see only 1 pixel vertical line of the object, the apparent position of a flash presented around the object is shifted horizontally to the direction of the object's motion. The FDE also occurs during transformational apparent motion, an illusion of motion without any real change in position over time (Whitney, 2006). Watanabe, Sato, and Shimojo (2003) further showed that the FDE can be induced even by a moving object that is completely invisible behind an occluding surface. In these three cases, subjects inferred the object's motion behind the occluding surface although there was no real directional motion. Thus, these results suggest that low-level motion is not necessary and that high-level motion analysis is important for the FDE. Shim and Cavanagh (2004) presented a flash around bistable quartet motion and measured the FDE, and they also found that the perceived position of the flash presented around the bistable quartet motion was significantly shifted in the

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perceived apparent motion direction and not shifted in the other possible motion direction. Shim and Cavanagh (2005) and Tse, Whitney, Anstis, and Cavanagh (2011) investigated whether attention plays a major role in the occurrence of the FDE. In both cases, the FDE was consistent with the attended direction of motion, suggesting that attention-based motion processing (Cavanagh, 1992; Lu & Sperling, 1995) is sufficient or perhaps even responsible for the FDE.

Together, these accumulating results show that there is a strong contribution of top-down or attention-based motion processing to the FDE, but there still remains a question as to whether motion information mediated only by a low-level motion mechanism can induce an FDE. To shed some light on this question, we used random motion (cf. Murakami, 2001a) as an inducer of the FDE in this study. In the random motion sequence, a moving stimulus randomly displaces its position at a very rapid rate. Because the moving stimulus unpredictably changes its motion direction and velocity, it is impossible to track this random motion attentively or to attend to each motion direction reliably. Thus, one can exclude the contribution of any attention-based motion mechanism by using the random motion. In Experiment 1, we used the random motion and found that it indeed produced an FDE. In addition, we obtained the temporal tuning of the FDE by appropriately sorting the data based on the flash's onset time relative to the random motion sequence. In Experiment 2, we isolated two-frame apparent motion stimuli from the random motion sequence we used previously and measured the FDE again. Under this condition (unlike in the random motion condition), subjects could easily identify the direction of motion. Thus, the top-down motion mechanism should also mediate the FDE in this situation. The results of both experiments suggest that the FDE involves preattentive motion processing but that top-down processes may also be involved in modulating the FDE.

Experiment 1: The FDE in random motion

Methods

Subjects

Three subjects unaware of the purpose of the experiment and the first author (aged 18–24) participated in the study. All had normal or corrected-to-normal visual acuity.

Apparatus

The stimulus was presented in a dark room on a CRT monitor (Mitsubishi Electric RDF223H, 1024 × 768 pixels, mean luminance of 46.3 cd/m^2). The refresh rate of the monitor was 120 Hz, so whenever the time dimension is henceforth described in terms of "frames," one frame corresponds to 8.33 ms. Each subject placed his/her head onto a chin rest and used both eyes to view the stimulus. The viewing distance was 57.3 cm.

Stimuli

A schematic of the stimulus configuration is shown in Figure 1. A fixation point (a bull's-eye) was presented at the center of the display throughout the experiment. Two oppositely moving sinusoidal gratings (both had 0.33 cpd spatial frequency, 99% contrast) were used as the "inducer" of the FDE. Each grating occupied a rectangular region subtending 3.5 deg × 40 deg and was centered at 2.8 deg to the left and right of the fixation point. Outside of the gratings, a pair of Gaussian blobs, hereafter termed the "flash," was simultaneously presented for one frame (center-to-center distance was 11.5 deg when aligned; the *SD* of each Gaussian was 0.24 deg). The averaged vertical position of the two blobs was chosen randomly within the range of ±0.5 deg around the fixation point to prevent the subject from judging the offset direction based on the relationship between the central fixation point and either one of the two blobs.

Procedure

The sinusoidal phase of the inducer was randomly shifted every 15 frames. The two gratings simultaneously shifted their phases and the phase shift of the right-hand

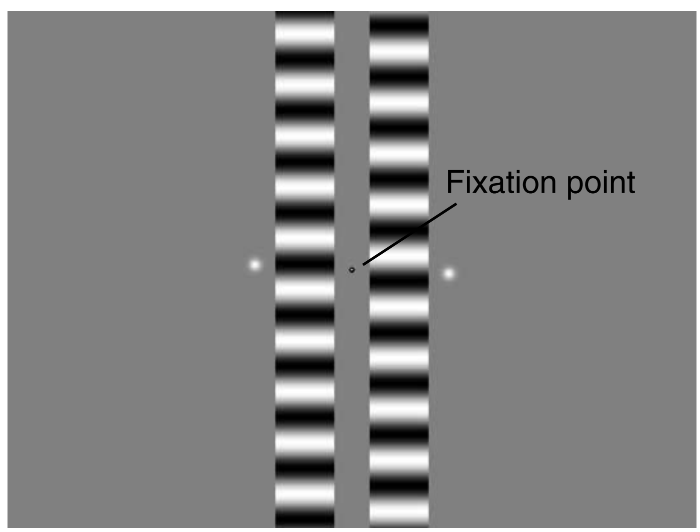

Figure 1. Schematic of the stimulus configuration. Two sinusoidal gratings were used as the inducer of the FDE. The inducer's phase was randomly shifted every 15 frames (1 frame = 8.33 ms). At a random timing, a pair of Gaussian blobs was presented as a flash.

grating was always in the opposite direction and by the same size compared with that of the left-hand grating; hence, their movements were rotation symmetric to each other. The flash was presented at a random timing (with the interflash interval within the range of 360 ± 120 frames). The vertical offset between the two flashes was randomly chosen from five distances (the range of distance was optimized for each subject) for every presentation. After the presentation of the flash, the subject performed two tasks. In the first task named the "flash-direction task," the subject judged whether the right-hand blob appeared above or below the left-hand blob. The next task called the "jump-direction task" was to judge which direction the inducer appeared to move at the instant the flash was presented. Both tasks were performed by pressing one of two keys in a two-alternative forced-choice fashion. The subject's key pressing in response to each flash was accepted until the presentation of the next flash. Such trials were repeated 2800 to 3000 times for each subject through 28 to 30 sessions, each lasting about 5 min.

A correlogram was drawn for visualizing the temporal tuning of the FDE. Schematic of the procedure of making the correlogram is shown in Figure 2. First, we categorized all of the inducer's random phase shifts into four categories: upward jump (phase shifts within the range of 30° to 150°), downward jump (phase shifts within the

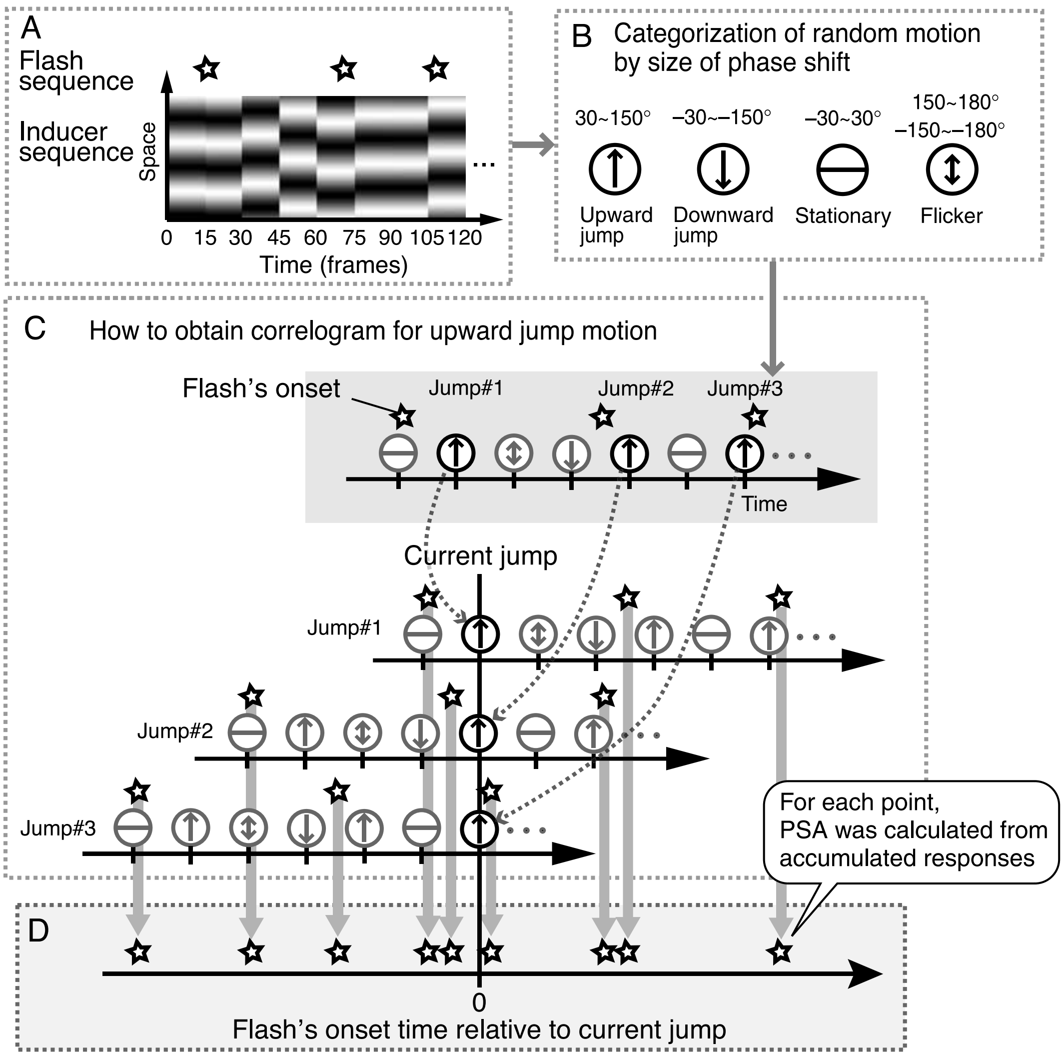

Figure 2. Schematic of the procedure of making the correlogram. (A) An example of the spatiotemporal plot of the inducer's random motion sequence and the temporal plot of the flash sequence (for illustrative purposes, the scheme looks as if the flash occurred in very rapid succession; actual interflash interval was chosen from the range of 360 ± 120 frames). After the presentation of each flash (indicated by each star symbol), the subject judged the flash position and the inducer's motion direction. (B) In the analysis, we categorized all of the inducer's random phase shifts into these four categories. (C) To make a correlogram for "upward jump," all the responses were replotted based on the flash's onset time (star symbols) relative to the "current" upward jump. (D) The correlogram of the FDE was obtained by calculating the point of subjective alignment (PSA) from the accumulated responses at each point in time relative to the "current jump."

range of −150° to −30°), stationary (phase shifts within the range of −30° to 30°), and flicker (phase shifts within the range of 150° to 180° and −180° to −150°). Second, we sorted all of the responses of the flash-direction task based on the flash's onset time relative to the "upward jump" or "downward jump." Each flash's onset time relative to each jump is hereafter referred to as the "stimulus onset asynchrony" (SOA). Phase shifts classified as "stationary" and "flicker" were considered as not having dominant motion information and were ignored from the analysis. For each SOA, the point of subjective alignment (PSA), namely, the physical alignment corresponding to the 50% point of a psychometric function, was obtained by the maximum likelihood estimation based on the data of the method of constant stimuli. We merged responses to flashes presented at each SOA, at one frame before that SOA, and at one frame after that SOA to estimate more robust psychometric functions representing the behavior at that SOA. We derived a PSA from a psychometric function at each SOA when a downward jump occurred at time 0, derived another PSA from another psychometric function at the same SOA when an upward jump occurred at time 0, and halved the distance between the two PSAs to represent the misalignment of the flash at that SOA that occurred in relation to the current jump at time 0. The same procedure was repeated for all SOAs. As there was no correlation between successive phase shifts, the correlogram of the FDE should stay at zero if the flashes are too far in the past or future compared with the current jump. Any change above or below zero should be ascribable to the pure effect of the current jump.

Results and discussion

The data are shown in Figure 3, plotted separately for each subject. The positive misalignments indicate that the flashed blobs appeared to shift their positions in the same direction as the current jump of the inducer grating that occurred at time 0. The negative and positive SOAs indicate the flashes physically presented before and after, respectively, the current jump of the inducer at time 0. Note that these misalignments were only correlated with the current jump because the phase offsets of the inducer grating occurred completely randomly. If the jump of the inducer grating phenomenally dragged only the simultaneously

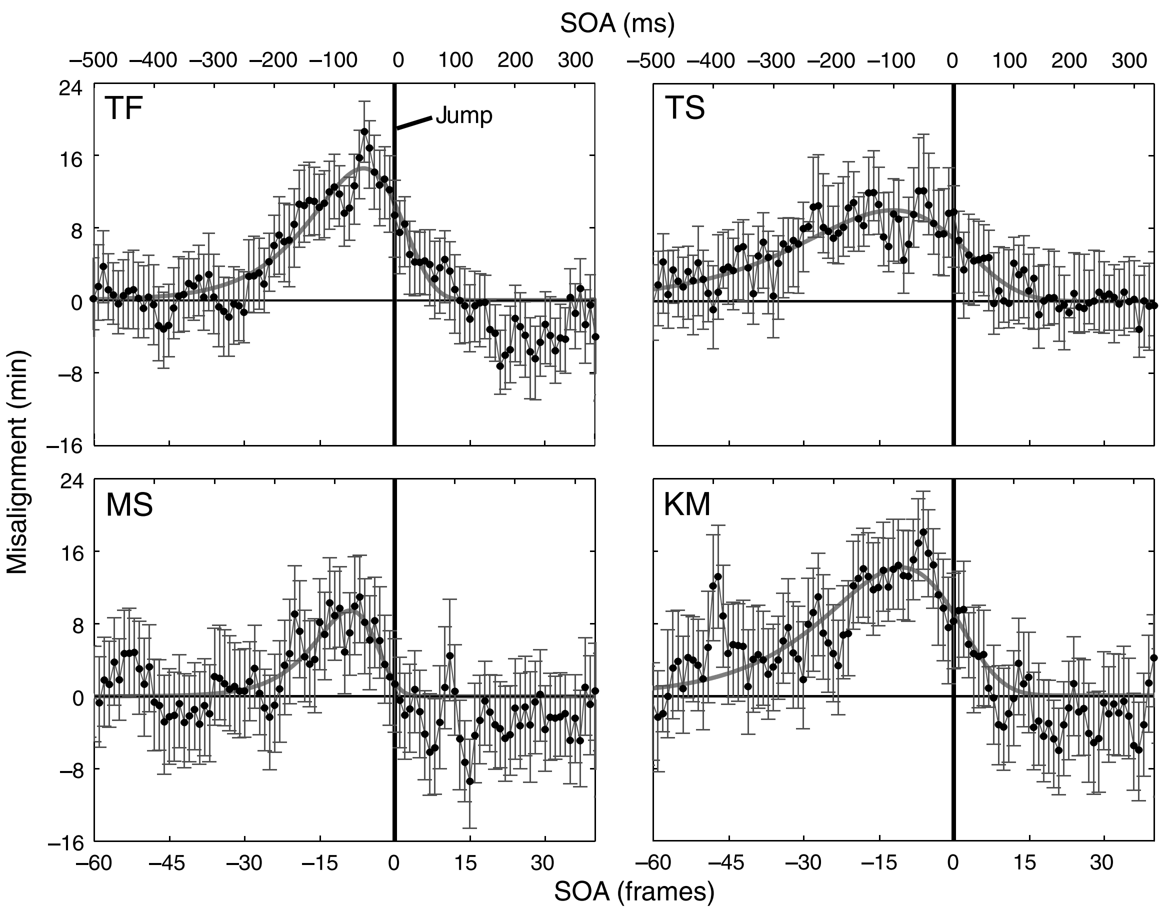

Figure 3. The FDE plotted as a function of SOA. The filled circles indicate actual data. Error bars show 95% confidence interval. The solid curve indicates the best-fit model according to the extreme value distribution.

presented flash in the jump direction, we would obtain a positive misalignment at time 0 and zero alignment at all other SOAs. However, if the FDE is not so severely time-locked, we might obtain a temporally distributed profile of the FDE indicating the time window within which the current jump is influential.

That is exactly what we found. A large FDE (i.e., positive misalignment) with a broad temporal tuning occurred 50 to 150 ms before the current jump and the temporal tuning seemed to have an asymmetric form: large broadening in the past direction and relatively small broadening in the future direction. Individual data showed similar tendency. This pattern of asymmetry has also been seen in the previous FDE studies (Durant & Johnston, 2004; Shim & Cavanagh, 2005; Watanabe et al., 2003). Thus, we used the extreme value distribution rather than the Gaussian curve as a model to characterize the temporal tuning of the FDE. The model we used was formulated as

$$f(t) = s \times P(t; \mu, \sigma), \tag{1}$$

where $P(t;\ \mu,\ \sigma)$ denotes the probability density function of the extreme value distribution, which is defined as

$$P(t; \mu, \sigma) = \sigma^{-1} \exp\left(\frac{t-\mu}{\sigma}\right) \exp\left(-\exp\left(\frac{t-\mu}{\sigma}\right)\right), \tag{2}$$

t represents SOA, and s is a proportionality coefficient that scales the overall magnitude of the FDE. The solid curve in Figure 3 was obtained by fitting this model to the data for each subject. The best-fit parameters were (μ, σ) = (−51.5, 74.1) ms for subject TF, (μ, σ) = (−101.9, 133.7) ms for subject TS, (μ, σ) = (−74.1, 50.9) ms for subject MS, (μ, σ) = (−86.9, 106.7) ms for subject KM. The R^2 values of the fit were 0.767 for subject TF, 0.794 for subject TS, 0.478 for subject MS, and 0.706 for subject KM.

Because the random motion sequence could not be tracked attentively, the results obtained here indicate that preattentive motion processing can cause an FDE with substantially broad temporal tuning. Indeed, the responses

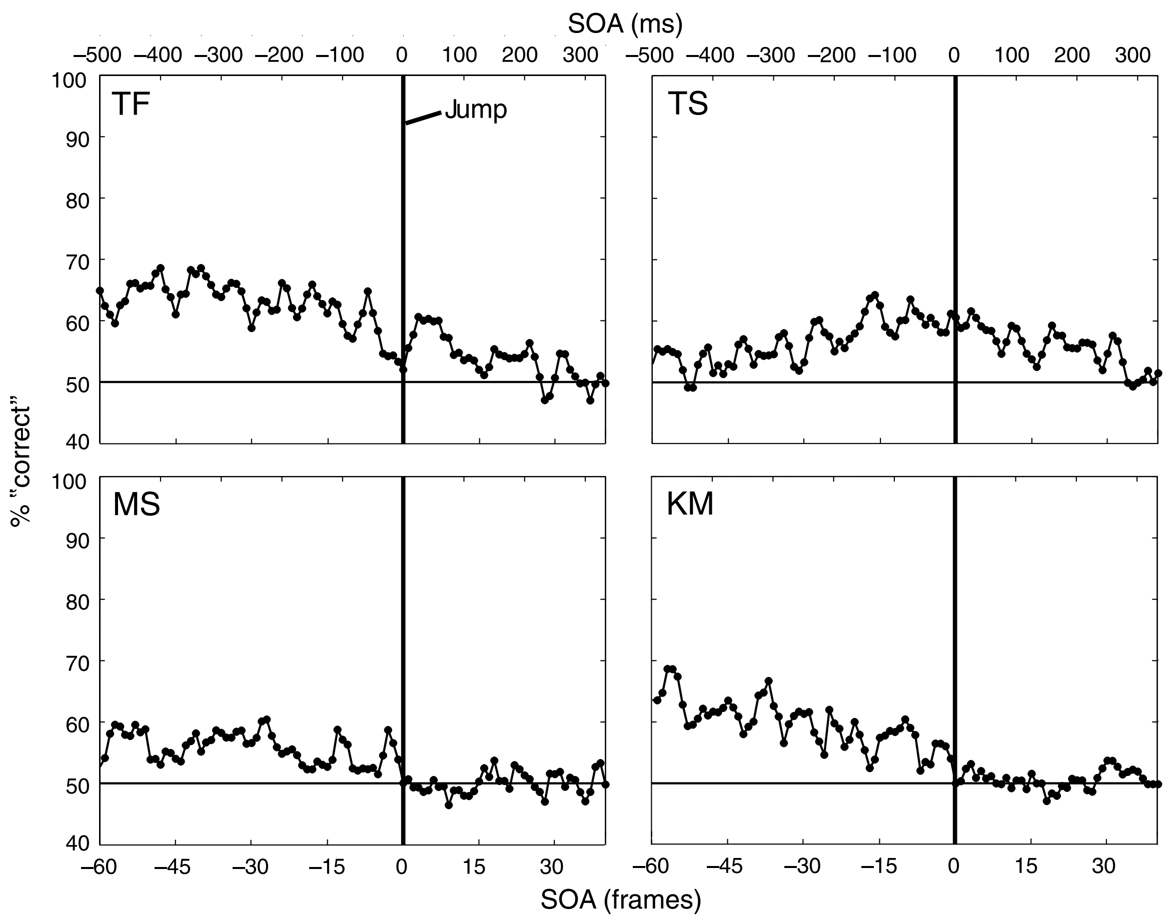

Figure 4. The percentage of "correct" responses for the jump-direction task plotted as a function of SOA. A "correct" response indicates that a subject's judgment agreed with the current jump direction and does not mean that it agreed with the jump closest to the flash. For example, a response was counted as "correct" if the subject's judgment agreed with the current jump even when the flash was presented 45 frames before the current jump (SOA = −45) or 30 frames after the current jump (SOA = 30).

of the jump-direction task did not correlate with those of the flash-direction task (Figure 4). In Figure 4, the percentage of trials in which the response of the jump-direction task was "correct" with respect to the current jump is plotted as a function of SOA. The percentage of "correct" responses fluctuated around 50 to 60% for all subjects and the patterns of the fluctuation were very dissimilar to those of the FDE in Figure 3. Thus, the influence of the current jump on the flash misalignment in the direction of the FDE occurred independently even though the subject could not consciously individuate the jump that was seen simultaneously with the flash. However, there was a possibility that the subject could correctly guess the motion direction in a small subset of trials, in which case the subject may have exhibited some bias in flash misalignment in favor of the FDE. To see more clearly whether the subject's reports on jump directions were correlated with the amplitude and the temporal tuning of the FDE, we separated the responses of the flash-direction task depending on whether the response of the jump-direction task in the same trial was correct with respect to the current jump direction and obtained two temporal tunings of the FDE, each derived from "correct" trials and "incorrect" trials. The results (a representative result is shown in Figure 5) are odd at first sight because the estimated FDE from "correct" and "incorrect" trials are very similarly shaped but are vertically shifted from each other at all SOAs (including extreme SOA conditions). This vertical shift would naturally result from the subjects' strategy or tendency to make the same report for the jump-direction task as the flash-direction task. That is, when uncertain, there was a bias to report that the motion was consistent with the perceived flash misalignment. Because the jump-direction task was very difficult (near chance performance), it is likely that the subjects adopted some criterion to report consistent. If the subjects have such a bias, the correlation between the responses of FDE direction and those of jump direction will become necessarily higher (vertically shifted) irrespective of the actual FDE. To verify this idea, we conducted a chi-square test and found a significant correlation between the perceived offset direction of the flash pair and reported jump direction of the inducer. This happened for each vertical offset condition, and for each subject, indicating a uniform bias. Chi-square values for each vertical offset conditions were $\chi^2(1) = 83.2$ ($p < 0.01$), $\chi^2(1) = 197.8$ ($p < 0.01$), $\chi^2(1) = 90.6$ ($p < 0.01$) for subject TF; $\chi^2(1) = 427.2$ ($p < 0.01$), $\chi^2(1) = 497.5$ ($p < 0.01$), $\chi^2(1) = 454.2$ ($p < 0.01$) for subject TS; $\chi^2(1) = 95.7$ ($p < 0.01$), $\chi^2(1) = 298.3$ ($p < 0.01$), $\chi^2(1) = 158.3$ ($p < 0.01$) for subject MS; $\chi^2(1) = 129.0$ ($p < 0.01$), $\chi^2(1) = 247.2$ ($p < 0.01$), $\chi^2(1) = 152.8$ ($p < 0.01$) for subject KM. Thus, we employed the average of the data from 80- to 120-frame SOAs as baselines and subtracted these baselines from each of the "correct" and "incorrect" profiles (Figure 6). The solid line represents the data from "correct" trials and the broken line represents the data from "incorrect" trials. Neither the amplitude relative to the baseline nor the temporal tuning was different between the profiles for the "correct" and "incorrect" trials. In other words, the FDE did not correlate with jump-direction judgment. Thus, the possibility that the flash drag occurred only when the subject could attentively track the jump direction is excluded. This demonstrates that the FDE in random motion was caused by preattentive motion processing.

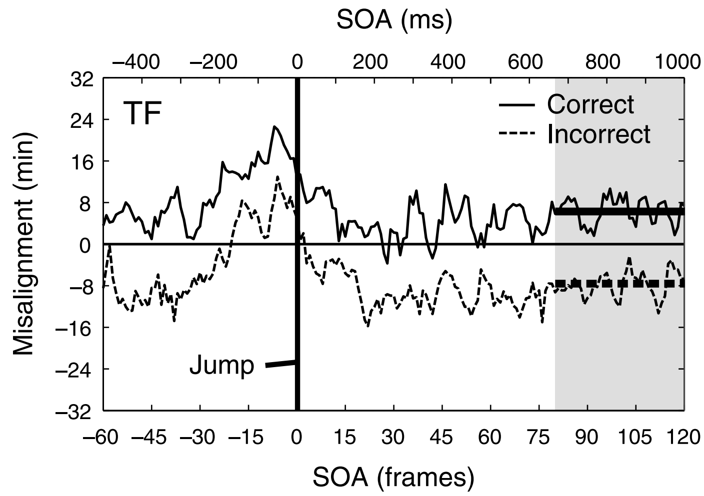

Figure 5. The FDE obtained only from "correct" trials or "incorrect" trials plotted as a function of SOA (only subject TF's result is shown as a representative). The solid line represents the FDE profile calculated only from those trials in which the subject could report "correctly" the jump direction. The broken line represents the FDE profile calculated only from those trials in which the subject could not report "correctly" the jump direction. The difference of the FDE between these two conditions is not surprising, as it naturally results from the subject's bias in the jump-direction task; it does not reflect a difference in the temporal tuning of the actual FDE. Thus, we employed the average of the data of 80- to 120-frame SOAs (the range shown as gray field) for the baseline. The thick solid line and the thick broken line in the gray field represent the baseline for "correct" profile and the baseline for "incorrect" profile, respectively. We subtracted these values from each data of "correct" and "incorrect" profiles, which are plotted in Figure 6.

In the jump-direction task, however, subjects might not individuate a jump that was closest to the flash's onset even if they could attentively track the inducer motion since it is known that temporal relationship between an event in the sequence and another event occurring outside the sequence is difficult to judge even when the sequence change is slow enough to recognize the individual sequence events (Fujisaki & Nishida, 2010; Reeves & Sperling, 1986). Therefore, the result of the jump-direction task alone cannot necessarily indicate that the FDE does not require attentive tracking process. As a more direct testing to rule out the possibility that the FDE occurred only when the subjects could attentively track the inducer, we

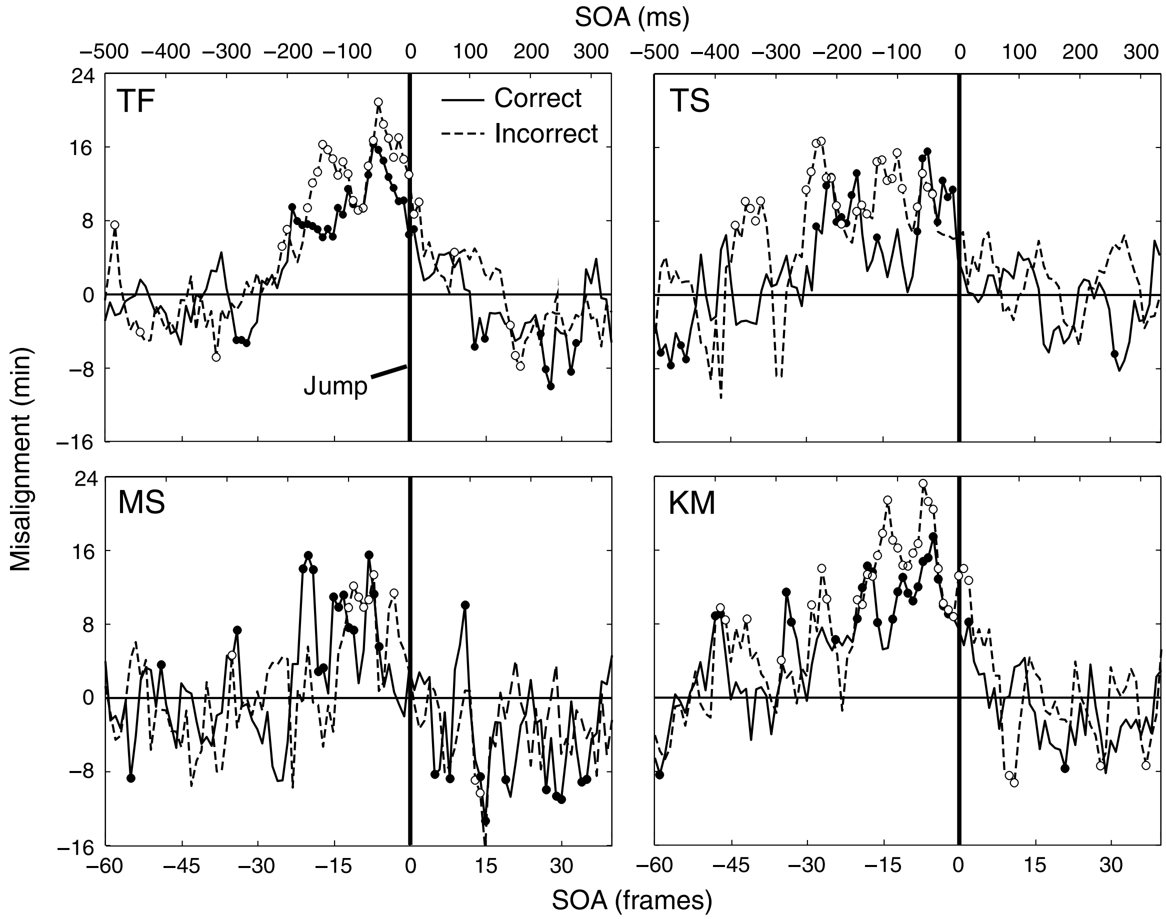

Figure 6. The FDE profiles normalized to the baseline that is calculated as the average of the data of 80- to 120-frame SOAs (Figure 5). The solid line represents the data from "correct" trials and the broken line represents the data from "incorrect" trials. The filled circles on the solid line and the open circles on the broken line represent data points that are significantly larger or smaller than each baseline.

examined whether there was any interaction in the FDE size between two successive jumps. If the subjects could attentively track the inducer only when the inducer happened to jump twice in the same direction successively, and if the FDE occurred only in such cases, a strong interaction would be observed. Thus, we sorted the data depending on whether the next jump just after the current jump occurred in the same direction (referred to as "same-as-current" trials) or occurred in the opposite direction (referred to as "opposite-to-current" trials) compared with the current jump direction. The data from "same-as-current" trials are plotted as filled circles, whereas the data from "opposite-to-current" trials are plotted as open circles (Figure 7). If there was no interaction, the data would be equivalent to linear summation of an FDE profile correlated with the current jump and an FDE profile correlated with the next jump. More specifically, the results would be described as the sum of the profile shown in Figure 3 and the same profile temporally shifted to the future by 15 frames (i.e., a jump-to-jump interval), in the "same-as-current" case. In the "opposite-to-current" case, the results would be described as the sum of the profile shown in Figure 3 and the same profile temporally shifted to the future by 15 frames and vertically flipped with respect to the zero misalignment level. The actual data indeed supported the linear prediction. For all subjects, "same-as-current" and "opposite-to-current" data were perfectly explained by the linear summation of the correlogram for the current jump at time 0 and that for the next jump (the solid line in Figure 7 represents the prediction for "same-as-current" and the broken line in Figure 7 represents the prediction for "opposite-to-current"), which means that no interaction between two successive jumps was observed and that every jump induced the FDE independently of each other. Therefore, it is concluded that two-frame apparent motion is sufficient to preattentively induce an FDE with a broad temporal tuning.

Experiment 2: The FDE in two-frame apparent motion

Is there any difference between the FDE mediated only by preattentive processing and that also mediated

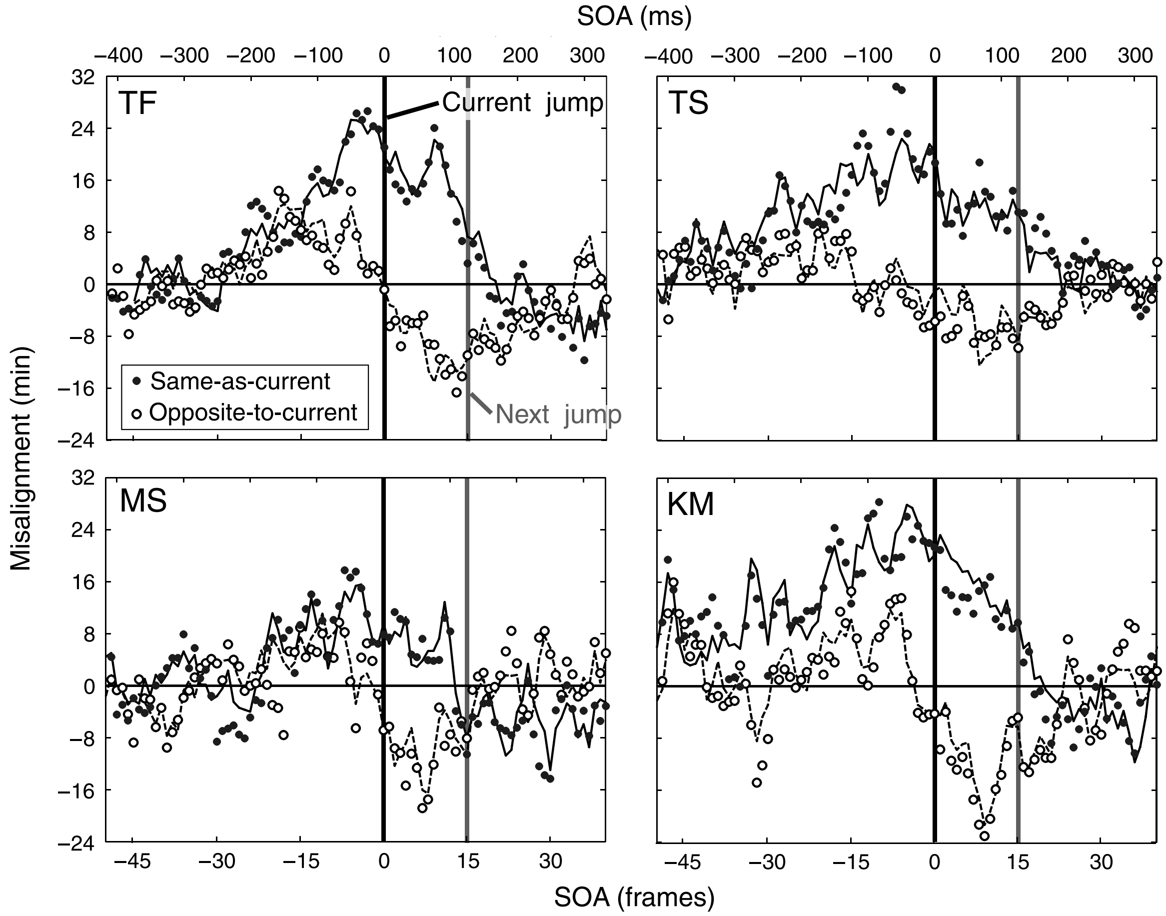

Figure 7. The FDE obtained from "same-as-current" trials and "opposite-to-current" trials plotted as a function of SOA. The original data were sorted depending on whether the jump occurred in the same direction ("same-as-current") or occurred in the opposite direction ("opposite-to-current"). The filled circles indicate the actual data from "same-as-current" trials. The open circles indicate the actual data from "opposite-to-current" trials. The solid and broken curves represent the predictions for the "same-as-current" and "opposite-to-current" data, respectively. Each prediction was the linear summation of the correlogram calculated for the current jump at time 0 and that calculated for the next jump.

by top-down motion processing? To examine this, we isolated two-frame apparent motion pairs from the random motion sequence we used in Experiment 1 and measured the FDE by presenting the flash at various timings relative to the jump. Under this condition, observers could easily individuate the jump that might possibly affect the flash misalignment and could also easily identify the jump direction. Thus, the FDE caused by these apparent motion stimuli would necessarily involve top-down motion processing in addition to the preattentive motion processing that was revealed in Experiment 1.

Methods

Subjects

The same four subjects as in Experiment 1 also participated in Experiment 2.

Apparatus

The same apparatus as in Experiment 1 was also used in Experiment 2.

Stimuli and procedure

The stimulus configuration was the same as in Experiment 1 except that only one jump occurred in one trial. At a random timing within the range of 180 ± 120 frames after the beginning of each trial, the pair of two flashes (the same as in Experiment 1) was presented. The combination of jump size and SOA in each trial was kept the same as those presented in Experiment 1. The absolute phase shift comprising each jump was always within the range of 90 ± 60° as in Experiment 1. Actually, the random sequence of phase shifts generated for each subject in Experiment 1 and stored for offline analysis was read out to generate the stimulus sequence for this experiment, such that only a subset of all the phase shifts was played back, substituting all other phase shifts in the past and future with 0°. Approximately 30% of the combinations of jump and SOA in Experiment 1 were used to produce about 3,300 to 3,600 trials of two-frame apparent motion sequence in Experiment 2. The subject's tasks were also identical to those in Experiment 1; each subject was asked to judge the direction of misalignment between two flashed blobs and to judge the jump direction of the inducer. The subject performed the two tasks successively by pressing one of two keys in a two-alternative forced-choice fashion. These responses triggered the next trial. The inducer was always presented through the experimental session and the subject did not see any motion except the jumps.

Results and discussion

We sorted the data based on SOA and obtained the FDE profile in the two-frame apparent motion. The results are shown in Figure 8. At each SOA, we merged responses of neighboring −2, −1, 0, 1, and 2 frames relative to that SOA to estimate more robust psychometric functions representing the behavior at that SOA. The performance of the jump-direction task was substantially higher than the chance level at all SOAs for all subjects (the correct response rate averaged across all SOAs was 96.5% for subject TF, 97.0% for subject TS, 86.8% for subject MS, and 92.3% for subject KM); thus, when asked to indicate the jump direction of the inducer grating at the instant the flash appeared, the subjects were able to identify the only jump that was present in temporal proximity to the flash and to report its direction much better than chance.

We fitted the same model as in Experiment 1 to the individual data (the solid curve in Figure 8) because the temporal tuning obtained in Experiment 2 seemed to have a qualitatively similar pattern to that obtained in Experiment 1. The best-fit parameters are (μ, σ) = (−38.7, 84.2) ms for subject TF, (μ, σ) = (−63.0, 103.2) ms for subject TS, (μ, σ) = (−65.9, 123.7) ms for subject MS, and (μ, σ) = (−35.7, 99.2) ms for subject KM. The R^2 values of the fit were 0.905 for subject TF, 0.872 for

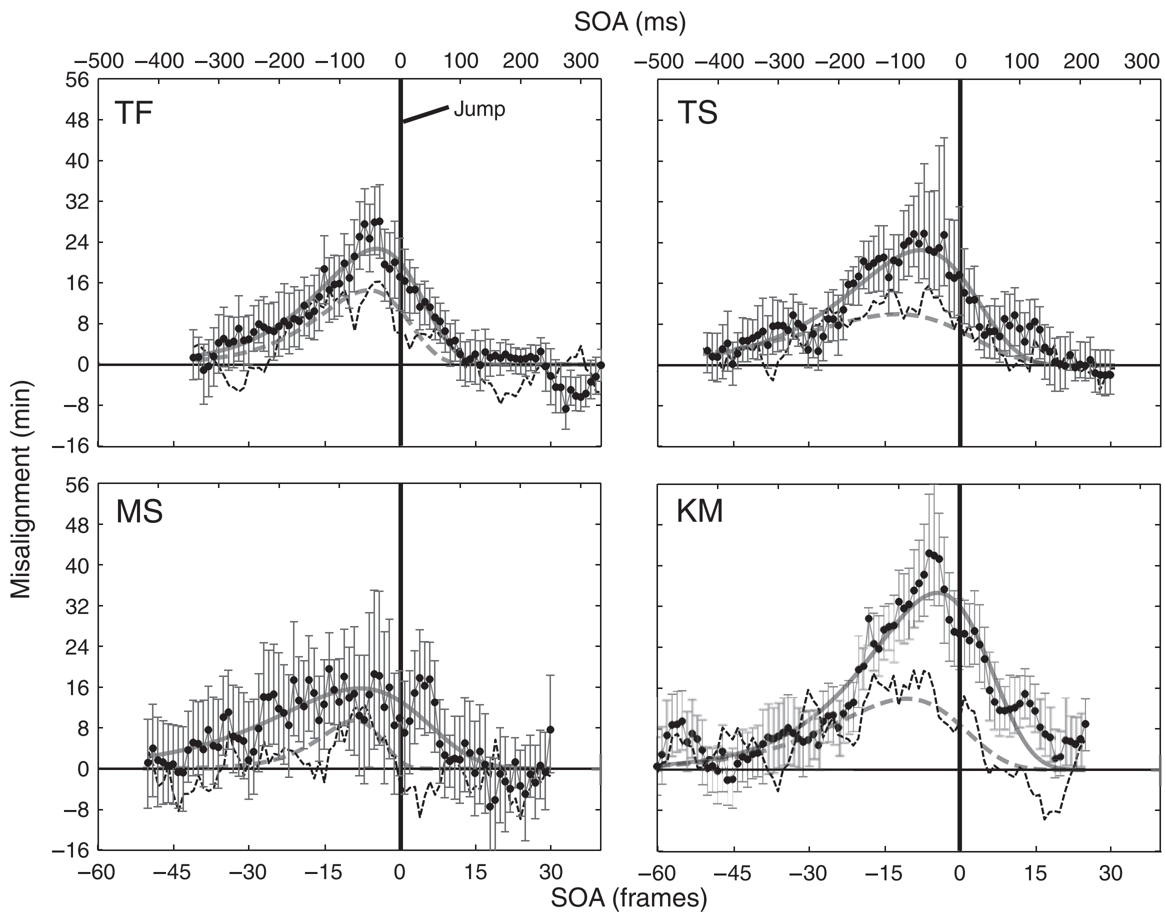

Figure 8. Comparison between the FDE in two-frame apparent motion and the FDE in random motion. The filled circles indicate the actual FDE induced by two-frame apparent motion in Experiment 2. Error bars show 95% confidence intervals. The solid curve indicates the best-fit extreme value distribution to the actual data obtained from two-frame apparent motion. The thin broken curve indicates the random motion FDE data in Experiment 1 reanalyzed by limiting the trials used to produce the two-frame motion sequence in Experiment 2. The thick broken curve is identical to the curve in Figure 3 and indicates the best-fit extreme value distribution to the original random motion FDE profile.

subject TS, 0.718 for subject MS, and 0.858 for subject KM. The profiles of the random motion data in Experiment 1 are superimposed in Figure 8 as the broken curves. When comparing these two model curves in Figure 7, one can find that the amplitude of the FDE was substantially larger than the effect originally found with the random motion sequence. This suggests that some top-down process, which does not work in the random motion case but works in two-frame apparent motion, may be involved as a facilitatory control of the flash-drag effect.

General discussion

Summary of the experiments

In Experiment 1, we found that random motion also induces an FDE with a broad temporal tuning. In this random motion sequence, subjects could not reliably discern the jump direction that was perceptually most proximal to the flash onset time, and whether the subjects could report the correct jump direction did not correlate with the FDE. Therefore, we concluded that preattentive motion processing also contributes to the occurrence of the FDE. Moreover, the FDE in random motion correlated with the current jump but had no higher order correlation with any other jumps in the past or future. This means that only two frames of apparent motion stimuli can preattentively cause the FDE. In Experiment 2, we isolated two-frame apparent motion stimuli from the random motion sequence we used previously and measured the FDE by presenting the flash at various timings relative to the jump. Under this condition, observers could easily identify the jump direction that was perceptually most proximal to the flash onset time. An FDE found under this condition had a similar temporal tuning curve, but its amplitude was substantially larger than the effect originally found with the random motion sequence. Overall, the results of this study suggest that the FDE involves preattentive motion processing but that top-down processes may also facilitate the FDE.

Both bottom-up and top-down processing can contribute to the FDE

Our research question was partly motivated by the conclusion by Whitney (2005, 2006), who used an adaptation paradigm to demonstrate that awareness of motion direction was not necessary for an illusory position shift to occur. Subjects were adapted to several patches of stimuli moving leftward or rightward randomly. Because of crowding, subjects could not identify the motion direction of any of the patches. Still, a stationary test patch subsequently presented within one of these adapted regions appeared to shift its position in the direction opposite to that of the motion adaptation. This experiment indicates that a low-level motion system can cause the illusory position shift even though a higher attentive system does not have access to visual information of motion direction. However, the stimulus configuration used in Whitney's (2005) study is radically different from the FDE situation in that the test patch of a relatively long duration was presented at the same location as the adapted region, a typical situation for the phenomenon of motion-induced position shift after motion adaptation (McGraw, Whitaker, Skillen, & Chung, 2002). Our study is the first to demonstrate that a flash presented at a remote location from a moving stimulus appears positionally shifted without conscious access to the motion direction of the inducer. Although Whitney and Cavanagh (2000) have already shown that motion at above 8 Hz, which is too fast to track attentively (Verstraten, Cavanagh, & Labianca, 2000), can induce an FDE, observers are still able to recognize the motion direction reliably and there remains a possibility that some higher order mechanism, which only works in conjunction with conscious access to the motion direction, is necessary to induce the FDE. Our study showed the contrary. However, the results of the present study do not necessarily mean that only preattentive motion processing contributes to the FDE. Indeed, there is a line of evidence that only attentional or top-down motion processing can induce the FDE (Shim & Cavanagh, 2004, 2005; Tse et al., 2011; Watanabe et al., 2002, 2003; Whitney, 2006). Our study also showed that the amplitude of the FDE substantially increased when only two-frame apparent motion was presented such that subjects could easily individuate jump directions. Therefore, both bottom-up and top-down motion processing stages contribute to the occurrence of the FDE.

Is there any qualitative difference between the temporal tunings of the FDE mediated by top-down motion processing and that mediated only by bottom-up motion processing? If there are substantial differences, it might imply that more than one position-coding mechanism independently mediate interactions between motion and position representations. In our study, only subject MS showed such a qualitative difference. As a result of bootstrap analysis, the best-fit model parameter σ for subject MS's temporal tuning obtained in Experiment 2 was significantly larger compared with that obtained in Experiment 1. By contrast, the temporal tunings of the other three subjects did not show such significant differences. Thus, their temporal tunings obtained in Experiment 1 and those obtained in Experiment 2 did not essentially differ from each other except for amplitude. However, it should be noted that most of the previous experiments, in which top-down motion processing was deemed to mediate the FDE, revealed much broader temporal tuning than those we found. For example, Whitney and Cavanagh (2000) presented a flash at various timings relative to the time of reversal of the inducer's motion direction and found that the reversal of the FDE direction was 200–300 ms before the reversal of the motion direction. This lag is fairly larger than those we found (70 ms to maximally 150 ms). Shim and Cavanagh (2005) asked subjects to attentively track an equiluminant rotating pattern and measured the FDE by presenting flashes at various timings. The largest FDE occurred for attended motion that preceded the flash by around ~500 ms. The temporal tuning they obtained had a similar asymmetric pattern but was substantially broader than the tuning we found. Whitney (2006) used the illusory transformational apparent motion (Tse & Logothetis, 2002) to examine the contribution from high-level motion processing to the FDE. Their transformational apparent motion consisted of a two-frame sequence in which an object was perceived as moving its boundaries from one position to another, although no physical motion was contained. The FDE was measured by using flashes presented at various timings relative to the switch of the two frames. The peak time of the obtained temporal tuning was at around 50 ms before the switch. This value is close to our estimates, but the broadening of the tuning in their study seems larger than ours. One possibility that explains these discrepancies is that our two-frame apparent-motion sequence was too brief to fully activate the top-down mechanism that is responsible for the extremely broad temporal tuning revealed in the past studies. The difference in amplitude between Experiments 1 and 2 might also result from motion adaptation, because the random motion sequence in Experiment 1 contained far stronger total power of motion energy than the stimulus in Experiment 2, presumably weakening the effect of the inducer on the flash after prolonged observation. Therefore, in those studies mentioned above, motion–position interactions may depend on a different mechanism than the underlying mechanism of the FDE in the present study.

What mechanism is responsible for the broad temporal tuning?

How does the motion–position interaction in the FDE in random motion occur? In other words, what mechanism is responsible for the broad temporal tuning of the FDE induced by preattentive motion information? The pattern of the temporal tuning similar to those we found has often been observed and discussed in the previous FDE literature (Durant & Johnston, 2004; Shim & Cavanagh, 2005). As mentioned above, Shim and Cavanagh (2005) found a much broader temporal tuning than those we found, but there are also similarities in that both temporal tunings had an asymmetric pattern and a bias in the past direction. In their study, Shim and Cavanagh attributed this pattern of the temporal tuning to a directionally modulated attentional repulsion effect. Because subjects attentively tracked the pattern of the rotating disk in their study, this covert movement of the attentional focus might cause the mislocalization of the flash more often when presented ahead of the tracking target than behind, as in the case of the mislocalization effect seen with actual eye movements (Matsumiya & Uchikawa, 2000). However, this cannot be the case in our study because we used a random motion sequence, in which attentional tracking is impossible. Durant and Johnston (2004) used a rotating bar as an inducer of the FDE and obtained a temporal tuning that is very similar to our results. They proposed that feedback signals from extrastriate areas like MT/V5 to area V1 is necessary for the FDE to occur and argued that the temporal tuning reflects the peak latency of the V1 cell responses. These authors argued that when feedback signals from MT/V5 arrive at the right time around the peak latency of the V1 cell responses, the maximal FDE occurs. This is surely a possibility, but a more parsimonious idea may be that the broad temporal tuning might reflect stochastic fluctuation of temporal binding between a jump and a flash. The lag and asymmetric form may reflect a time-consuming computational process that binds a flash to motion, which gets activated only after the flash is processed at a certain level in the visual system. This explanation shares common characteristics with the explanations of the flash-lag effect that have been proposed by several researchers. The flash-lag effect is a phenomenon in which a flash presented adjacent to a moving stimulus appears to lag behind it (MacKay, 1958; Mateeff & Hohnsbein, 1988; Nijhawan, 1994), and the main cause of this effect is thought to be that the perceived timing of the flash is delayed relative to the moving stimulus (Brenner & Smeets, 2000; Murakami, 2001a, 2001b; Whitney, Cavanagh, & Murakami, 2000; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000). Several studies suggest that the flash-lag effect is caused by a sluggish computational process that binds the flash and the moving stimulus rather than by the simple differential latency between the flash and the moving stimulus (Arnold, Durant, & Johnston, 2003; Arnold, Ong, & Roseboom, 2009; Brenner & Smeets, 2000; Cai & Schlag, 2001; Fukiage & Murakami, 2010). It should be noted that the flash-lag effect is different from the FDE in that the task in the flash-lag effect requires an explicit comparison between the positions of the flash and the moving stimulus, and it might be that this explicit comparison more directly reflect the temporal property of the binding process. Nevertheless, the time constant we estimated in this study is similar to those of distributed differential latency obtained in the studies of the flash-lag effect that also used random motion as the inducer (Fukiage & Murakami, 2010; Murakami, 2001a, 2001b). Although Durant and Johnston found that the flash-lag effect was smaller than the delay measured with the FDE, using their stimuli, the smooth motion they used might activate more than one mechanism that can influence position judgments. Unpredictability of random motion might be best to extract the pure effect of a bottom-up mechanism mediating both the FDE and the flash-lag effect. Therefore, a common mechanism, which binds a stationary object with a moving one or allocates objects to a kind of spatiotemporal map, might be responsible for both the FDE and the flash-lag effect. This idea is largely speculative, but there is also another study that suggests the existence of a high-level binding mechanism with large temporal imprecision (Linares, Holcombe, & White, 2009).

Account for above-chance performance in the jump-direction task

In the jump-direction task in Experiment 1, the subjects judged the motion direction at the flash's onset time during the random motion sequence. We confirmed that the performance was as poor as 50 to 70% (Figure 4). However, all subjects performed above chance at several SOAs though they could not attentively track the random motion sequence. What made this performance possible? We argue that this is a natural consequence of stochastic stimulation, given the fact that in the random motion sequence, the statistics of motion direction in several successive phase shifts can often incline toward one side. If the subjects judged the inducer's motion direction based on the net motion change over a broad time scale, the performance of the jump-direction task should necessarily be higher than the chance level in a broad range of SOAs. To test this possibility, we extracted the statistics of the random motion sequence around the flash's onset time based on the responses of the jump-direction task. As a result, we found that the inducer jumped more often in the same direction as the subject's response than the chance level in a range from −30 to 80 frames relative to the flash's onset. Therefore, it is plausible that the subjects judged the inducer's motion direction based on the net motion change around the flash's onset, and such behavior should have raised the correct response rate. This argument accounts for the extremely broad distribution of the above-chance data in Figure 4. As we already mentioned, however, this response bias has nothing to do with the occurrence of the FDE because the FDE in random motion did not correlate with motion direction judgment (Figures 5 and 6).

Conclusion

In Experiment 1, we demonstrated that random motion can induce the FDE with a broad temporal tuning. This suggests that the FDE involves preattentive motion processing. In Experiment 2, we presented only two-frame apparent motion as the inducer and found an FDE larger than that found in the random motion sequence. This means that some top-down process may facilitate the FDE. The estimated time constant of the FDE is similar to those of distributed differential latency obtained in the studies of the flash-lag effect that also used random motion as the inducer (Fukiage & Murakami, 2010; Murakami, 2001a, 2001b). Thus, there is a possibility that a common mechanism, which binds a flash with a moving stimulus, is responsible for both the FDE and the flash-lag effect. The broad temporal tuning might reflect stochastic fluctuation of temporal binding between a flash and motion.

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