A motion-induced position shift that depends on motion both before and after the test probe

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Two versions of the flash grab illusion were used to examine the relative contributions of motion before and motion after the test flash to the illusory position shift. The stimulus in the first two experiments was a square pattern that expanded and contracted with an outline square flashed each time the motion reversed producing a dramatic difference in perceived size between the two reversals. Experiment 1 showed a strong illusion when motion was present before and after the flashed tests or just after the flashes, but no significant effect when only the pre-flash motion was present. In Experiment 2, motion always followed the flash, and the duration of the pre-flash motion was varied. The results showed a significant increase in illusion strength with the duration of pre-flash motion and the effect of the pre-flash motion was almost 50% that of the post-flash motion. Finally, Experiment 3 tested the position shifts when the linear motion of a disk before the flash was orthogonal to its motion after the flash. Here, the results again showed that the pre-flash motion made a significant contribution, about 32% that of the post-flash motion. Several models are considered and even though all fail to some degree, they do offer insights into the nature of the illusion. Finally, we show that the empirical measure of the relative contribution of motion before and after the flash can be used to distinguish the mechanisms underlying different illusions.

Introduction

If a probe is flashed briefly on a moving pattern when it reverses direction, the apparent position of the flash shifts in the direction of the following motion (Figure 1A; Cavanagh & Anstis, 2013; Hogendoorn, Verstraten, & Cavanagh, 2015; Kohler, Cavanagh, & Tse, 2015; Anstis & Cavanagh, 2017; Kohler, Cavanagh, & Tse, 2017; van Heusden, Harris, Garrido, & Hogendoorn, 2018; Blom, Liang, & Hogendoorn, 2019; Coffey, Adamian, Blom, van Heusden, Cavanagh, & Hogendoorn, 2019; Ge, Zhou, Qian, Zhang, Wang, & He, 2020). This “flash grab” effect has been related to extrapolation that compensates for neural delays (van Heusden et al., 2018) or to an averaging of position that predicts a shortened path (see Figure 1C; Sinico, Parovel, Casco, & Anstis, 2009; Cavanagh & Anstis, 2013). Additional models developed for the flash-lag effect (Metzger, 1932; Mackay, 1958; Nijhawan, 1994) may be relevant (position averaging, Krekelberg & Lappe, 2000; integration, differential latency, Purushothaman, Patel, Bedell, & Öğmen, 1998; Whitney, Murakami, & Cavanagh, 2000). Unlike the flash lag, there is an additional step in the flash grab where the flash’s position is transferred to the perceived

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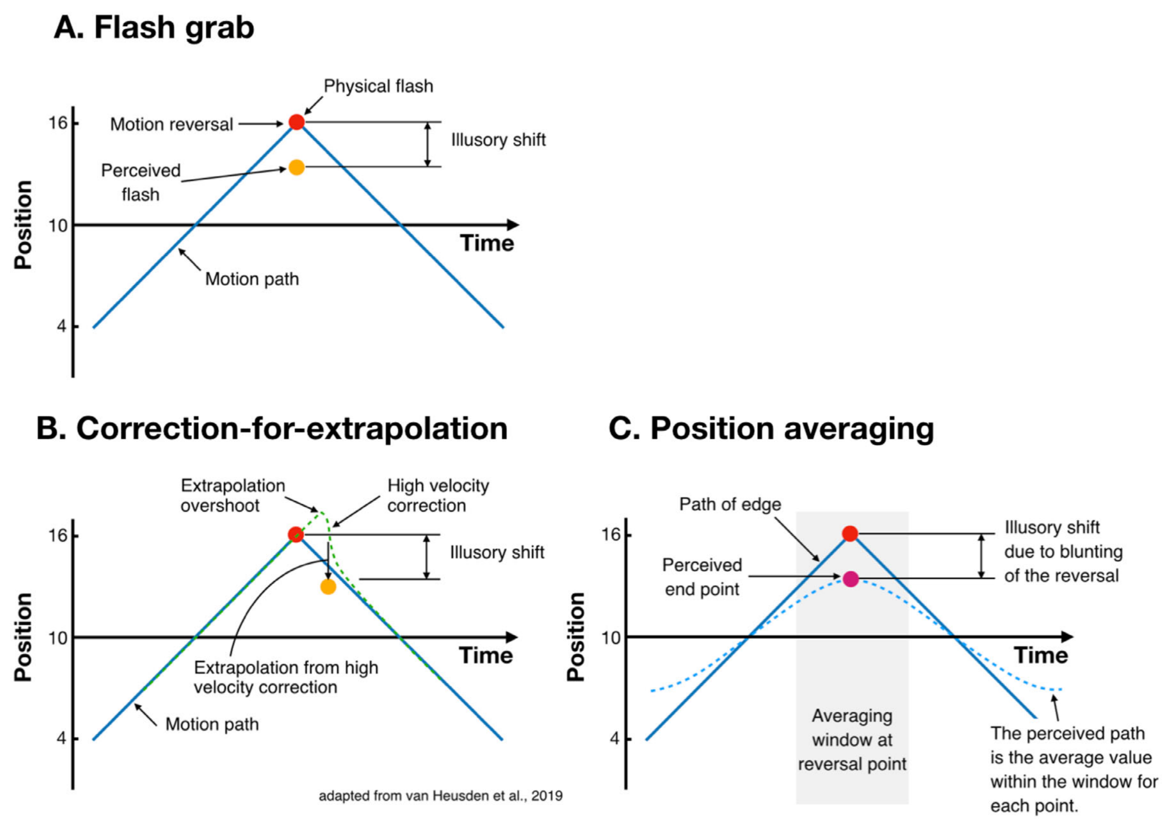
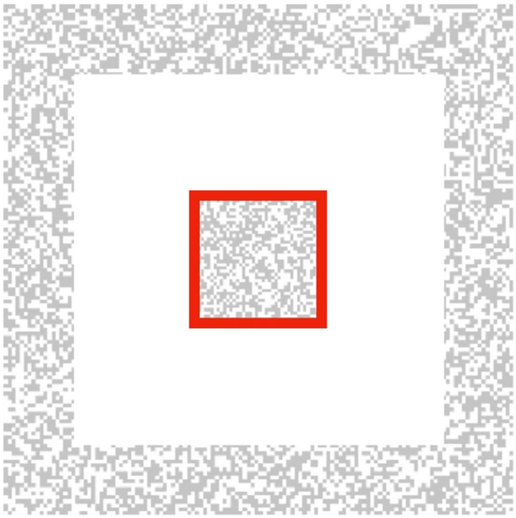


Figure 1. **Models of the flash grab**. A flash is presented each time a moving stimulus reverses direction. (**A**) The perceived location of the flash is shifted away from the actual end of the motion path but falls on the perceived reversal point of the path. The perceived location of the flash moves to the apparent path end point – it is not seen separated from it. (**B**) **Correction-for-extrapolation**. Extrapolation would predict an overshoot but van Heusden, Harris, Garrido, and Hogendoorn (2019) propose that there is a rapid correction for this overshoot and the high velocity return motion produces a larger extrapolation in the other direction. (**C**) **Position averaging**. The perceived position of the moving target is given by the average value within the window and this averaging will blunt the sharp reversal into a rounded one (e.g. Sinico et al., 2009). The end point then moves away from the physical location, taking the flash location with it, producing the illusory shift.

location of the motion reversal, so that they are seen together rather than separated. This process may rely on the binding of the flash to the motion reversal as both transients occur in synchrony. Indeed, if the synchrony is broken by presenting the flash before or after the reversal, there is a steep decrease in the illusory shift (Cavanagh & Anstis, 2013).

Whatever its source, the illusory shift is quite large and easy to report. The question we address here is the relative contribution of the motion before versus motion after the flash. Previous evidence has suggested that only the motion after the flash generates the illusion. The illusory shift is in the direction of the motion after the flash and when motion is presented only after the flash, the illusion is similar in magnitude compared to when motion is present both before and after the flash (Cavanagh & Anstis, 2013). In addition, when the flash is presented at the end of the motion (a flash-terminated condition), there is little or no offset seen from its physical location (Cavanagh & Anstis, 2013). Although these results show that the motion after the test flash is necessary for producing the illusion, they have not shown that it is the sole determinant of the shift. In addition, the results for motion terminating with the flash may be confounded by effects of the temporal offset of motion. A similar argument has been made in the case of the flash lag effect (Nijhawan, 2002; Nijhawan, 2008; Shi & Nijhawan, 2012). As a result, it is critical to assess the relative contributions of motion before and after the flash under conditions that avoid interference from the offset of motion.

Recently, Blom, Liang, and Hogendoorn (2019) addressed this directly with motion present both before and after the flash. This avoided any issue of the interference caused by the temporal offset of motion. To compare the effects of motion before and after the flash, they manipulated the directions so, for example, in two of their conditions, the motion after the flash was orthogonal to the motion before. This meant that the judged position of the flash would show the effect of pre-flash motion along one axis and the effect of post-flash motion along the orthogonal axis. They



Movie 1. Basic effect of the motion induced size change from Anstis and Cavanagh (2017). Movie available here: https://cavlab.net/Demos/Before/Movie1.m4v.

reported that the illusory position shifts were again dominated by the motion after the flash. However, they also found a small but significant contribution from motion before the flash, an effect of about 12% that of the motion after the flash. Interestingly, the position shift from the motion before the flash was opposite to the direction of the pre-flash motion whereas the effect of motion after the flash was in the same direction as the post-flash motion. Their result is the first to suggest that motion before the test can have an effect but the effect size for motion before the test was small.

Here, we re-examine the effect of motion before the test in the context of a particularly strong version of the flash grab illusion that, as a result of its larger effect size, offers a more sensitive measure. In this version, the probe is flashed at the same time that the motion of the background reverses (Cavanagh & Anstis, 2013) but here with an expanding and contracting square (Anstis & Cavanagh, 2017). This configuration gives the strongest motion-induced position shift reported to date (Movie 1). Because of the geometry of the stimulus, these position shifts are experienced as changes in the size of the flashed squares so that one square appears larger than the other even though they are physically identical.

We first replicate the large size changes seen when the motion is present for the full cycle – both before and after the test flash – and when motion is present only after the test. Importantly, we again found no illusion for the flash-terminated condition (with motion present only before the flash). The effect of motion before the flash can also be derived from the difference between the full cycle (before and after) and the motion only after the flash. Like Blom et al. (2019), these two conditions both have motion after the flash and so avoid the interference of the offset of the motion (e.g. Shi & Nijhawan, 2012) or the persistence of its offset location. However, unlike Blom et al. (2019) this difference, although in the direction of a contribution of motion before, was not significant.

The next experiment investigated this difference between the full cycle and the motion only after the flash by varying the duration of the motion before the flash while keeping the motion after the flash fixed. Here, we found evidence that the motion before the flash boosts the illusion strength, contributing almost 50% of the effect produced by the motion after the flash.

The contribution of motion before the flash in Experiment 2 was significant ($p = 0.03$). To verify this, we ran a third experiment following Blom et al.'s (2019) technique of orthogonal motions before and after the flash to measure their contributions independently. In this experiment, the contribution of motion before the flash was significant and unequivocal. Motion before contributed about 32% of the effect produced by the motion after the flash.

These results therefore support Blom et al.'s (2019) findings and increase the estimate of the importance of the motion before the flash. This suggests that absence of an effect in the motion terminated conditions ("Motion Before" here) in previous studies, and, here, was due to the abrupt termination of the motion at the same time as the flash. This transient may overwrite or veto the shift that is produced by the motion before the flash, as first suggested by Shi and Nijhawan (2012) for the flash terminated conditions in the flash lag effect. Alternatively, there may be a persistence of the offset location when not followed by additional motion that dominates the perception of the flash location (Öğmen, Patel, Bedell, & Camuz, 2004, figure 12). This result raises three significant questions. First, why does motion before the flash shift the perceived location in the direction opposite to the pre-flash motion, whereas the motion after the flash shifts the position in the same direction as the post-flash motion? Second, if there is a contribution of motion before the flash, why does it disappear when the motion terminates at the same time that the flash is presented? Third, why is the motion after the flash more effective than the motion before? The answers to these questions will constrain viable models of the flash grab and other motion-induced position shifts.

Experiment 1

We compared illusion strength for motion before the flash, motion after, and motion before and after to determine if the motion before the flash would have any impact on the illusion. The effect of only motion before the flash is equivalent to the flash terminated conditions tested for the flash lag (e.g. Eagleman & Sejnowski, 2000) and for the flash grab (Cavanagh & Anstis, 2013). Subtracting the illusion strength for motion only after the flash from motion both before and after will estimate the contribution of motion before, if any, in the absence of any interference from the simultaneous offset of motion and the presentation of the flash (Shi & Nijhawan, 2012).

Method

Participants

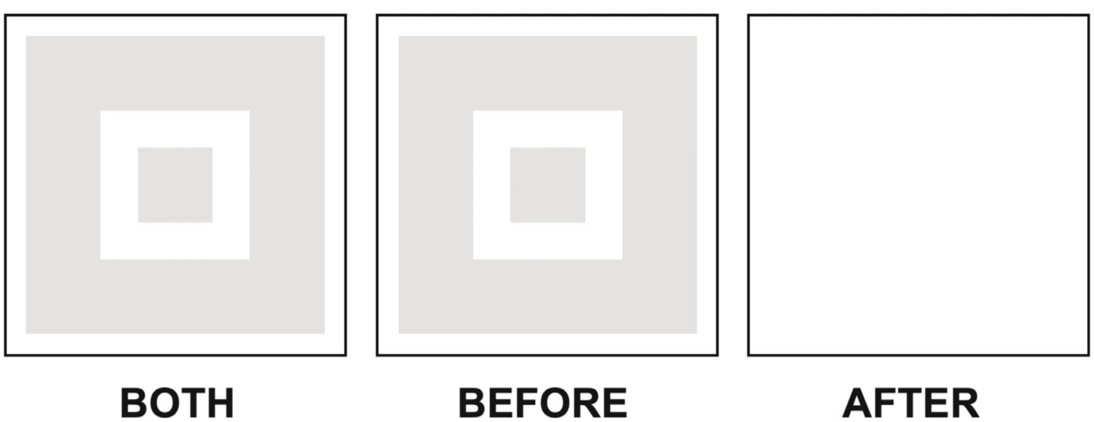
Eight students (6 men and 2 women, aged between 18 and 25 years old) and two of the authors (1 man and 1 woman, aged between 29 and 74 years old) participated. All participants had normal or corrected-to-normal vision. Written informed consent was obtained from each participant before the experiment. This study was approved by the internal review board of Waseda University.

Stimuli

All stimuli were presented on a 23-inch LCD monitor (1920 × 1080 pixels) with the refresh rate of 100 hertz (Hz). Participants observed the stimuli from 57 cm away using a chin rest while fixating a central cross (0.5 degrees of visual angle in diameter [dva]). The frame made up of two nested gray squares (Figure 2) was presented at 7.25 dva to the left or right of fixation on a uniform, mid-gray background. The width of the frame's inner gray square was always one quarter that of the outer square as the pattern expanded and contracted. The two squares were a uniform dark gray on the white background (Movie 2). The frame expanded then contracted or vice versa over a four-fold range in size (4.8 dva and 19.2 dva) with each phase taking 500 ms. The test was a single outline square of fixed size (4.8 dva in width and contour width 0.5 dva) that flashed for 100 ms at the reversal point. During the 100 ms of test presentation the background remained static. The outline square was colored blue when the frame was at its smallest size (when the first half cycle was contraction), or red when the frame was at its largest size (the first half cycle was expansion). Only one colored square was flashed within each cycle and there was a 600 ms gap between cycles. In the before condition, the second 500 ms of each cycle, following the 100 ms flashed test, was left blank; in the after condition the first half of each cycle was left blank and the 100 ms flashed test and the subsequent 500 ms of motion were shown; in the both condition, both 500 ms motion segments were present (either contraction, then expansion, or vice versa), separated by the 100 ms test. Two comparison stimuli, superimposed red and blue squares, were present continuously throughout the trial 7.25 dva from fixation on the opposite side of the expanding/contracting frame. Their relative size was under the control of the participant.

Procedure

Participants fixated on the central plus (+) sign and adjusted the relative size of the red and blue squares on one side to match the perceived sizes of the red and blue squares flashed on the expanding/contracting square on the other side. The participants used the up-arrow on the keyboard to make the blue comparison square larger and the red one smaller or the down-arrow to make the red square larger and the blue one smaller. The up and down arrow keys were only enabled after two full cycles of the stimulus sequence. The stimulus cycled continuously while the participant made adjustments, and when they were satisfied with their setting, they pressed the space bar to register their setting and began



Movie 2. Sample trials for motion both, before, and after the flash in Experiment 1. Each condition displays three cycles of the red and blue tests before beginning the next condition. Movie available here: https://cavlab.net/Demos/Before/Movie2.m4v.

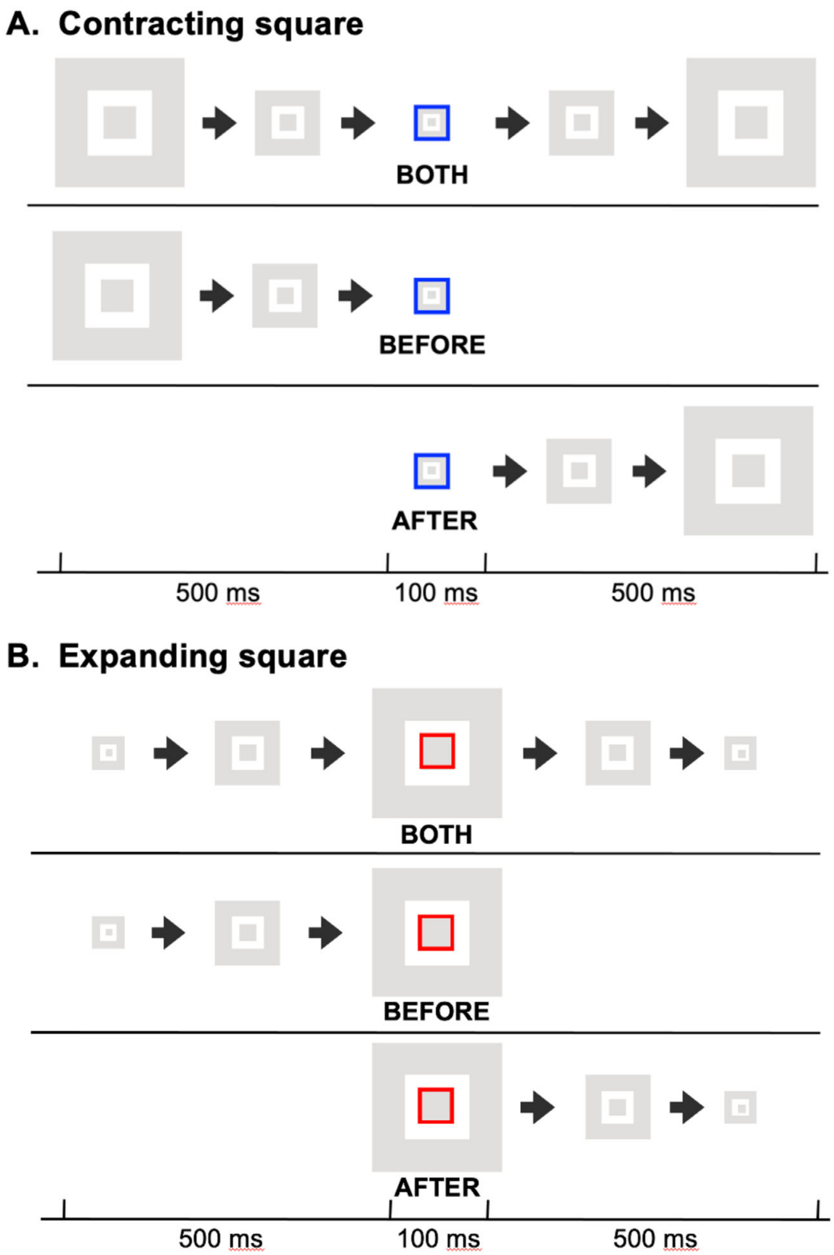


Figure 2. The three conditions: both, before, and after (see Movie 2). The both condition has 500 ms of contraction first, a 100 ms blue flash at the reversal followed by 500 ms of expansion. For the before condition, the stimulus is blanked for the second segment (600–1100 ms) whereas for the after condition, the first segment (0 to 500 ms) is blank. (**A**) There is only one colored square in a cycle, here, it is blue and the two cycles alternated so that both blue and red squares were seen in each sequence. (**B**) For the cycle with the red square, the background would start at its smallest size and reverse direction when it was at its largest size. The red outline square in that case exactly matched the size of the inner square of the background as well as the size of the blue outline square seen in every second cycle.

the next trial. Three conditions of background motion (before, after, and both) were presented in random order in each session, combined with two orders of inducer motion (expanding first, so with a red test square, or contracting first, with a blue test square), and two locations of the expanding/contracting stimulus (left or right). There were eight repetitions of each of these three combinations for a total of 24 trials per session which lasted approximately 10 to 15 minutes. Each participant completed three sessions.

Data analysis

The illusion magnitudes were calculated as the percent change of the size of the blue comparison square compared to that of the red, so that a change of

0% would indicate equal sizes for the two squares and no illusion. A perceived increase of blue relative to red would indicate an illusion in the same direction as that found in the previous study of this illusion (Anstis & Cavanagh, 2017).

Results

The mean percent change between the two adjusted squares was taken as the illusion magnitude and this value was averaged over trials for each condition and participant. These values are plotted in Figure 3. For the baseline condition (both) when the inducing backgrounds were present for the entire cycle, the blue comparison square was set 42.0 ± 8.83% (mean ± 1 SE) larger than the red comparison square. The size change was 33.4 ± 5.56% for the after condition and 4.78 ± 6.18% for the before condition.

We performed an analysis of variance (ANOVA) for the mean of the illusion magnitudes over the three conditions of background motion. The analyses showed that the effect of motion conditions was significant ($F(2,18) = 27.49$, $p < 0.001$). Then, multiple comparisons showed the significant difference between motion before and motion after ($t(9) = -5.55$, $p = 0.001$, and both $t(9) = -7.83$, $p < 0.001$). However, there was no significant difference between motion after and motion both ($t(9) = 1.48$, $p > 0.05$, Bonferroni corrected). Illusion magnitudes significantly greater than 0% were found for the after and both cycle conditions (both: $t(9) = 4.76$, $p = 0.003$, and after: $t(9) = 6.02$, $p < 0.001$, Bonferroni corrected) but the illusion did not differ significantly from zero with motion only before (before: $t(9) = 0.774$, $p > 0.999$).

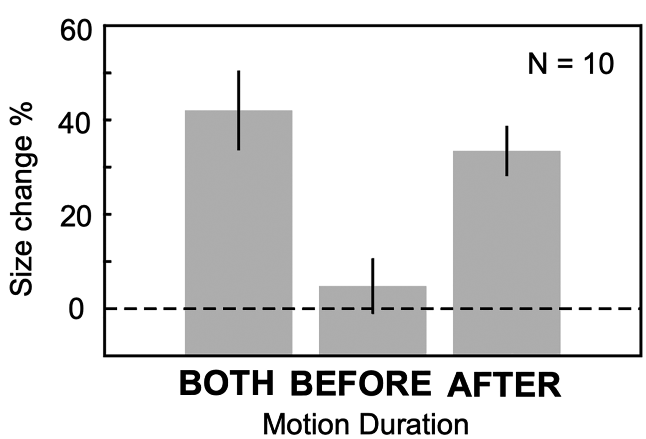


Figure 3. Illusion magnitude (blue–red/red) is plotted in percent as a function of motion timing. The vertical bars represent ±1 SE.

Discussion

The results show that our side-by-side technique replicates the original findings of Anstis and Cavanagh (2017) showing an illusion of 42% when the expanding and contracting backgrounds completed the full cycle. Anstis and Cavanagh (2017) reported an illusion of 120 ± 50% for their three participants. Our smaller value may be due to the single test flash per cycle used here rather than the continuous cycling through both tests in the earlier study. Or it may be a difference in participants.

The results also showed a loss of the illusion when the motion preceded the flashed squares but did not follow them, replicating Cavanagh and Anstis (2013). This motion-before test has the drawback that the motion and test disappear together, which could mask or interfere with any effect the motion before the flash may have had (e.g. Shi & Nijhawan, 2012). As planned, we can also evaluate the contribution of the motion before the flash without any offset by subtracting the illusion strength in the after condition (33.4%) from its strength in the both condition (42.0%). These two differ only in the presence of the motion before the test in the both conditions. Although the 8.59% difference in illusion strength was not significant, it was consistent with a contribution of motion before the test that was about 25.7% of the contribution of motion after the flash (8.59/33.4). In the next experiment, we evaluate the contribution of the motion before the flash as a function of its duration.

Experiment 2

In this experiment, we examined how the illusion strength would change with increasing duration of motion before the flash while always leaving the complete half cycle of motion after the flash. This eliminated any suppression or persistence that might arise in the flash terminated condition (motion before) of the first experiment.

Method

Participants

Nine students (6 men and 3 women, aged between 20 and 24 years old) and one of the authors (1 woman, 29 years old) ran this experiment. They had not participated in Experiment 1 except for the author. All participants had normal or corrected-to-normal vision. Written informed consent was obtained from each participant before the experiment. This study was approved by the internal review board of Waseda University.

Stimuli, procedure, and data analysis

The settings were identical to that of Experiment 1 except that five ranges of background motion before the test probe were presented, along with the motion after the test: therefore, 0, 125, 250, 375, and 500 ms of motion before the test, followed by the 100 ms test and then the 500 ms motion after the test.

Results

The mean percent change in size between the two adjusted squares was again taken as the illusion magnitude and this value was averaged over trials for each condition and participant. These values are plotted in Figure 4.

We performed a linear mixed model for the mean of the illusion magnitudes with the duration of motion before as a fixed effect and participants as a random effect. This analysis indicated that the linear effect of duration of motion before the test was significant ($F(1,398) = 4.51$, $p = 0.03$), showing that the duration of motion before the flash did have a significant effect when the motion after the flash was added.

The linear regression for the group's data was:

$$Size\,Change\,(\%) = 41.2 + 0.04 \times Motion\,Before\,(ms).$$

The illusion was significantly larger than 0 for all ranges [all p values < 0.001] and reached a value of 59.4% ± 7.67 for the full cycle (similar to the both condition of Experiment 1). The value for motion only after the flash was 40.7% ± 10.2. We used the regression to estimate the size change between the blue and red tests for the full cycle as 61.2% (= 41.2 + 0.04 • 500). For motion only after the flash, the estimated change is 41.2%. The difference between these two values gives us the contribution the motion before: 20.0%. This suggests that contribution of the motion before the flash was 48.5% of that from the motion after the flash (20.0/41.2), a substantial fraction. For comparison, in Experiment 1, this ratio was 25.7%.

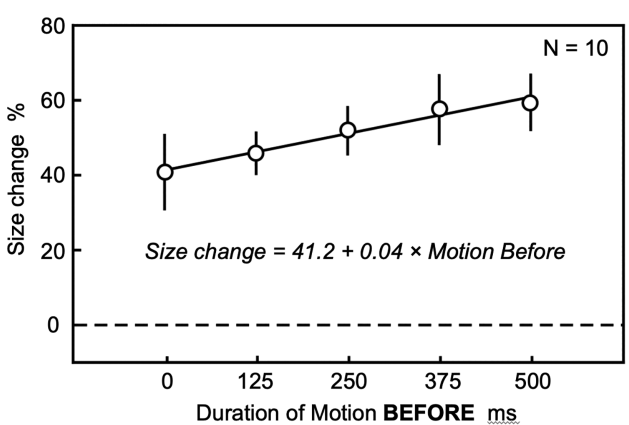


Figure 4. Illusion magnitude (blue–red/red) is plotted in percent as a function of duration of motion before the test flash. The straight line is the regression fit. The vertical bars represent ±1 SE.

Discussion

The second experiment examined the contribution to the illusion strength of motion before flash, varying its duration from none to complete (500 ms) always with the full 500 ms of reversed motion after the test flash. The results showed that the illusion strength increased significantly with the duration of motion before the flash. Both the regression result and the main effect of duration were significant. To verify this, we ran a third experiment.

Experiment 3

Here, we returned to a more conventional flash grab experiment, and we borrowed Blom et al.'s (2019) logic making the motion after the flash orthogonal to the pre-flash motion (Figure 5). This will allow us to judge the two contributions independently.

Method

Participants

Eleven people participated in this online experiment (7 men, aged between 28 and 59 years old) including four of the authors (3 men and 1 woman, aged between 29 and 74 years old). Other than the co-authors, they had not participated in Experiments 1 and 2 and were naive to the purpose of the experiment. All participants had normal or corrected-to-normal vision. Informed consent was obtained from each participant before the experiment. This study was approved by the internal review board of Waseda University.

Stimuli, procedure, and data analysis

The experiment consisted of a set of movies presented to the participants in their web browser accessed at this URL https://cavlab.net/Demos/Elbow. The recruitment email outlined the experiment and specified that only those who consented to participate

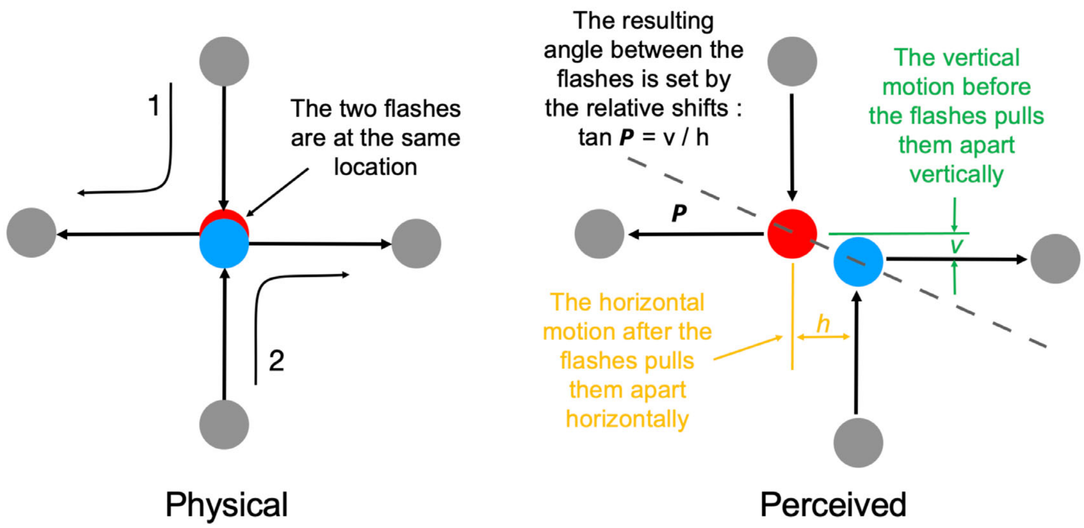


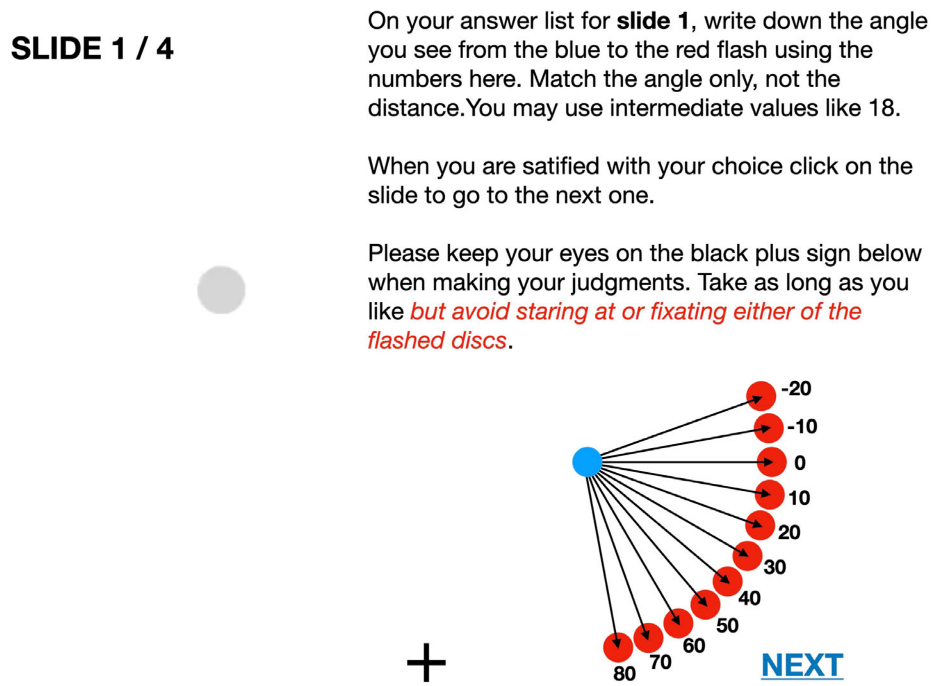
Figure 5. **Left panel**. The first disk moved down to the common center location, flashed blue, then moved away to the left. The second disk moved up to the common location, flashed red, then moved away to the right. **Right panel**. Even though superimposed the two flashes appeared offset pulled apart vertically by the effects of the motion before the flashes and horizontally by the effects of motion after the flashes. This created a perceived angle between the two flashes that was reported by participants using a response choice shown in Movie 3 below. The perceived angle is set by the relative strengths of the vertical and horizontal offset (tan $\theta = v/h$). The other three conditions were 90 degrees rotations of this first one.

could load the experiment web pages and return their responses. Figure 4 shows the layout and logic of the tests. The disk sizes were 5% of the browser window, the disk paths center to center from onset to flash (and flash to offset) were 16% of the browser window. The monitor size, browser window size, and viewing distance were not controlled. In the first of the four conditions, a grey disk appeared at the top of the motion area and moved down vertically for 167 ms. It paused for 116 ms while the disk flashed red, and then returned to grey and continued to the left horizontally for another 167 ms, and disappeared. The second grey disk appeared at the bottom of the display area at the same time the first disk flashed blue and moved up vertically to the same location where the previous disk had stopped. The second disk also stopped there and turned red for 116 ms. It then became grey again and moved to the right horizontally for 167 ms, and disappeared. These two grey disks continued to make the alternating right angle turns with the common turning point until participants were ready to respond. Because of the effects of motion on the perceived locations, the two positions appeared offset and, in this first condition, the vertical offset was caused by the motion before the flash (which had only vertical motion), whereas the horizontal offset was caused by motion after the flash (which had only horizontal motion). These combined horizontal and vertical offsets created a perceived angle between the two flashes, even though they were physically superimposed. The participants reported this angle by selecting one of the angle lines above and to the right of the motion display area. The three other conditions were 90 degrees rotations of the first (see Movie 3 for the first condition) and each condition was shown once for a total of four responses. The experiment took about 10 minutes to complete. The four responses were averaged for each participant for the analysis.

Results

The perceived angle between the two-colored circles reflects the relative contributions of motion before and motion after the flashes (but not their absolute magnitudes). If the contributions are equal, the perceived angle between the two flashes would be 45 degrees; if the motion after the flash is more effective, the angle will be less than 45 degrees. If the motion before the flash has no effect, the angle will be 0 degrees. These values are plotted in Figure 6.

One sample t-test was performed against 0 degrees, which would indicate no contribution of the motion before the flash. The mean angles were significantly greater than 0 degrees for the group mean ($t(10) = -10.6$, $p < 0.001$) and, individually, for eight of the 11 participants. This showed that the motion before the flash did contribute to the illusion and the mean angle of 17.6 degrees corresponds to a contribution of the motion before, that is 31.7% that of the motion after.



Movie 3. A sample test slide from the experiment. The two flashes seen in the Movie are always physically superimposed but may appear offset. The angle of the offset reveals the relative contributions of the vertical motion before and horizontal motion after the flash as described in Figure 5. Movie available here: https://cavlab.net/Demos/Before/Movie3.m4v.

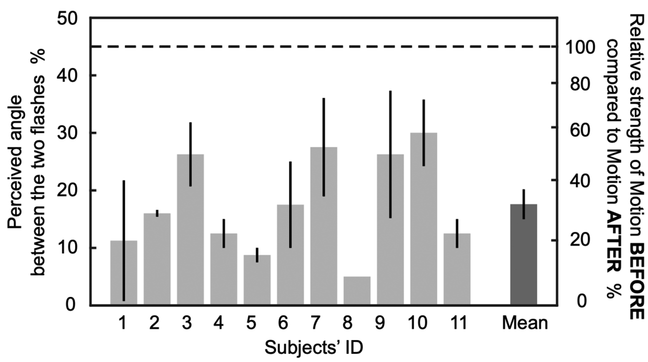


Figure 6. The perceived angle (left hand vertical axis) between the two flashed probes first for individual participants then for the group mean. The righthand axis gives the relative strength of motion before compared to motion after that corresponds to these angles. The vertical bars represent ±1 SE.

Discussion

Using a perceptual judgment of the angle between the two flashes, we obtained a direct estimate of the relative weights of motion before and motion after the flash. This supported the result of the previous experiment and indicated that the effect of motion before the flash was about 32% that of the motion after the flash. This was lower than the value from Experiment 2 (49.7%) but similar to the value from Experiment 1 (25.7% but nonsignificant).

General discussion

Here, we have examined the role of the motion before and after the flash in producing the flash-grab illusion. When there was motion both before and after the flash, the motion before the flash contributed between 25% and 50% of the effect from the motion following the flash. This supports the results of Blom et al. (2019) but points to a much larger contribution of motion before the flash than they had reported (12%). The result again suggests that the temporal offset of motion in flash-terminated conditions (Cavanagh & Anstis, 2013) was responsible for suppressing the illusion in this condition. This suppression was avoided here in the conditions with motion both before and after the flash. Blom et al. (2019) had measured the effect of the motion before and after the flash using orthogonal directions of the two motions to isolate their contributions and avoid any flash-terminated suppression or persistence. Their estimate of the contribution of the motion before the flash was small (12%) but significant. The theoretical importance of their finding combined with its small effect size led us to re-examine the question in a series of three experiments.

Our experiments used two versions of the flash-grab stimuli. In the first, a pattern expanded and contracted to produce a very large illusory position shift that was seen as a size change (Anstis & Cavanagh, 2017). We did replicate the absence of an illusion in the

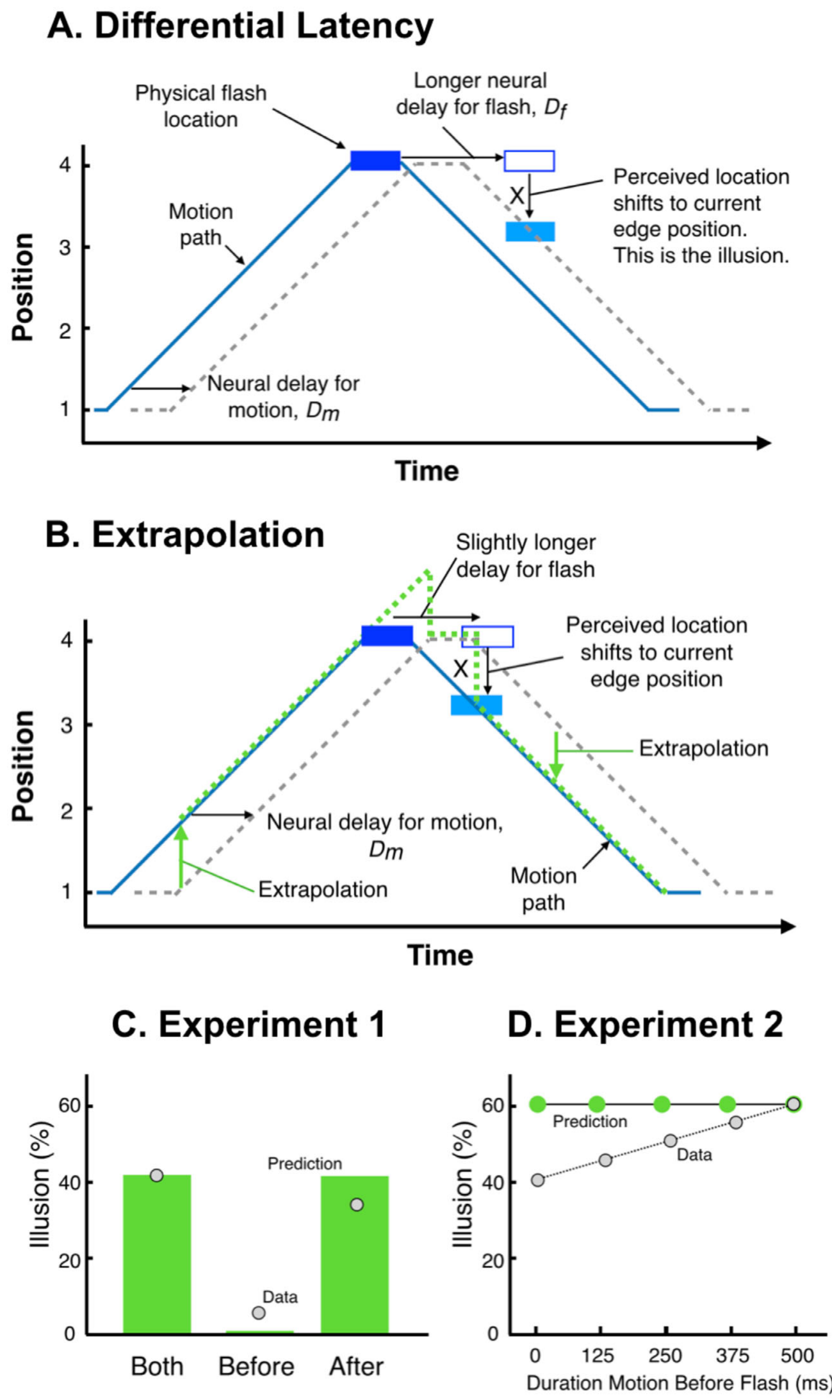


Figure 7. Panels (**A**) and (**B**) show the differential latency and extrapolation models for the condition of motion before and after the flash. In both cases, the perceived location of the flash is assigned to a position ahead of the perceived reversal (the peak of the dashed profile) rather than coincident with it. Panels (**C**) and (**D**) plot the predictions of these models for the data of Experiments 1 and 2.

flash-terminated condition (motion only before the flash), as had been previously shown for the flash-grab stimulus (Cavanagh & Anstis, 2013). We also compared the both condition (both pre- and post-flash motion) to the after condition (motion only after the flash) in this experiment to estimate the contribution of the pre-flash motion. Specifically, these conditions differ only in the presence of the pre-flash motion and because both have post-flash motion, they also avoid the issue of the offset of the motion concurrent with the flash. However, the difference between the two was not significant. It was, nevertheless, in the direction of a contribution of

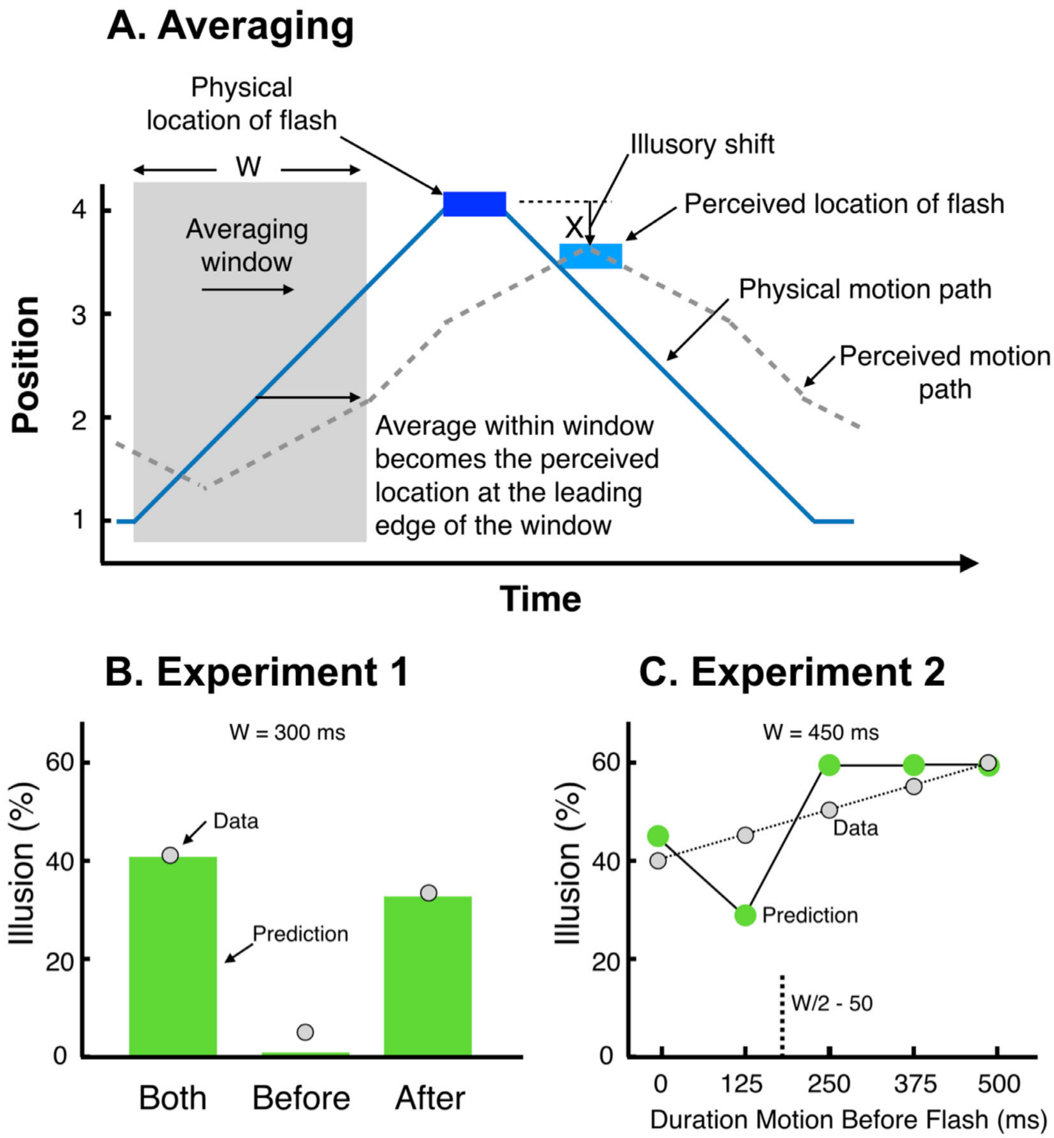


Figure 8. (**A**) Averaging model for the condition of motion before and after the flash. The perceived location of the flash is assigned to the maximum of the dashed profile, the perceived location of the motion reversal. Panels (**B**) and (**C**) plot the predictions of the model for the data of Experiments 1 and 2.

pre-flash motion and so it left the status of Blom et al.'s finding undecided. In our second experiment, we varied the duration of the pre-flash motion, leaving the duration of post-flash motion fixed. Here, we found a significant contribution of the motion before the flash that increased linearly with its duration. The relative weight of the pre-flash motion was almost 50% of that of the post-flash motion. This suggests that the pre-flash motion does contribute and does so with a weight that exceeded the value of 12% reported by Blom et al. (2019).

Although this finding was significant, it was not strongly so and we proceeded with a third experiment using a standard flash grab stimulus, with motion before and after the flash. Importantly, we adopted Blom et al.'s (2019) technique of using orthogonal directions for the pre-flash and post-flash motions. This allowed the two contributions to be isolated in the reports of the relative flash locations. The results were clear – there was again a contribution of the pre-flash motion that was now about 32% that of the post-flash motion. Overall, the three experiments support Blom et al.'s (2019) finding that the motion before the flash does contribute to the position shift, and we find that its strength is two to four times larger than the effect that they reported.

This result leaves three outstanding questions. The first concerns the opposite direction of the effect relative to the motions before and after the flash. Specifically, the pre-flash motion is toward the flash, but its effect

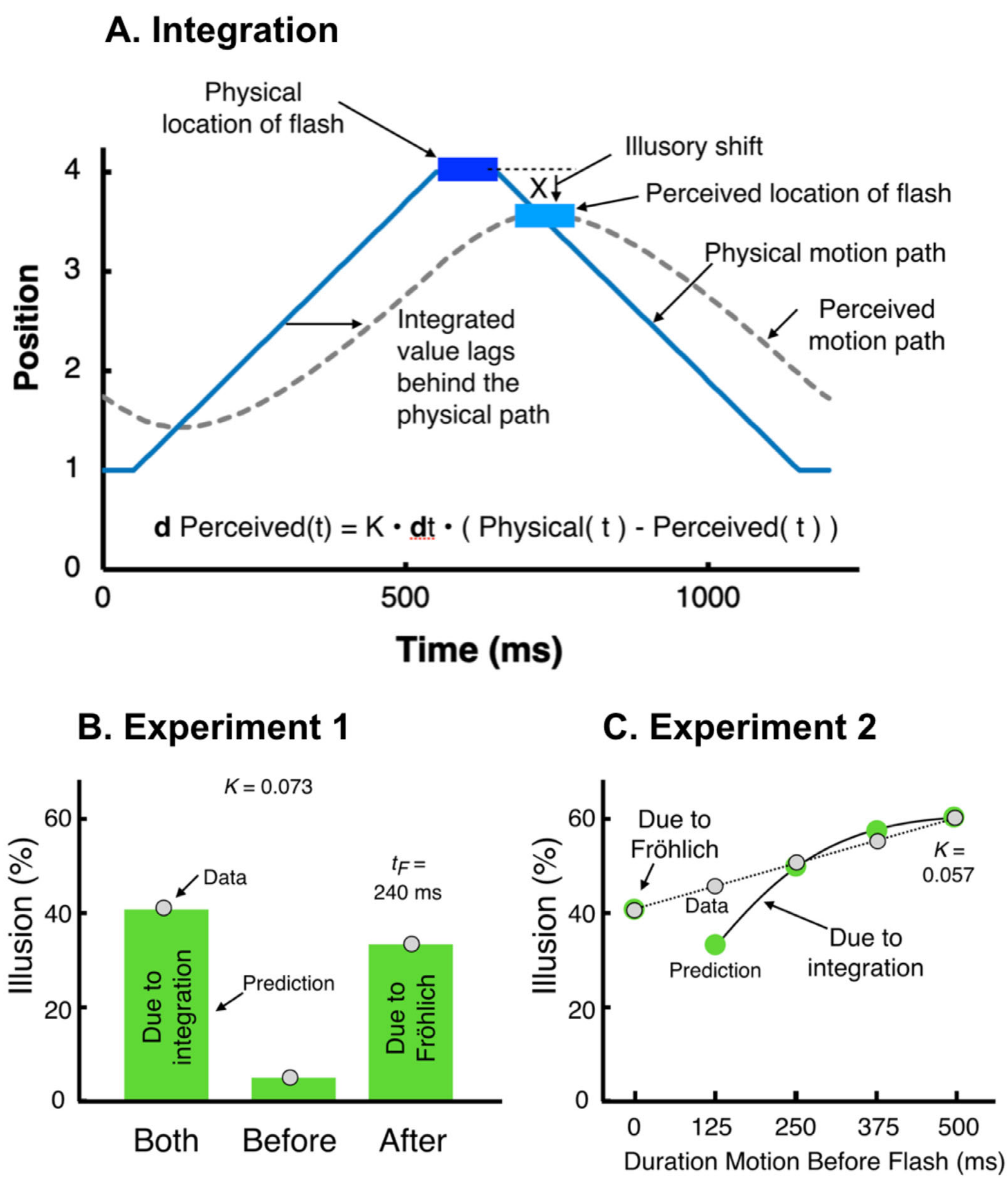


Figure 9. (**A**) Integration model for the condition of motion before and after the flash. The perceived location of the flash is assigned to the maximum of the dashed profile, the perceived location of the motion reversal. Panels (**B**) and (**C**) plot the predictions of the model for the data of Experiments 1 and 2.

on the perceived location of the flash is in the opposite direction – the flash is seen shifted against the direction of motion. In contrast, the post-flash motion is away from the flash and the position shifts the same direction as the motion. This pattern was seen consistently across the three experiments. The second question concerns the absence of effect when the motion is only before the flash (flash terminated). If there is a contribution of motion before the flash, why does it disappear when the motion terminates at the same time that the flash is presented? Finally, there is a significant contribution of motion before the flashed test when there was also motion after but the motion following the flash was in general more than twice as effective as the motion before the flash. What accounts for this imbalance?

We looked first at modeling to address these questions, making a comparison across several possible models: differential latency, extrapolation (see Figures 7A, 7B), averaging (see Figure 8), and integration (see Figure 9). Many of the details of these models have been proposed and extensively debated since Nijhawan's 1994 revival of the flash lag effect (see Nijhawan, 2008 for an overview of the controversies). The modeling results shown in our figures here analyze the illusory shifts of a single edge of the flashed red square. The combined illusion strength between the red and blue squares is then derived from this single shift.

The description of the modeling and the simulations are presented in the Supplementary Materials. The final result of this comparison is mixed: no model can fully account for the data and the perceptual phenomena, although the averaging and integration models do better. Importantly, only the averaging and integration models can place the flash at the shifted location of the motion reversal where it is actually seen. For Experiment 1, the differential latency and extrapolation models predict the results of the three conditions with a single free parameter. In contrast, the averaging and integration models require three free parameters for these three data points. Only the both condition with motion before and after the flash is predicted directly by the averaging and integration processes. The other two conditions of Experiment 1 require independent assumptions of delay. For Experiment 2, the differential latency and extrapolation models cannot predict any effect of motion before the reversal whereas averaging and integration can. However, these last two do not predict the linear effect very well or at all (see Figures 7, 8, 9).

Although these models fail to provide any broad explanation of the data, they do offer several insights into our three main questions that we raised to begin with.

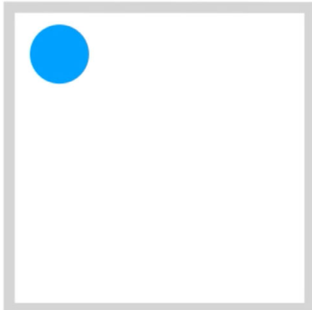
First, why is the illusion in the direction opposite to the motion before the flash but in the same direction as the motion after the flash? The answer most likely is due to some averaging or integration process, as these are based on position, not motion. They generate an illusory shift due to the shorter extent of travel of the averaged or integrated location. This shift brings the flash closer to the center of the motion path and so it is shifted in the direction opposite to the pre-flash motion and in the same direction as the post-flash motion.

Second, if there is a contribution of motion before the flash, why does it disappear when the motion terminates at the same time that the flash is presented? Our results confirm this effect but the modeling did not add any new insights compared to the many previous articles on flash-terminated conditions. Instead of no illusion, both averaging and integration models predicted a strong illusion if the perceived offset was registered with the same delay as the rest of the motion path. The integration model therefore had to add an extended persistence of the temporal offset of motion to account for the lack of illusion, as did Öğmen et al. (2004). This persistence was 370 ms, compared to the integration delay of 110 ms at most other points along the motion path. The averaging model also required a longer delay in assigning the perceived value to the temporal offset of motion (320 ms) to allow the illusion to converge to the veridical location. The averaging delay for other points on the motion path was 185 ms. Whatever the source, these additional delay or persistence effects are not integral parts of the averaging or integration processes. The actual mechanism that suppresses the illusion in the flash-terminated case remains an open question. Recall that the flash-terminated position does show a flash lag illusion (overshoot) if the offset signal is weakened (Maus & Nijhawan, 2009) or absent (Maus & Nijhawan, 2009).

Finally, we have derived the contribution of motion before the flash by subtracting the case with only motion after the flash from the case with motion both before and after. This gave us an empirical estimate of the relative contribution of motion before versus after the flash that favored the motion after the flash. However, the modeling showed that the case of motion only after the flash was never predicted by the averaging or integration models. Contrary to the results, both models predicted no illusion in this case. Both models had to add a Fröhlich effect to produce an illusion in these flash-initiated conditions (Experiment 1 = motion only after and Experiment 2 = 0 ms before). Therefore, our subtraction (motion after illusion minus the motion before and after illusion) does not give a true measure of the contributions of motion before because it is the difference of two independent processes. The relative weight of motion before and after therefore depends on the process, for example, motion before and after the reversal are weighted equally in the averaging model when both are present. Even though the question gets no conclusive answer here, the before versus after ratio is an important empirical signature of the illusion, as we will describe below.

Clearly, the more complex paths for the flash grab illusion are beyond the ability of these basic models. It is probable that two or more processes are operating to produce these illusions – the models suggest that some averaging or integration process may be combined with some delay of visibility of motion onset and offset. The simpler stimuli of the flash lag effect were better fit by these models. Our results in Experiment 2 not only challenged all these models but also point to some process with a very long time constant to produce this linear result over a 500 ms range of motion durations.

Finally, we want to close by drawing attention to the utility of the empirical measure that we have developed here: the relative strength of the motion before versus after the flash. We will show that it can serve as a signature of common mechanisms underlying different illusions. We are investigating two other size and position illusions with motion before and after a flashed test: the Dynamic Ebbinghaus illusion (Mruczek, Blair, Strother, & Caplovitz, 2015; Takao, Watanabe, & Cavanagh, 2021) and the Frame Effect (Özkan et al., 2021; Cavanagh, Anstis, Lisi, Wexler, Maechler, 't Hart, Shams Ahmar, & Saleki, 2022). Movie 4 shows an example for the frame effect that is matched to the right-angled flash grab effect in Experiment 3



Movie 4. The frame follows a square trajectory with a red and blue flash in the same location as the square changes direction. As in Experiment 3, the motion before each flash is vertical and the motion after is horizontal. Due to the frame effect (Özkan et al., 2021), the flashes may appear separated and the angle between them indicates the relative contribution of motion before and motion after the flashes. If the contributions are equal, the flashes will appear to lie on a 45 degree angle. Movie available here, click on slide to start: https://cavlab.net/Demos/Before/Movie4.m4v.

and Movie 3. The motion before the flash is vertical and after the flash it is horizontal. Unlike the case with the flash grab, the offset of the two flashed probes appears to have an angle of about 45 degrees, indicating an equal contribution from motion before and after, rather than the lesser contribution from motion before seen with the flash lag in Experiment 3 here. If verified formally, this suggests that the frame effect does not share underlying mechanisms with the flash grab effect. We will extend this comparison to the Dynamic Ebbinghaus illusion as well as others to determine which do share common mechanisms.

In summary, this study compared the contributions of motion before and after the flash to the flash-grab illusion. The pre-flash motion was found to contribute significantly to the illusion, by as much as 48.5% relative to the contribution of the post-flash motion, as measured by the difference between the both and after conditions in Experiments 1 and 2, and by the effects in orthogonal directions (Experiment 3). Position averaging or integration models provided suggestions for underlying mechanisms.

Keywords: motion induced illusion, position shift, timing, averaging model

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Supplementary Material: Modeling.

Here we summarize the results of the modeling. The predictions are shown in the graphs of the main text and the simulations underlying the modeling are shown in the spreadsheet that is also available with the supplementary material. We examine the predictions of models that have been proposed for the flash grab: extrapolation (van Heusden et al., 2019) and averaging (Cavanagh & Anstis, 2013; Sinico et al, 2009). We also examine models developed for the flash lag effect that can be applied to the flash grab as well. These models compute where the moving stimulus would be at the time of the flash. For the flash *lag*, this gives an offset or lag – a separation between the moving stimulus and the flash. In the case of the flash *grab*, the flash is instead seen transposed to the location of the moving stimulus, not separated from it. Nevertheless, the same computations can be used to predict where the flash *will move to.* These models have been proposed and extensively debated in the decade following Nijhawan's 1994 revival of the flash lag effect. What is new here is that the motion path for the flash grab effect is more of a challenge for these models, especially the results of our Experiment 2. Some of the earlier flash lag models are specific to its dual task nature – that is, first detecting the flash and then attending to the motion (e.g., Baldo & Klein, 1995) so we will not consider these. But we will include the differential latency models which assume different temporal properties for the flash and the motion and the integration (Whitney et al., 2000; Öğmen et al., 2004) and averaging models (Krakelberg & Lappe, 2000).

This generalization of the flash lag models to the flash grab is likely valid for flashes presented at the motion reversal, as is true for our experiments here. In this case, the flash location appears to migrate to the location of the motion reversal. But this migration or "grabbing" process undoubtedly depends on the synchronicity of the flash and the motion reversal that binds them together (Cavanagh & Anstis, 2013). For a flash that is not at the reversal point in time and space, the binding weakens and the flash shift decreases dramatically (Cavanagh & Anstis, 2013). The effect then becomes a separation of the no longer shifted flash from the motion – the flash lag. For the case where the flash is synchronous with the motion reversal, as it is in our experiments, we believe several flash lag models are relevant.

First, we describe how we model the illusion in the expanding and contracting stimulus. The stimulus produces a doubled effect as the blue flashed square becomes larger and the red flashed square, smaller. For simplicity, we will model only a single moving edge of the inner square and the superimposed red flash. We can calculate the size of the shift for that one edge that contributes to the combined illusion reported in experiment 1 and 2.

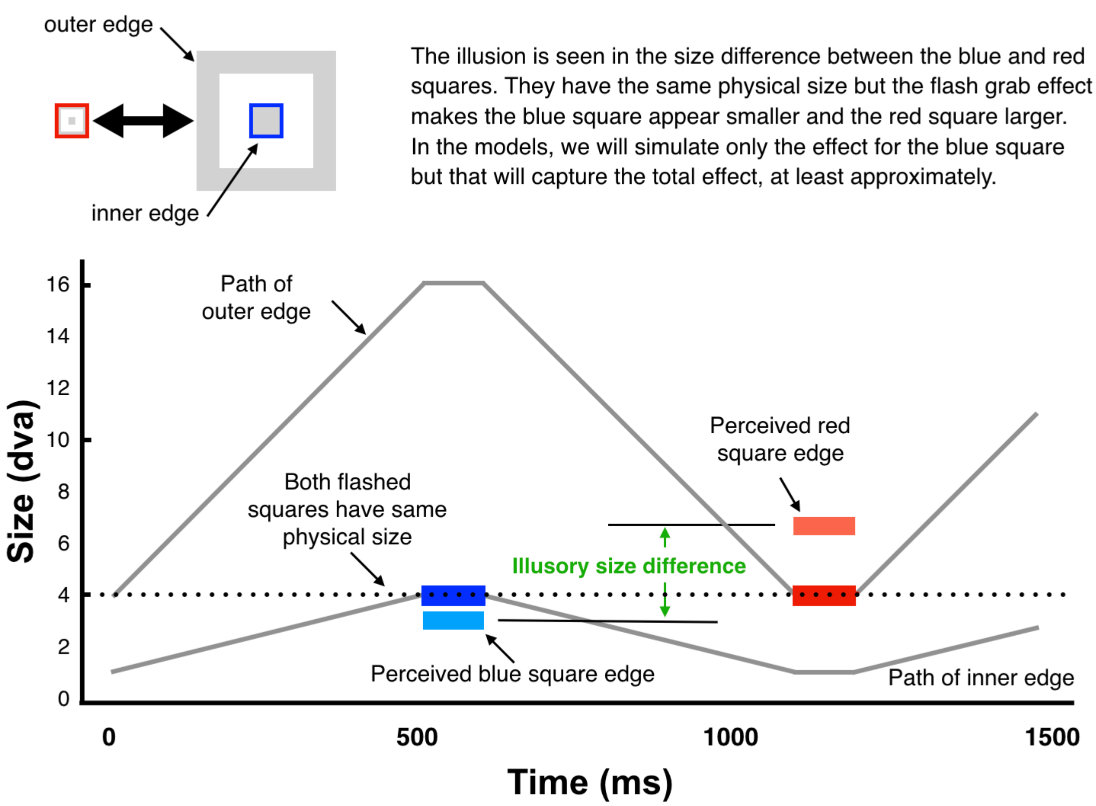

Figure S1. The expanding and contracting square version of the flash grab illusion.

To do so, we link the shift of the modelled flash to the measured illusion between both flashes. In the illusion, the red square gets smaller and the blue square larger. We assume that the size increase for the blue square is four times the decrease in the red square. That is because the outer background edge where the blue square flashes travels four times farther than the edge of the smaller, inner square where red flashes. In Figure S2, these differences are shown below as a change of +4X for the blue square from the starting value of 4 dva, but -X for the red square, again starting from size 4 dva.

The illusion magnitude, M, is the % increase of Blue relative to Red:

$M = 100 \cdot (B / R - 1) = 100 \cdot ((4 + 4X) / (4 - X) - 1)$

$M = 500 \cdot X / (4 - X)$

So the shift X needed to produce the illusion magnitude M is given by

$X = 4 \cdot M / (500 + M)$

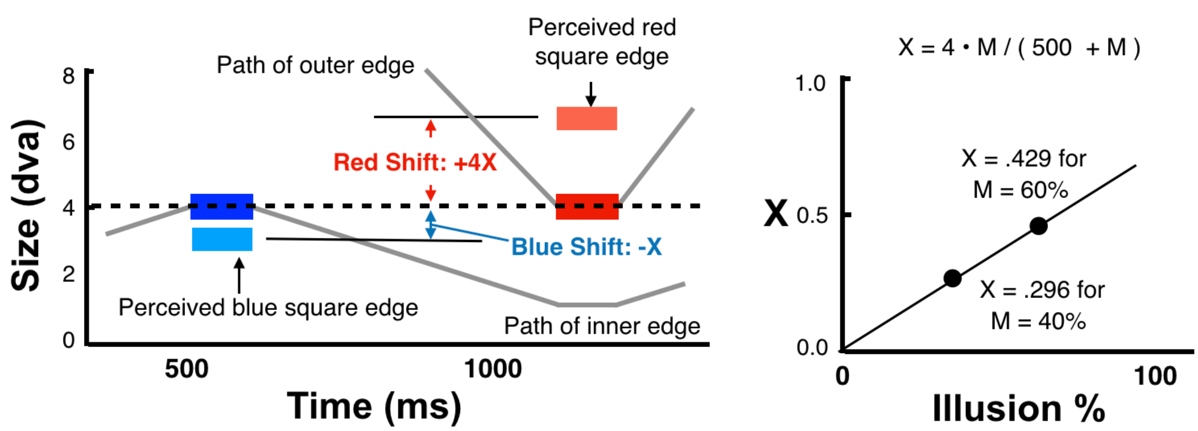

Figure S2. Linking the measured illusion strength M to the modeled shift X of the red flash.

Differential latency.

The differential latency model deals with the neural delays for registering two signals – the flash and the position of the moving stimulus (e.g., Metzger, 1932; Whitney & Murakami, 1998;

Whitney, Murakami, & Cavanagh, 2000). The delay for the motion is shorter because it is a predictable signal that is already being processed. The difference in latencies creates a forward shift in the perceived location of the moving stimulus compared to the flash. Other than being delayed, this version here assumes no other changes in the neural representation of the position of the moving stimulus (some differential latency models apply an integration process to the motion path, e.g, Öğmen et al., 2004, which we will evaluate later). In the case of the flash lag, once the flash is detected, the position of the moving stimulus can be accessed, and the slower latency for

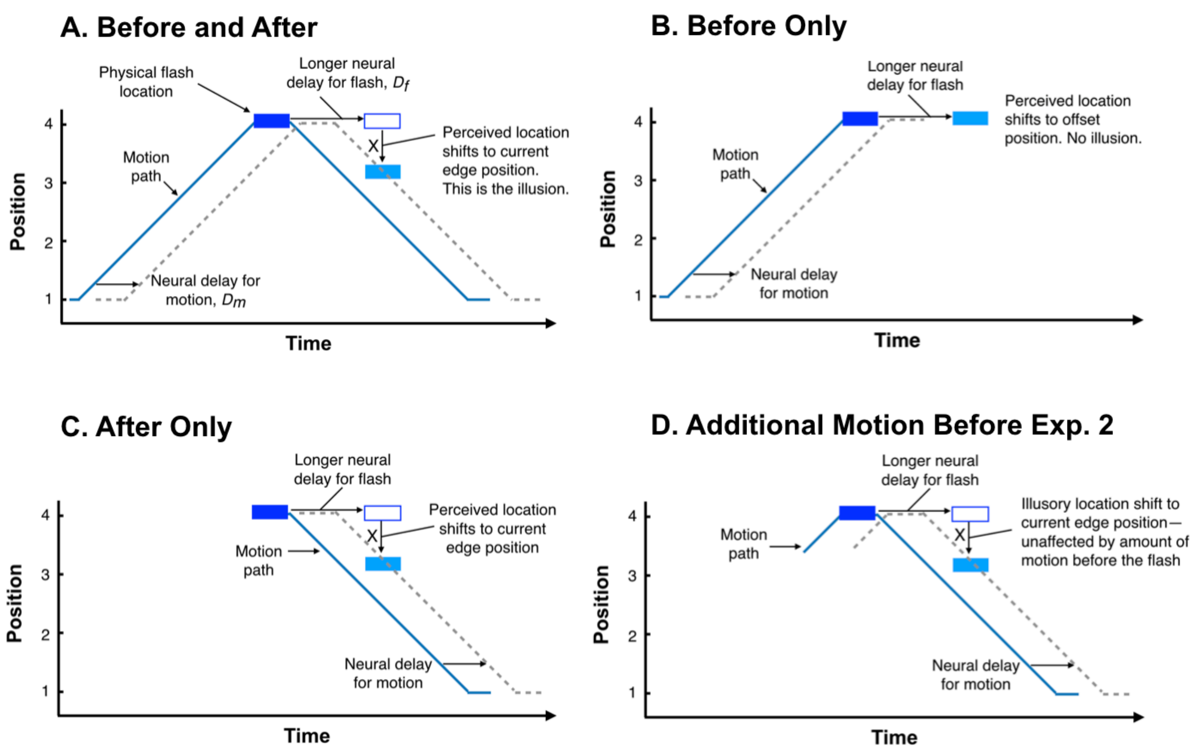

Figure S3. Differential latency model. The gray dashed line represents the delayed neural representation for the motion. The dark red rectangle is the physical flash and the light red rectangle the perceived flash. The illusory position shift is shown as X.

the flash means that the position of the moving stimulus has moved farther along on its path. For the flash grab, in contrast, we assume that once the flash is registered, its position is assigned to the current position of the moving stimulus. Because of the longer delay for the flash, it will be assigned to a location farther along the motion path after the reversal, producing an offset (Fig.

S3A). For Experiment 1, a delay difference of 50 ms produces an illusion of 40%, whereas a delay difference of 74 ms produces an illusion of 60% for Experiment 2. This transfer of the flash location to the position of the moving edge only involves events at and after the time of the flash, so it predicts no illusion for motion present only before the flash (flash terminated, Fig. S3B) and equal illusions for the conditions of motion both before and after the flash, and motion only after the flash (Fig. S3C). It therefore also predicts no change of illusion (Fig. S3D) for additional motion before the flash (Experiment 2).

Overall, the model accounts for some aspects of the data but is unable to account for the contribution of motion before the flash seen in Experiment 2. It also shifts the perceived location of the flash away from the reversal point, something that is never reported. There are also additional drawbacks to the differential latency model that have been discussed in the flash-lag literature. For example, even though this model depends on a delayed perception of the flash relative to the moving bar, temporal order judgements do not reveal any relative delay (e.g., Eagleman, 2000). Given these failures, we can exclude differential latency as a plausible model.

Extrapolation.

The extrapolation model of Nijhawan (1994) proposes that the perceived location of a moving stimulus is extrapolated ahead to compensate for neural delays. The motion is then perceived at its current location. This extrapolation predicts an overshoot when motion stops or reverses whereas the data show an undershoot (Whitney et al., 2000). Hogendoorn and colleagues (Blom, Liang & Hogendoorn, 2019; van Heusden, Harris, Garrido, & Hogendoorn, 2019) have modified this extrapolation model for the flash grab stimulus by assuming that there is a compensation for this overshoot that actually overcompensates – producing an illusion in the correct direction. However, this extra step involves the unlikely process of extrapolation based on an already extrapolated path. Moreover, it is not necessary as the extrapolation naturally corrects itself. Specifically, the extrapolation returns to zero as soon as the motion stops and it reverses when the motion reverses. These properties match closely the effects from van Heusden et al. (2019), although here without any smoothing of the extrapolated path. With a small adjustment for a slightly longer latency for the flash, extrapolation generates the same predictions as differential latency and has the same shortcomings (Fig. S4). It shifts the perceived location of the flash away

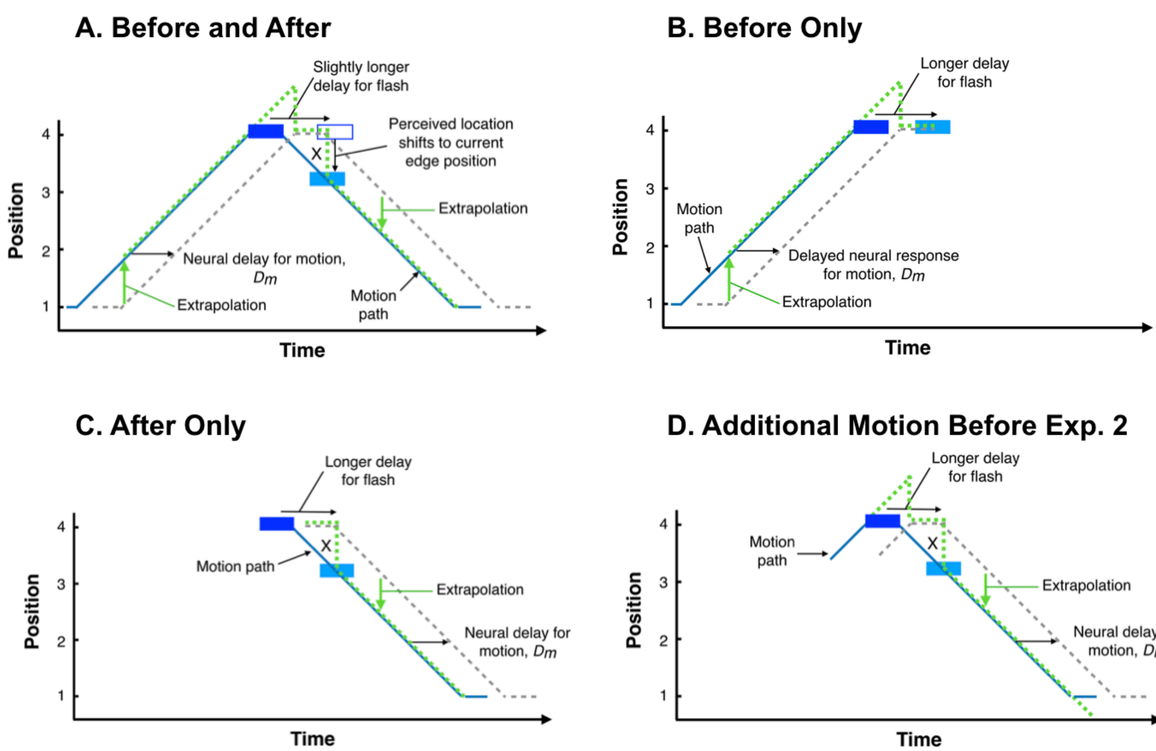

Figure S4. Extrapolation model. The gray dashed line represents the delayed neural representation for the motion and the dashed green line the extrapolated positions shifted in the direction of the motion to compensate for the delay. During part of the motion trace, the green line lies on top of the physical motion path. Other conventions as in Fig. S3

from the reversal point, which is even earlier than the physical reversal due to the early overshoot before the motion stops. It is unable to account for the contribution of motion before the flash (Experiment 2).

Averaging.

Averaging (Krakelberg & Lappe, 2000; Cavanagh & Anstis, 2013; Whitney et al., 2000; Sinico et al., 2009) computes the average value of position within a time window and assigns that value as the perceived location for the time point of the leading edge of the window. Note that position averaging must operate on a higher order representation of position, not the image itself as the averaging would make the moving background appear as little more than a smear if it were applied to the image. When applied to back-and-forth motion, averaging shortens the apparent extent of the path (Whitney et al., 2000; Sinico, et al., 2009; Cavanagh & Anstis, 2013), shifting the location of the motion reversal and delaying it by half the window width (Fig. S5A). We assign the perceived location of the flash to the shifted location of the reversal. Because the averaging model is based on position, not motion, it answers the first of our three points and generates an offset that is opposite to the direction of the pre-flash motion and yet in the same direction as the post-flash motion.

Overall, the averaging model has several good points. It can assign the flash location to the perceived location of the motion reversal. It also explains why the illusion is in the direction of the motion following the flash but also in the direction of motion before the flash (because it is based on a position average, not motion). However, in Experiment 1, the averaging cannot account for the flash initiated or flash terminated results, both of which require separate assumptions about the delay in visibility (Fig. S5B and C). For the motion onset, averaging gives the veridical location. Öğmen et al. (2004) dealt with this for the similar integration model by delaying the point where the moving stimulus becomes visible (equivalent to the Fröhlich effect). Here we use a delay in visibility of half the window width, the same delay as for the reversal point. This matches the data reasonably well. For motion offset, the flash terminated condition, a delay of the full window width is required to give no illusion.

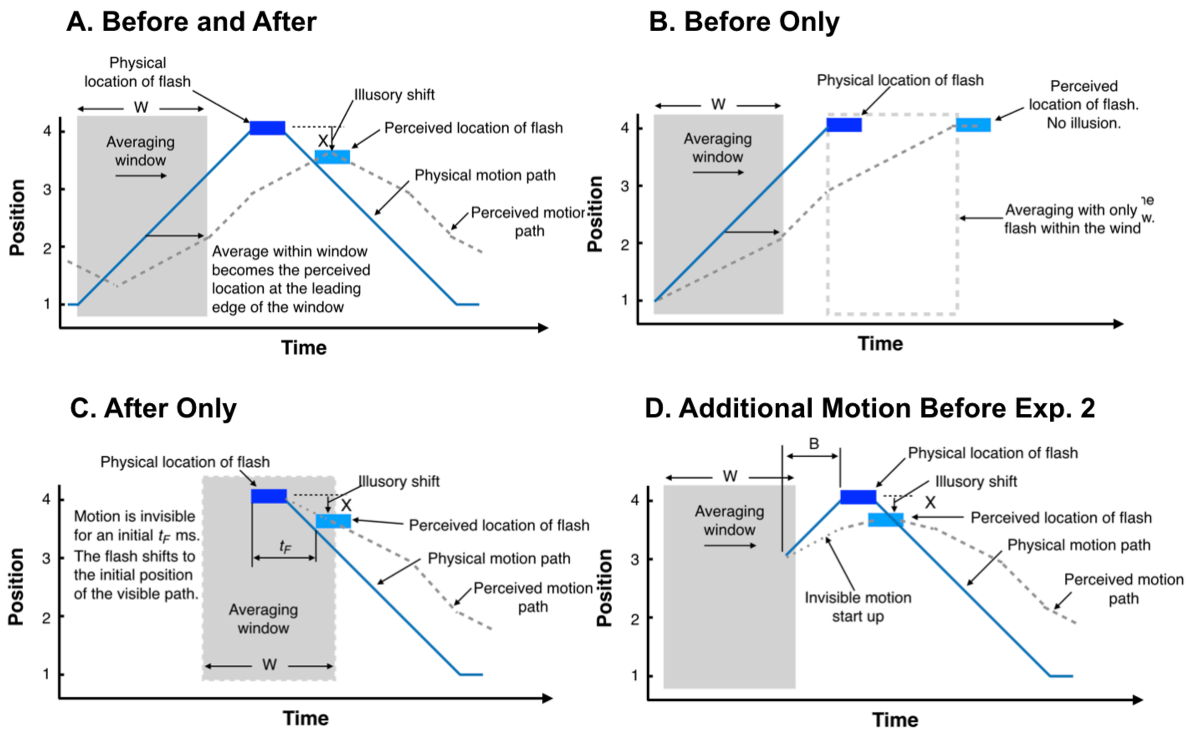

Figure S5. Averaging model. The gray dashed line represents the averaged representation of position within the window. The perceived location of the flash is assigned to the maximum of the position trace, the perceived location of the reversal in direction in panels A and D. The flash location is set by delay parameters in panels B and C. Other conventions as in Fig. S3.

The width of the temporal window to predict the Both result is 370 ms in Experiment 1 and 450 ms in Experiment 2. This is shorter than the 600 ms averaging period reported by Krekelberg and Lappe (2000). The delay in visibility for the window centered on the flash (W/2 + 50) is 235 ms in the Motion After condition of Experiment 1 and 275 ms in Experiment 2. These values are long compared to published values for the equivalent Fröhlich effect (80 ms, Adamian & Cavanagh, 2017; 110 ms, Krischfield & Kammer, 1999). The averaging also predicts no illusion for motion only before the flash (flash terminated) as it continues to give the veridical location once only the motion reversal location is at the trailing edge of the window. To do so, however, it requires a delay in the perceived flash equal to the window width (370 to 450 ms), twice the delay it gives for the reversal point in the other conditions. The averaging model also predicts additional illusory position shift for additional motion before the flash (Fig. S5D), but only over a restricted range – for up to 175 ms of additional motion before the flash (W/2-50). Its overall prediction for Experiment 2, even though better than the previous two models, still does not give a good match to the data (Fig. 8B, main text). Also, the result for 0 ms of motion before the flash (equivalent to the Motion Only After condition of Experiment 1) is again dependent on an arbitrary delay of one half the window width.

Integration.

The integration model was originally proposed for the flash lag (Öğmen et al, 2004) but is applicable for the flash grab as well given that the flash position does not lag the motion but is instead transferred to the shifted location of the motion reversal. The perceived location is the integral of difference of the input position and the current perceived location (adapted from Öğmen et al., 2004). This again blunts the reversal in the flash grab and produces a delay. In Experiment 1, the integration model, like the averaging model, predicts no effect for motion that starts with the flash, and a delay of 180 ms (Exp. 1) or 205 ms (Exp. 2) in the visibility of the onset is required to give the observed result (equivalent to the Fröhlich effect). Also, we have to assume that when motion is present only before the flash (flash terminated), there is a continuing activity of the motion offset location to drive the integration toward it (as in Öğmen et al, 2004 for flash terminated condition, Fig. 12). This persisting trace of the motion offset is problematic as it must be quite long, 370 ms, whereas Whitney et al. (2000) have demonstrated with masking that persistence does not contribute to the flash lag persistence.

Overall, the flash is seen at the reversal point, and there is some effect of motion before the flash as seen in Experiment 2. However, the Experiment 1 data require 3 parameters for 3 data points and two of these parameters are for delays unrelated to integration process. The effect for additional motion before the flash is close but not fully linear like the data and also relies on a second, separate delay parameter for the 0 ms condition.

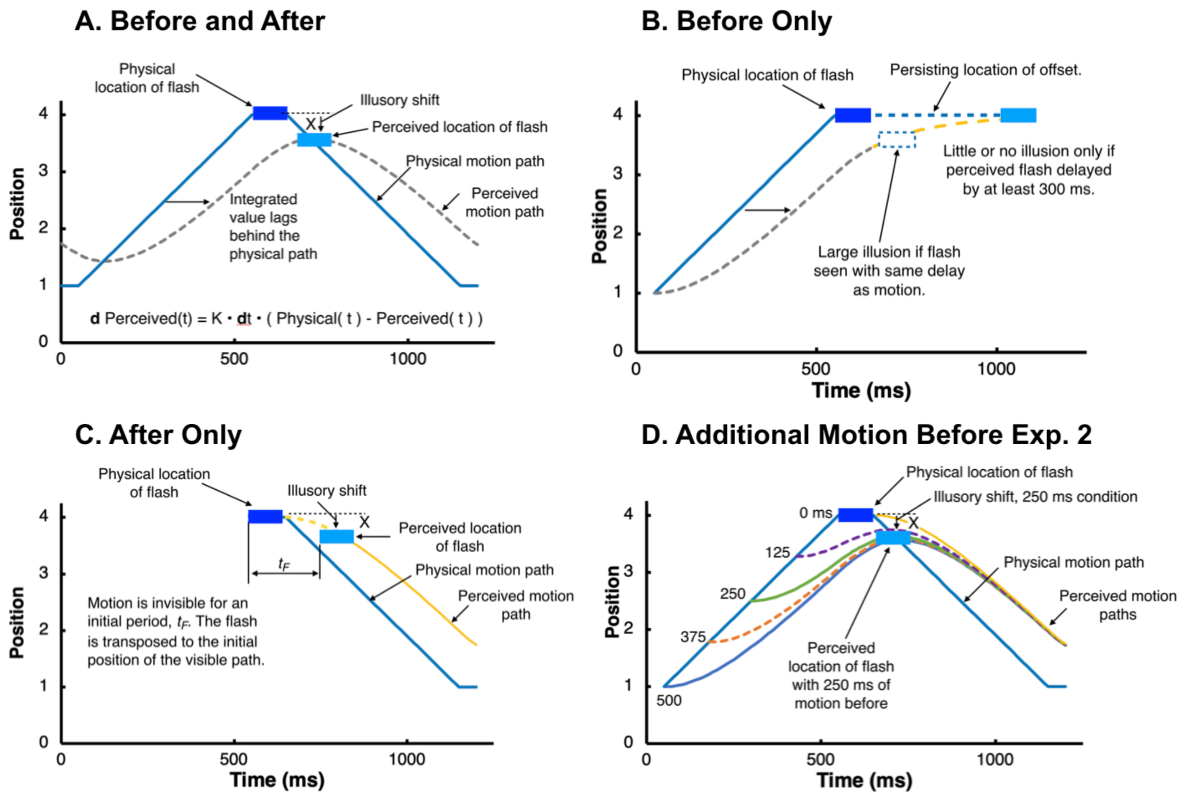

Figure S6. Integration model. The gray dashed line represents the integrated representation of position within the window in panels A and B. The perceived location of the flash is assigned to the maximum of the position trace, the perceived location of the reversal in direction in panels A and D. The flash location is set by delay parameters in panels B and C. Panel D shows the predicted motion traces for the 5 conditions and the flash shift for 250 ms of additional motion before the flash. Other conventions as in Fig. S3.

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