Motion extrapolation in the flash-lag effect depends on perceived, rather than physical speed

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Acknowledgements

This study was supported by an Australian Research Council (ARC) Discovery Projects Grant awarded to H.H. (DP180102268).

Commercial relationships: none.

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Abstract

In the flash-lag effect (FLE), a flash in spatiotemporal alignment with a moving object is often misperceived as lagging behind the moving object. One proposed explanation for the illusion is based on predictive motion extrapolation of trajectories. In this interpretation, observers require an estimate of the object's velocity to anticipate future positions, implying that the FLE is dependent on a neural representation of perceived velocity. By contrast, alternative models of the FLE based on differential latencies or temporal averaging should not rely on such a representation of velocity. Here, we test the extrapolation account by investigating whether the FLE is sensitive to illusory changes in perceived speed when physical speed is actually constant. This was tested using rotational wedge stimuli with variable noise texture (Experiment 1) and luminance contrast (Experiment 2). We show for both manipulations, differences in perceived speed corresponded to differences in the FLE: dynamic versus static noise, and low versus high contrast stimuli led to increases in perceived speed and FLE magnitudes. These effects were consistent across different textures and were not due to low-level factors. Our results support the idea that the FLE depends on a neural representation of velocity, which is consistent with mechanisms of motion extrapolation. Hence, the faster the perceived speed, the larger the extrapolation, the stronger the flash-lag.

Keywords: position perception, flash-lag effect, perceived speed, motion extrapolation, noise texture, luminance contrast, spatial vision, motion

1. Introduction

In the process of visual perception, delays incur as information encoded by the retina is transmitted to the visual cortex (Schmolesky et al., 1998). Neural processing across the visual hierarchy subsequently takes time. By the time a time-varying stimulus—such as a moving object—is processed, its position information will already be outdated (De Valois & De Valois, 1991). More importantly, the object will continue to move in the physical world and its perceived position will lag at any given time (Maunsell & Gibson, 1992). The impact of such delays should be significant when localizing moving objects, but despite this, we seem to be able to accurately pursue and interact with even fast-moving objects (Smeets & Brenner, 1995). One proposed explanation is that neural delays are partly, perceptually compensated by motion extrapolation (Nijhawan, 1994, 2002). The visual system is thought to predict the trajectory of an object by actively extrapolating future positions so that observers can perceive it as closely as possible to its veridical positions.

A strong case for motion extrapolation has been made as the basis of a motion-induced position shift known as the flash-lag effect (FLE), which was first described by Metzger (1932) and rediscovered by MacKay (1958). It was reinterpreted by Nijhwawan (1994), who demonstrated that a flashed target presented as physically aligned to a continuously moving bar is misperceived as spatially lagging behind the bar. Although the illusion is argued to have many possible causes, Nijhawan proposed that the perceived position of the bar is actually shifted forward along its trajectory, resulting in a displacement between the two stimuli. That is, the observer's percept of the moving object is already extrapolated. Insofar as motion extrapolation compensates for the distance traveled during the time required for neural transmission and processing, then this sort of shift would be expected for the moving object but not for the flash (Nijhawan, 2002).

The illusion appears to be stronger with increasing speed, although not necessarily linearly (Wojtach, Sung, Truong, & Purves, 2008). This implies that the brain might rely on a symbolic, neuronal representation of motion—where an object is (position) and how fast it is moving (velocity)—in the computation of predicting current or future positions based on its motion history (Rosenbaum, 1975; Nijhawan & Wu, 2009; Crick and Koch, 1995; Pollen, 2003). Theoretically, the extrapolation process could depend on representations of physical velocity or, alternatively, of

perceived velocity. Even though the two share many properties, speed perception is often influenced by various factors such as contrast (Stone & Thompson, 1992), transiency/duration (Treue, Snowden, & Andersen, 1993), and spatial (Smith & Edgar, 1990) and temporal frequency (Shen, Shimodaira & Ohashi, 2003), so observers tend to under/overestimate the speed at which objects are moving. According to this model, the FLE could vary with perceived speed.

In alternative explanations of the FLE, however, the illusion has been generally attributed to temporal processes that cause the moving object and the flash to appear misaligned only in time (see Krekelberg and Lappe (2001), Nijhawan (2002, 2008), Hubbard (2014), and Hogendoorn (2020) for reviews). The FLE has been described to result from attentional shifting (Baldo & Klein, 1995; but see Khurana & Nijhawan, 1995; Khurana, Watanabe, Nijhawan, 2000), differential processing latencies (Purushothaman, Patel, Bedell, & Ögmen, 1998; Eagleman & Sejnowski, 2000; Whitney, Murakami, & Cavanagh, 2000; Ögmen, Patel, Bedell, & Camuz, 2004; but see Nijhawan, Watanabe, Khurana, & Shimojo, 2004; Eagleman & Sejnowski, 2000; Arnold, Ong, & Roseboom, 2009), temporal averaging of positions (Krekelberg & Lappe, 1999; Whitney et al., 2000; Brenner & Smeets, 2000), or postdiction mechanisms (Eagleman & Sejnowski, 2000; Eagleman & Sejnowski, 2007). In these accounts, the magnitude of the FLE would also be expected to increase with speed of the moving object—but only in the form of a temporal offset which translates into a spatial error (Krekelberg and Lappe, 1999, 2000). Nijhawan's (1994) motion extrapolation account therefore uniquely requires an explicit calculation to estimate the distance the object will travel, and only it predicts that the magnitude of the FLE modulates as perceived speed is altered. Here we test this unique prediction based on motion extrapolation.

2. Experiment 1

One method of manipulating perceived speed is by adding noise to a moving object (Treue et al., 1993). Carlson, Schrater, and He (2006) presented a moving object comprising a smaller square with static noise texture superimposed on a larger square with dynamic noise texture. When the object moved (i.e. the two squares moved 'together' in the same direction), the area of static noise consistently appeared to lag behind the area of dynamic noise, causing an illusory percept that they called the Floating Square illusion. Importantly, they found that dynamic noise appeared to move

faster than static noise at the same physical speed, to which they concluded that the lag was due to a difference in the perceived speeds of the two textures. The results of this experiment are consistent with the idea perceived speed influences motion extrapolation, and in line with this study, our motion stimuli contained either static or flickering dynamic noise. Participants carried out a spatial localization task where they reported, in a two-alternative forced-choice task (2AFC), whether a rotating stimulus or a flashed target appeared ahead of the other, i.e. leading in the direction of motion. This task is hereafter referred to as the flash-lag task (Experiment 1A), which served to measure extrapolation performance. A control speed-discrimination task (Experiment 1B) was used to test if the noise textures actually differed in perceived speed. We hypothesized that if the FLE is sensitive to a change in perceived speed, then both the perceived speed and perceived flash-lag would increase for dynamic noise relative to static noise stimuli. If the FLE is not dependent on perceived speed, then there should be no difference in the FLE magnitudes between the two noise textures.

2.1 Participants

A total of 30 observers participated in Experiment 1A, and 20 observers participated in Experiment 1B. A further 49 observers participated in both experimental tasks, who were intended for correlation analysis (see *2.4.3 Individual differences*). Two observers were excluded from Experiment 1A because their results significantly violated normality (Shapiro-Wilk: $p < 0.001$; Kolmogorov-Smirnov: $p < 0.001$). One observer was excluded from both tasks for ignoring the instructions and incorrectly performing the tasks. Together, this yielded a total of 76 observers in Experiment 1A (23 males, mean age 24.2 years and SD 6 years) and 68 observers in Experiment 1B (23 males, mean age 24.2 years and SD 5.6 years), with 48 of these observers having completed both tasks.

All observers were naïve to the purpose of the experiment, right-handed, and reported normal or corrected-to-normal vision. Observers gave informed consent and were reimbursed 10 AUD per hour for their participation in the experiment. The study was conducted in accordance with the Declaration of Helsinki and approved by the University of Melbourne Human Research Ethics Committee of the Melbourne School of Psychological Sciences (Ethics ID 1954146.2).

2.2 Stimuli

All stimuli were presented on a 24.5-inch ASUS ROG PG258Q monitor (1920 x 1080 resolution, 200Hz), controlled by an HP EliteDesk 800 G3 TWR running MATLAB R2017b (Mathworks, Natick, NA) with PsychToolbox 3.04.14 extensions (Kleiner et al., 2007). Participants sat in a light-attenuated room and viewed the stimuli from a headrest at a distance of 60 cm from the monitor.

The primary stimulus consisted of a wedge segment from an annulus, displayed around a centrally presented white fixation point (Figure 1). Its inner and outer edges were 4.05° and 6.75° of visual angle away from the fixation point and subtended 45° of polar angle along the radial axis. The wedge rotated within the annulus, in randomly interweaved clockwise or counter-clockwise circular motion at a fixed speed of 200° of polar angle/s.

The stimulus was defined by one of two textures: either a filtered noise texture or a square checkers pattern. Filtered noise was created by applying a low-pass filter on white noise at 0.5 cycles/degree, and square checkers were created using 5x5 pixel black and white checkerboard pattern. Dynamic noise textures were created using a new set of pixels, of no correlation with the previous set, chosen at every frame. The background annulus always contained absolutely static texture, because observers would be unable to distinguish the wedge from the background annulus if both textures were dynamic. Motion for static wedge against its annulus was thus defined as second-order motion.

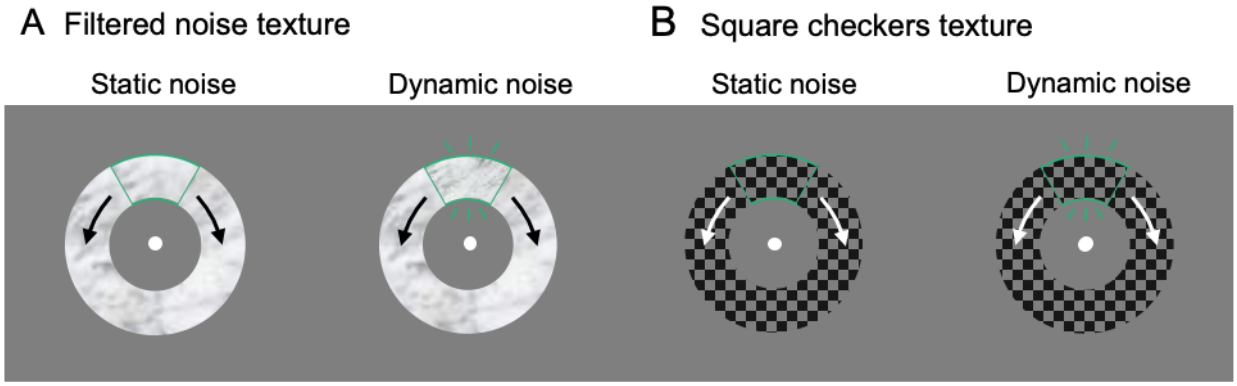

Figure 1. Example stimuli used in Experiment 1. For texture types (A) filtered noise and (B) square checkers, the primary stimulus consisted of a rotating wedge segment (green outline) superimposed onto an annulus with the same static noise. For illustrative purposes, the flashing effect of dynamic noise is highlighted using a starburst pattern in this figure.

In Experiment 1A, observers compared the position of the primary stimulus to a briefly flashed target stimulus. The target stimulus was defined by the same static texture as the primary stimulus and was flashed along the inner circumference of the annulus. Its inner and outer edges corresponded to 2.43° and 3.78° of visual angle from fixation and subtended 45° of polar angle along the radial axis.

In Experiment 1B, observers compared the speed of the primary stimulus to a previously presented reference stimulus. The reference stimulus was a solid black wedge the same size and shape as the primary stimulus, presented on a gray background. The speed of the moving stimulus was constant at 200° of polar angle/s, but the speed of the reference varied across trials according to a staircase procedure (see *2.3 Procedure* below). The primary and reference stimuli always rotated in the same direction on a given trial, which was randomly chosen at the start of each trial.

2.3 Procedure

2.3.1 Experiment 1A: Flash-lag task

Each trial consisted of a stimulation sequence of approximately 2s (Figure 2). The primary stimulus was presented against a gray background, and the wedge began rotating from a random position in the annulus. After 850, 1000, or 1150ms (chosen at random), the target stimulus flashed briefly for 15ms along the primary stimulus' trajectory. The primary stimulus continued rotating for the remainder of the sequence (1150, 1000, or 850ms) and then disappeared. Participants were instructed to fixate a white central point throughout all trials while they judged whether the rotating or flashed wedge was spatially ahead in the direction of motion. They had up to 5s to respond using a keypress as a method of two-alternative forced choice (2AFC) – 'i' for inner (target stimulus) or 'o' for outer (primary stimulus) – which prompted the next trial.

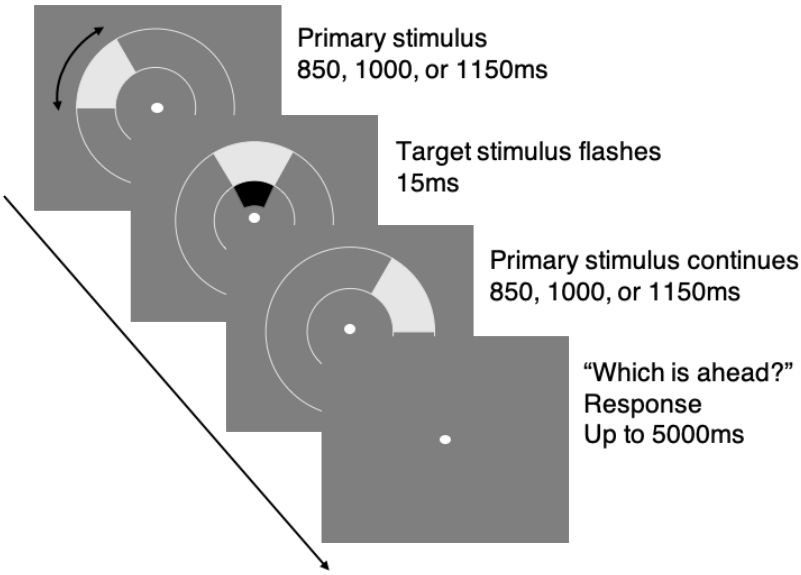

Figure 2. Schematic illustration of Experiment 1A. A fixation point was shown on the center of the screen at the onset of each block. The stimulation sequence began with the primary stimulus rotating inside an annulus. The target stimulus flashed at a randomly chosen moment during the sequence. At the end of the sequence, observers were asked to respond using a keypress. Once the response was made, the next trial began immediately. Each trial lasted up to 7s, the stimulation sequence lasting approximately 2s.

The physical alignment between the primary stimulus and the target was driven by a 1-up, 1-down staircase procedure, with trials randomly drawn from two interleaved staircases. One staircase started at +20° of polar angle difference (primary stimulus ahead of flash) and the other started at 0° (physically aligned) during the central presentation frame. Depending on the participant's response, the difference was adjusted by ±2° for the following trial drawn from that staircase. Observers completed 120 trials from each staircase, and the final 60 points of each staircase were averaged to estimate the point of subjective equality (PSE): the displacement at which the moving and flashed wedges were perceived to be aligned.

Trials were blocked into 4 conditions. Each condition block consisted of 120 trials lasting up to 7s, for a total of 480 trials over 4 blocks. The conditions were determined based on a combination of *noise type* (static or dynamic) and *texture type* (filtered noise or square checkers). All participants completed a practice block of 12 trials before completing the rest of the experimental

blocks. The order of experimental blocks was randomized for observers who completed only Experiment 1A and counterbalanced for those who completed both Experiment 1A and 1B. Between each block, participants could take a self-paced break. The total testing duration was approximately 30 minutes.

2.3.2 Experiment 1B: Speed-discrimination task

Each trial began with the presentation of the reference stimulus at a random position against a grey background (Figure 3). The reference stimulus rotated for either 1500, 1750, or 2000ms (randomly chosen) and then disappeared. The primary stimulus from the above flash-lag task (herein test stimulus) appeared from a random position within the annulus and rotated for 1500, 1750, or 2000ms (randomly chosen) until the sequence ended. We varied the presentation duration to ensure observers could not reliably base their responses on the difference between distance traveled. Participants were instructed to fixate the white central point throughout all trials while they judged whether the reference or test wedge rotated faster around the fixation point. They had up to 5s to respond using a keypress to indicate which of the two stimuli was perceived to move faster: '1' for first (reference stimulus) or '2' for second (test stimulus).

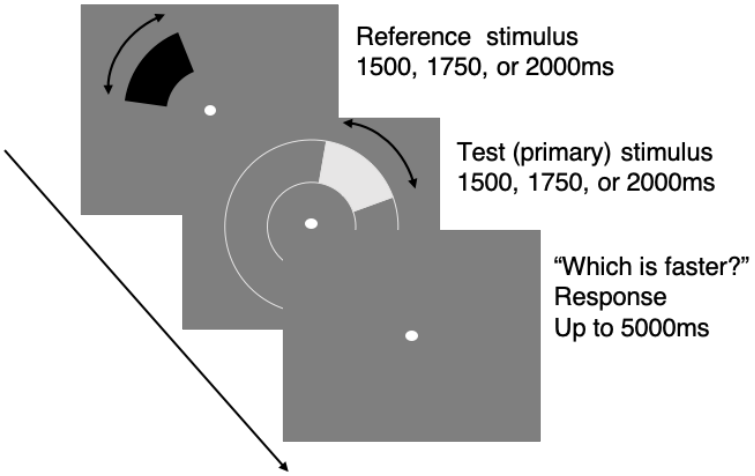

Figure 3. Schematic illustration of Experiment 1B. A fixation point was shown on the center of the screen at the onset of each block. During the stimulation sequence, the reference and test wedges were presented sequentially. At the end of the sequence, observers were asked to respond using a keypress. Once a response was made, the next trial began immediately. Each trial lasted up to 9s, the stimulation sequence lasting up to 4s.

The speed of the test stimulus was constant at 200° of polar angle/s. The speed of the reference stimulus changed using a similar staircase procedure to vary the speed ratio of the two stimuli, and trials were drawn from one of two interleaved staircases. Because speed perception follows a logarithmic function, staircases were adjusted by multiplying and dividing, rather than adding and subtracting. The first staircase was initialized at 1.075^{7}, and the second started at 1.075^{-7}, with step size set to 1.075 for both. The value of the staircase on a given trial was proportionate to the relative speed of the reference stimulus compared to the test stimulus. For example, 1.075^{7} (~1.66) indicated that the reference wedge rotated at 166% of the speed of the test wedge (166% of 200°/s). Depending on the observer's response, the speed on the next trial drawn from a given staircase was adjusted by multiplying or dividing by 1.075. Observers completed 72 trials from each staircase, and the geometric mean of the last 36 trials from both staircases determined the PSE: the speed at which the reference was perceived to match the speed of the test wedge.

Trials were blocked into the same 4 conditions used in Experiment 1A (*noise type* (static or dynamic noise) and *texture type* (filtered noise or square checkers)). All observers completed a total of 4 blocks. Observers who completed only Experiment 1B completed 72 trials per block (for a total of 288 trials) and observers who completed both Experiment 1A and 1B completed 144 trials per block (for a total of 576 trials). The total testing duration was 25 and 50 minutes, respectively.

2.4 Results

We tested for perceived flash-lag and/or perceived speed differences in each condition using a two-way repeated measures ANOVA, with the factor of *noise type* (static or dynamic noise) and *texture type* (filtered noise or square checkers). We then performed post hoc paired-samples *t*-tests (two-tailed) with Bonferroni corrections to estimate the differences in the FLE magnitudes and/or perceived speed of the primary stimulus when it was presented in static noise compared to dynamic noise.

2.4.1 Experiment 1A: Effect of noise texture on perceived flash-lag

A repeated measures ANOVA revealed a significant main effect of noise type ($F_{1,75} = 5.14$, $p = 0.026$), with greater FLE magnitudes observed for dynamic noise than for static noise wedges (Figure 4A). There was no significant main effect of texture type ($F_{1,75} = 1.61$, $p = 0.209$) or an interaction effect between the two factors ($F_{1,75} = 0.81$, $p = 0.37$). Follow-up *t*-tests showed that mean FLE magnitudes was significantly larger for dynamic noise compared to static noise stimuli in the filtered noise condition ($t_{75} = 2.49$, $p = 0.015$), but the difference did not reach significance in the square checkers condition ($t_{75} = 1.03$, $p = 0.309$).

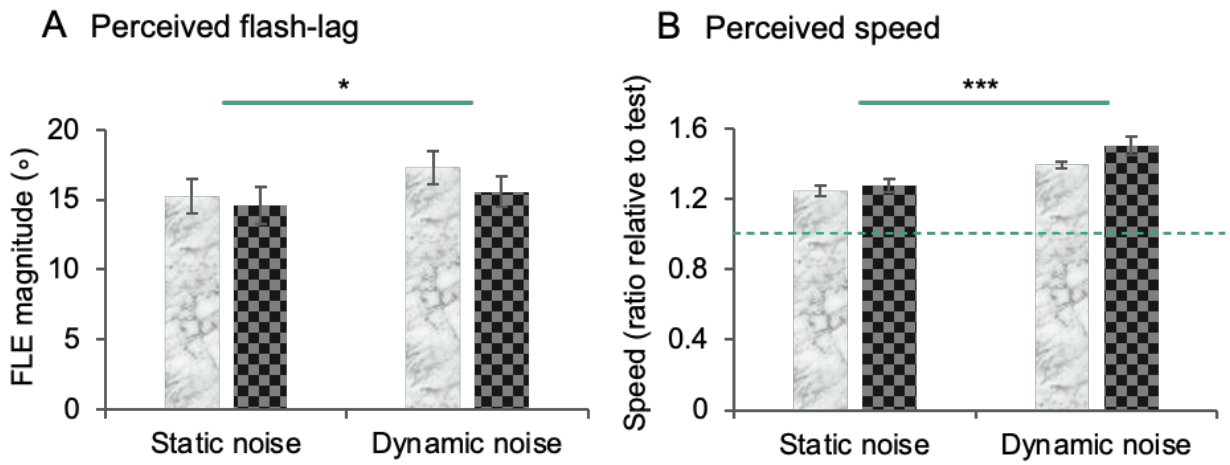

Figure 4. Results of Experiment 1A and 1B. For illustrative purposes, the bars are highlighted with corresponding textures in this figure. (A) Bar graph comparing mean FLE magnitudes between static and dynamic noise wedges across both texture conditions in Experiment 1A. (B) Bar graph comparing mean perceived speeds of static and dynamic noise wedges across both texture conditions in Experiment 1B. Perceived speed was calculated as a ratio of the reference speed relative to the test speed. The baseline speed is indicated as y = 1. Error bars represent standard errors across observers. Asterisks above the bars indicate statistically significant main effect of noise type. * denotes $p < 0.05$. *** denotes $p < 0.001$.

2.4.2 Experiment 1B: Effect of noise texture on perceived speed

A repeated measures ANOVA showed a significant main effect of noise type on perceived speed ($F_{1,67} = 35.82$, $p < 0.001$), with greater perceived speeds reported for dynamic noise than for static noise wedges (Figure 4B). Follow-up *t*-tests showed that this effect was significant in both filtered noise ($t_{67} = 4.08$, $p < 0.001$) and square checkers ($t_{67} = 5.33$, $p < 0.001$) conditions. We also

observed a main effect of texture type ($F_{1,67}$= 11.5, p = 0.001) but no significant interaction effect ($F_{1,67}$ = 2.518, p = 0.117).

2.4.3 Individual differences

To further investigate the possible relationship between perceived speed and the FLE, we examined correlations for the 48 observers that completed both Experiment 1A and 1B. We hypothesized that the effects of dynamic noise on the FLE magnitudes and perceived speed might correlate across observers. Observers for whom dynamic noise greatly increased perceived speed would also be expected to report large changes in the FLE; and conversely, observers with minimal (or negative) effects of dynamic noise on perceived speed would be expected to show corresponding small or negative effects on the illusion. However, Pearson's correlation (two-tailed) revealed no significant correlation between the two measures in either filtered noise (r = 0.15, p = 0.3) or square checkers (r = 0.07, p = 0.64) conditions.

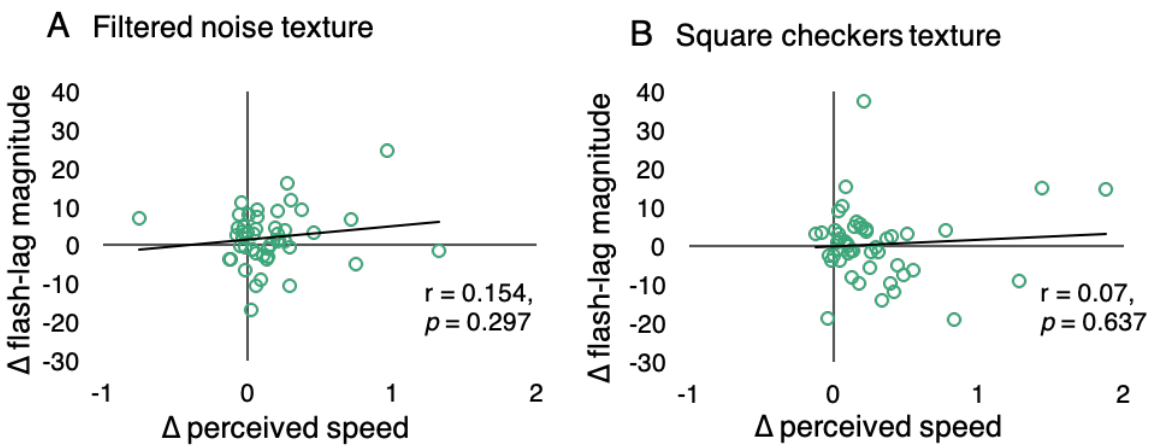

Figure 5. Mean [dynamic-static] differences in the FLE plotted as a function of mean differences in perceived speed for (A) filtered noise and (B) square checkers texture conditions.

3. Experiment 2

The results from Experiment 1 demonstrate that, in line with the motion extrapolation account, adding dynamic compared to static noise is accompanied by increases in the magnitude of the flash-lag effect (FLE). To provide confidence that the effect is due to changes in perceived speed

rather than unknown low-level factors, we carried out a parallel set of experiments using a different manipulation in Experiment 2: by varying luminance contrast. It is widely reported that speed is underestimated at low contrasts (Thompson, 1982; Blakemore & Snowden, 1999; Anstis, 2003), which has been argued to explain why drivers frequently drive too fast under foggy conditions (as over-compensation; Snowden, Stimpson, & Ruddle, 1998; Anstis, 2003; but see Owens, Wood, & Carberry, 2010; Pretto, Bresciani, Rainer, & Bülthoff, 2012). However, the effect of contrast also appears to depend on velocity and luminance, reversing direction for high physical speeds (Thompson, Brooks, & Hammett, 2006; Hawken, Gegenfurtner, & Tang, 1994) and low luminance (Vaziri-Pashkam & Cavanagh, 2008, 2011). Here we changed the contrast of the moving object against a uniform background. Observers completed identical flash-lag and speed-discrimination tasks as in Experiment 1 to explore whether an independent manipulation of perceived speed similarly affects the FLE.

3.1 Participants

As for Experiment 2, we opted for small-N methods. Seven observers (3 males, mean age 25.3 years, SD 3.4 years) participated in the experiment. All observers had previously participated in psychophysical experiments and completed both Experiment 2A (Flash-lag) and 2B (Speed-discrimination).

3.2 Stimuli

Stimuli were similar to those used in Experiment 1, with the following exceptions (Figure 6). Observers viewed the primary stimulus moving on a rotational trajectory around the fixation point, as in Experiment 1, with the exception that the wedge was presented on a blank gray background without the annulus that was presented in Experiment 1. This controlled for potential mediation effects due to context, which would require observers to distinguish between the contrasts of the wedge and annulus at the same time (e.g., Blakemore & Snowden, 2000). Observers viewed the stimuli from a distance of 50 cm. The inner and outer edges of the primary stimulus were 4.75° and 7.92° of visual angle away from the fixation point and subtended 3.17° of polar angle along the radial axis. The inner and outer edges of the target stimulus in Experiment 2A were 3.46° and 4.44° from fixation, subtending 1.58° of polar angle along the radial axis.

Stimuli were filled with filtered noise or square checkers, as in Experiment 1, and always presented in static texture. The main experimental manipulation of Experiment 2 was that on each trial, the primary stimulus was presented at either high (100%) or low (10%) luminance contrast relative to the gray background.

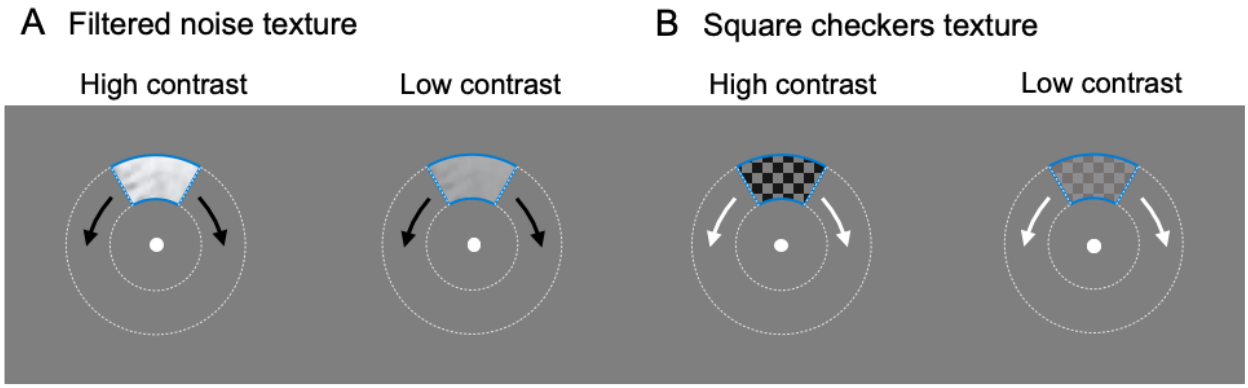

Figure 6. Example stimuli used in Experiment 2. For texture types (A) filtered noise and (B) square checkers, the primary stimulus consisted of a rotating wedge segment (blue outline) against a gray uniform background. The different contrast levels and missing background annuli are illustrated in this figure.

3.3 Procedure

Observers completed the experiment in a light-attenuated room in their own homes, with the same high-performance monitor set-up as in Experiment 1 but a chinrest, to accommodate restrictions during the 2020 COVID-19 pandemic. As per Experiment 1, in Experiment 2A we probed the perceived flash-lag for each condition, and in Experiment 2B we probed the perceived speed for each condition.

Trials were blocked into 4 condition blocks determined by *contrast level* (high or low) and *texture type* (filtered noise or square checkers). All observers completed a total of 4 blocks: 120 trials per block (for a total of 480 trials) in Experiment 2A and 144 trials per block (for a total of 576 trials) in Experiment 2B. The total testing duration was approximately 80 minutes.

3.4 Results

As in Experiment 1, we submitted all FLE magnitudes (Experiment 2A) and perceived speeds (Experiment 2B) to repeated measures ANOVAs with two factors: *contrast level* (high or low) and *texture type* (filtered noise or square checkers).

3.4.1 Experiment 2A: Effect of contrast on perceived flash-lag

A repeated measures ANOVA revealed a significant main effect of contrast level ($F_{1,6} = 7.32$, $p = 0.035$), with greater FLE magnitudes observed for low contrast than high contrast wedges (Figure 7). There was a main effect of texture type ($F_{1,6} = 28.87$, $p = 0.002$), with greater FLE magnitudes observed for square checkers than for filtered noise stimuli. There was no significant interaction effect between the two factors ($F_{1,6} = 0.47$, $p = 0.52$). Post-hoc *t*-tests revealed a significant FLE magnitude difference in the filtered noise condition ($t_6 = 3.47$, $p = 0.013$), but the difference did not reach significance in the square checkers condition ($t_6 = 2.12$, $p = 0.078$). Figure 7B shows that the FLE was consistently larger at low contrast compared to high contrast for all but two observers (P6; filtered noise condition; P3; square checkers condition).

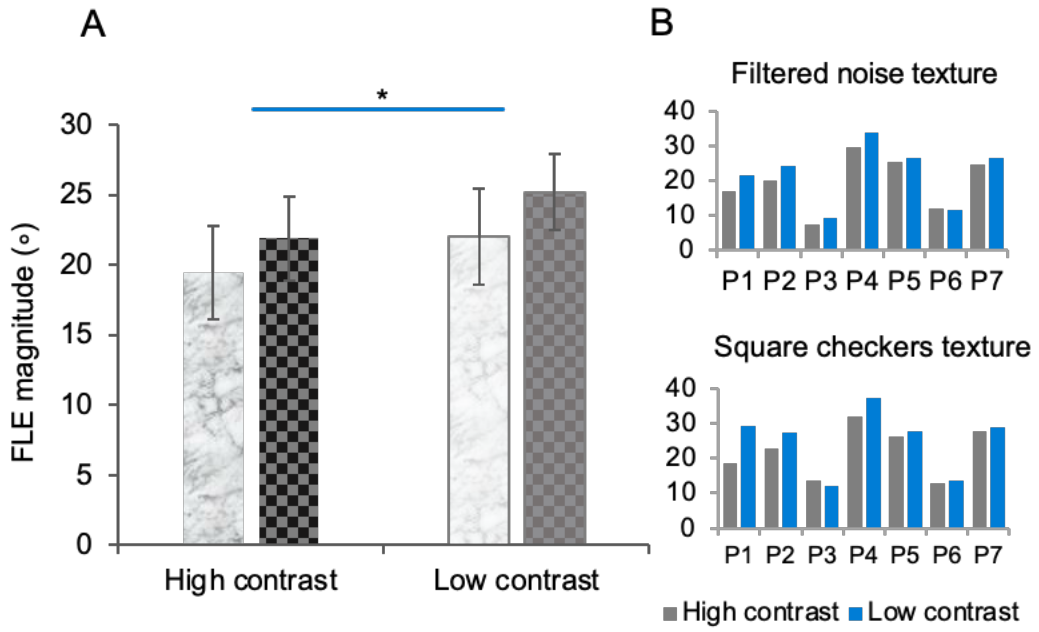

Figure 7. Results of Experiment 2A. (A) Bar graphs comparing mean FLE magnitudes between high and low contrast levels across both texture conditions, pooled over seven observers. (B) Bar graphs for individual observers. Error bars represent standard errors across observers. Asterisks above the bars indicate statistically significant main effect of contrast level. * denotes $p < 0.05$.

3.4.2 Experiment 2B: Effect of contrast on perceived speed

A repeated measures ANOVA revealed a significant main effect of contrast level on perceived speed ($F_{1,6}$ = 52.85, p < 0.001), with low contrast perceived to move faster than high contrast wedges (Figure 8). There was no significant main effect of texture type ($F_{1,6}$ = 0.086, p = 0.779) or significant interaction effect ($F_{1,6}$ = 4.68, p = 0.074). Post-hoc t-tests revealed that differences in perceived speed were significant in both filtered noise (t_6 = 5.72, p = 0.001) and square checkers (t_6 = 7.31, p < 0.001) conditions. Figure 8B shows that this effect was highly consistent across individual observers.

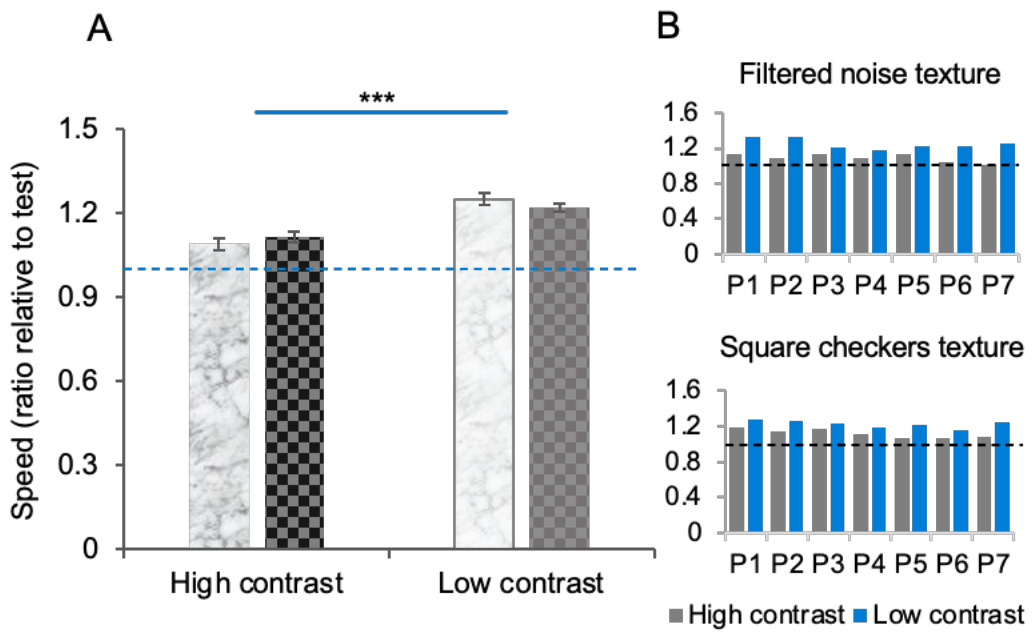

Figure 8. Results of Experiment 2B. (A) Bar graphs comparing mean perceived speeds between high and low contrast levels across both texture conditions, pooled over seven observers. (B) Bar graphs for individual observers. Perceived speed was calculated as a ratio of the reference speed relative to the test speed. The baseline speed is indicated as y = 1. Error bars represent standard errors across observers. Asterisks above the bars indicate statistically significant main effect of contrast level. *** denotes p < 0.001.

4. Discussion

The present study explored how the flash-lag effect (FLE) was modulated by changes in perceived speed. We achieved this by altering perceived speed of a moving object when physical speed was constant. The main findings were: (a) Experiment 1 showed that the dynamic noise increased perceived speed as well as FLE magnitude, compared to static noise, and (b) Experiment 2 confirmed a similar effect whereby low contrast increased perceived speed and FLE magnitude compared to high contrast. These findings demonstrate that the illusion is stronger for faster perceived speeds, consistent with the motion extrapolation account of the FLE.

Experiment 1 showed clear increases in perceived speeds as well as FLE magnitudes for dynamic noise relative to static noise stimuli. This was qualitatively similar across two textures, albeit more pronounced for filtered noise. Overall, these results replicate previously reported effects on perceived speed in gratings, Gabor patches, and the Floating Square illusion (De Valois & De Valois, 1991; Treue et al., 1993; Shen et al., 2003; Carlson et al., 2006), which supports our hypothesis that the observed changes in the FLE could be explained by the difference in perceived speeds of the two noise textures.

Our flicker manipulation, however, did not see a correlation between FLE magnitude and changes in perceived speed across observers. If a neural representation of perceived speed is used to fuel the extrapolation process behind the illusion, then, in principle, we would expect to see a causal relationship between the two measures. Of course, the observed patterns of results could suggest that even though the effect of perceived speed is robust within individuals, it can explain only a small proportion of the variance in the illusion across individuals. This could be noise, but a portion of observers also show a decrease in FLE magnitude despite clear increases in perceived speed. To explain this observation, one issue we could consider is whether observers make use of the same kind of speed information in both tasks of this study—when they make explicit speed judgments in a speed discrimination task versus when they perform extrapolation in a flash-lag task. For example, one study reported that varying stimuli contrast affected extrapolation judgments but not visuo-motor decisions (de' Seperti & Thornton, 2019). Observers showed contrast biases when they made saccades to an imagined target but not to avoid colliding with multiple targets, which suggests that they involve different mechanisms in the process of motion prediction. Possibly, we can infer that representations that support explicit reports of how fast an

object is could also be distinct from representations dedicated for implicit processing of where an object is. The nature of these representations could be fundamentally different and constitute separate processes, or they may represent different aspects of the same process, with similar relationships to physical speed and are subject to the same biases and manipulations as reported in the present experiments. If observers rely on such neural representations of speed, it seems likely that the same flicker manipulation can lead to a larger effect in perceived speed but to a less extent in the FLE task. It is entirely possible that other factors—indeed, including noise—could play a more important role in determining individual differences in the magnitude of the FLE than in speed judgments**.**

The results of Experiment 2 show a pattern consistent with Experiment 1. An interesting observation was that the perceived speed of the moving object increased at low contrast. This was surprising in regard to the classic 'Thompson effect' described in the literature (Blakemore & Snowden, 1999; Stone & Thompson, 1992; Anstis, 2003; Snowden et al., 1998) but supports a related observation in which low contrast actually increases perceived speed (Thompson et al., 2006; Hawken et al., 1994; Pretto et al., 2012). The reverse effect has been reported for objects with higher temporal frequencies (i.e. < 8Hz) or speeds (i.e. < 8° of visual angle (dva) per second; Thompson, 1982; Stone & Thompson, 1992; Blakemore & Snowden, 1999). Although we did not intend for the primary stimulus to move at such a rapid rate *per se*, 200° of polar angle/s (28.15 dva/s) is relatively fast compared to the range of speeds tested in studies outlined here (e.g., ~8-17 dva/s; Stone & Thompson, 1992; Blakemore & Snowden, 1999; Thompson et al., 2006). Our motion stimuli could validly appear faster at low than high contrast. However, we confirm that 28.15 dva/s still falls well within the range of speeds which observers perceive the FLE (3-50 dva/s; Wojtach et al., 2008), and the estimated FLE magnitudes that correspond to this speed are also close to the average FLE magnitudes reported here, ~15-22° of polar angle = ~2-3° of visual angle.

Moreover, the FLE shifts were in the hypothesized direction and were consistent with previously reported contrast effects in other flash-lag paradigms (e.g., flash-initiated condition; Khoei, Masson, & Perrinet, 2017; Kanai, Sheth, & Shimojo, 2004; Purushothaman et al., 1998). Kanai et al. (2004) interpreted their results based on differential latencies, explaining that motion stimuli

take longer to process at low contrast because they are harder to detect than at high contrast. This notion of stimulus uncertainty, in turn, gives rise to the displacement of the FLE. Our results, however, demonstrate that the extrapolation process underlying the FLE is unlikely to be driven by uncertainty. While making objects fainter (or noisier) could indeed affect visibility and spatial certainty, in principle, such a process based on uncertainty would depend on speed estimates that are less available or accurate. It would predict effects opposite to the ones presented here, whereby extrapolation is weaker and the FLE magnitudes are smaller for low contrast stimuli. In practice, uncertainty seems to have little impact on observers' speed judgments than previously thought (Stocker & Simoncelli, 2006), and observers are able to accurately perform extrapolation despite limited visibility (Graf, Warren, & Maloney, 2005). Possibly, this could hint at mechanisms that already factor some representations of uncertainty for optimal motion perception and/or subsequent decision-making (e.g., Tassinari, Hudson, & Landy, 2004), but that question is beyond the scope of this study. Here we observed that contrast modulates the FLE in the same direction as it modulates perceived speed, which implies that the change in FLE magnitude is perhaps more parsimoniously explained by the change in perceived speed rather than uncertainty.

These findings show evidence for behavioral motion extrapolation, which is consistent with neural implementations of motion extrapolation thought to compensate for neural delays. Extrapolation mechanisms have been identified in the form of pre-activations of neural representations, as the brain anticipates for moving objects in their next positions. For example, Hogendoorn and Burkitt (2018) showed in an EEG decoding paradigm that peak activity in the visual system occurs at shorter latencies for predictable than unpredictable motion stimuli. Blom, Feuerriegel, Johnson, Bode, and Hogendoorn (2020) extended these findings by demonstrating that this predictive representation is pre-activated even when a stimulus does not reach its anticipated position. The present effects complement these studies and the mechanisms underlying these instances of neural motion extrapolation.

In conclusion, we have shown in two experiments the putative role of perceived speed in the FLE. We reported subjective increases in FLE magnitude and perceived speed when the moving object contained dynamic noise relative to static noise, and when the moving object was presented in low contrast relative to high contrast. The results presented here suggest that a neural representation of

perceived speed is required to anticipate positions of moving objects while accounting for delays in visual processing. Therefore, motion extrapolation in the FLE depends on perceived, rather than physical speed.

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