

When predictions fail: Correction for extrapolation in the flash-grab effect

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Motion-induced position shifts constitute a broad class of visual illusions in which motion and position signals interact in the human visual pathway. In such illusions, the presence of visual motion distorts the perceived positions of objects in nearby space. Predictive mechanisms, which could contribute to compensating for processing delays due to neural transmission, have been given as an explanation. However, such mechanisms have struggled to explain why we do not usually perceive objects extrapolated beyond the end of their trajectory. Advocates of this interpretation have proposed a “correction-for-extrapolation” mechanism to explain this: When the object motion ends abruptly, this mechanism corrects the overextrapolation by shifting the perceived object location backwards to its actual location. However, such a mechanism has so far not been empirically demonstrated. Here, we use a novel version of the flash-grab illusion to demonstrate this mechanism. In the flash-grab effect, a target is flashed on a moving background that abruptly changes direction, leading to the mislocalization of the target. Here, we manipulate the angle of the direction change to dissociate the contributions of the background motion before and after the flash. Consistent with previous reports, we observe that perceptual mislocalization in the flash-grab illusion is mainly driven by motion after the flash. Importantly, however, we reveal a small but consistent mislocalization component in the direction opposite to the direction of the first motion sequence. This provides empirical support for the proposed correction-for-extrapolation mechanism, and therefore corroborates the interpretation that motion-induced position shifts might result from predictive interactions between motion and position signals.

Introduction

A broad class of visual illusions demonstrate that motion and position signals interact in the human visual pathway. In such illusions, the presence of visual motion distorts the perceived positions of objects in nearby space, causing motion-induced position shifts. The most-studied illusion in this category is probably the flash-lag effect (Nijhawan, 1994), in which a stimulus is flashed next to (and aligned with) a moving object. The result is that the flash appears to lag behind the position of the moving object. In the related flash-drag illusion, an object flashed adjacent to a moving texture is mislocalized in the direction of that texture’s motion (Whitney & Cavanagh, 2000a). Similarly, when motion is presented within a stationary patch, the perceived position of that patch is shifted in the direction of that motion (e.g., Anstis, 1989; De Valois & De Valois, 1991; Ramachandran & Anstis, 1990). Transient changes in an object’s visual properties (e.g., size or color) are perceived to occur further along the object’s trajectory than they actually do (Cai & Schlag, 2001), an effect that is sometimes dubbed the feature-flash lag or the flash-jump. In the Fröhlich effect, the initial position of an object that suddenly appears in motion is perceived as being shifted in the direction of its motion (Fröhlich, 1924; Kirschfeld & Kammer, 1999). Finally, in the related flash-grab effect, an object flashed on a moving background when that background unexpectedly changes direction is mislocalized in the background’s subsequent direction of motion (Cavanagh & Anstis, 2013).

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The neural basis of these illusions has been hotly debated over the past decades, particularly in the context of the flash-lag effect. Different groups have advocated explanations in extrapolation (Khurana, Watanabe, & Nijhawan, 2000; Nijhawan, 1994), latency differences (Patel, Ogom, Bedell, & Sampath, 2000; Whitney & Murakami, 1998; Whitney, Murakami, & Cavanagh, 2000), attention (Baldo & Klein, 1995; Brenner & Smeets, 2000), temporal averaging (Krekkelberg & Lappe, 2000) and postdiction (Eagleman & Sejnowski, 2000). Initial attempts to reconcile these interpretations have largely focused on identifying whether these effects are temporal or spatial, that is, identifying whether events are shifted in time or in space (Eagleman & Sejnowski, 2002; Khurana et al., 2000; Krekelberg & Lappe, 2001; Whitney, 2002). Later, Eagleman & Sejnowski (2007) proposed a unified explanation in which local motion signals collected over a brief time window are integrated to bias instantaneous position judgments. The first computational model uniting these effects was recently provided by Kwon, Tadin, and Knill (2015), which explained motion and position interactions in terms of a Bayesian inference process.

Altogether there seems to be consensus that motion-induced position shifts result from an interaction between position signals and motion signals. In particular, the importance of motion *after* the event is clear: in the flash-lag effect, there is no illusion without motion after the flash (Eagleman & Sejnowski, 2000; Maus & Nijhawan, 2009), and the same is true for the flash-grab effect (Cavanagh & Anstis, 2013), and by definition for the Fröhlich effect (Fröhlich, 1924). There is, however, still some debate surrounding how long after an event motion signals are integrated to influence the perceived position of that event: proposed values range from up to 50 ms following the event (Whitney et al., 2000), 80 ms (Eagleman & Sejnowski, 2000), 150 ms (Brenner & Smeets, 2000), 175 ms (Maus & Nijhawan, 2006), 200 ms (Cavanagh & Anstis, 2013; Kwon et al., 2015), all the way up to 500 ms (Krekkelberg & Lappe, 1999, 2001). Similarly, in the related flash-drag effect, in which a static flash is mislocalized by presentation on or near a moving texture, motion signals within a certain interval around the flash onset time affect the perceived location of the flash. The impact of motion signals within this interval is skewed towards the time after the flash (Durant & Johnston, 2004; Murai & Murakami, 2016; Roach & McGraw, 2009).

The role of motion *before* (and possibly concurrent with) an event is less clear. Proponents of the extrapolation hypothesis argue that it is prior motion that leads to extrapolation of the target when it is subsequently presented (Nijhawan, 1994, 2002, 2008). In support of this, a range of physiological studies

have revealed extrapolation mechanisms at various stages of the visual hierarchy, including the retina (Berry, Brivanlou, Jordan, & Meister, 1999), lateral geniculate nucleus (Sillito, Jones, Gerstein, & West, 1994), V1 (Jancke, Erlhagen, Schöner, & Dinse, 2004), V4 (Sundberg, Fallah, & Reynolds, 2006), MT (Maus, Fischer, & Whitney, 2013), and in both monocular and binocular populations (van Heusden, Harris, Garrido, & Hogendoorn, 2019). Using an electroencephalogram decoding approach, we recently showed that early cortical position signals are pre-activated ahead of predictably moving stimuli (Hogendoorn & Burkitt, 2018a), and argued that within the framework of hierarchical predictive coding (Rao & Ballard, 1999), such extrapolation mechanisms would be ubiquitous in the visual hierarchy (Hogendoorn & Burkitt, 2018b). We have previously argued that EEG correlates of the flash-grab effect are detectable so rapidly after presentation (~80 ms; Hogendoorn, Verstraten, & Cavanagh, 2015) that motion after the target could impossibly be processed on time to affect the (initial development of the) illusion. However, the Fröhlich effect, in which there is no motion before the target event at all, indicates that motion *prior* to the event is not necessary for mislocalization. This seems to undermine an explanation in extrapolation, except that the instantaneous velocity signal present concurrently with the target has been argued to be sufficient to drive extrapolation mechanisms (Nijhawan, 2008). This was corroborated by a study showing that eye movements made to a very briefly presented moving target are targeted at the extrapolated position of that target, in a place where the target is never presented (Quinet & Goffart, 2015). More recently, we demonstrated that the same is true when human observers make saccadic eye movements to a target whose position is shifted by the flash-grab effect: observers make saccades to the extrapolated position of the target (van Heusden, Rolfs, Cavanagh, & Hogendoorn, 2018).

The degree to which motion before an event affects the perceived position of that event is therefore still unclear. Indeed, even the role of static stimuli prior to the flash-lag stimulus is disputed (Chappell & Hine, 2004; Whitney & Cavanagh, 2000b). An additional point of contention is the role of abrupt transients, such as those caused by the appearance or disappearance of an object. Eagleman and Sejnowski (2000) have argued that such transients reset the integration window, destroying neural traces of motion prior to the transient such that only motion after the event is integrated. Conversely, in support of their extrapolation account, Nijhawan and colleagues have argued that transients generate a correction-for-extrapolation signal (Maus & Nijhawan, 2006; Nijhawan, 2002, 2008; Shi & Nijhawan, 2012). This

signal would shift the object's position back along the object's trajectory, reversing extrapolation that took place before the visual system detected the transient and thereby correcting for an expected future that did not come true. This would explain why the flash-lag effect is eliminated when there is no motion after the flash and why the perceived end of a motion trajectory has been reported to be mislocalized in the direction opposite to the motion (Maus & Nijhawan, 2009; Müsseler, Stork, & Kerzel, 2002; Roulston, Self, & Zeki, 2006).

Although plausible, and broadly consistent with neurophysiological evidence of reversal detection mechanisms in the retina (Chen, Chou, Park, Schwartz, & Berry, 2014; Schwartz et al., 2007), no direct evidence for a correction-for-extrapolation mechanism has been demonstrated in human observers. Here, we use a two-dimensional version of the flash-grab effect to isolate the correction-for-extrapolation mechanism in the flash-grab effect. By separating the relative contributions of motion before and after a target event to the perceived position of that event, we directly test the proposition that transients evoke correction-for-extrapolation signals. The rationale is that the moving background drives an extrapolation mechanism, which results in over-extrapolation when the background unexpectedly changes direction. If a corrective mechanism exists that prevents us from becoming aware of this overshoot by shifting the extrapolated position of the background back along its initial trajectory, it might also influence the perceived position of the (static) flash. We show that although the perceived position of the target is primarily influenced by motion after the target, motion before the target does indeed have a small but significant effect. Most importantly, we show that the direction of this effect is in accordance with the correction-for-extrapolation hypothesis, showing that the visual system indeed corrects for representations that are extrapolated but not subsequently substantiated by sensory input.

Experiment 1

Methods

Observers

Ten observers participated in this experiment. All observers had normal or corrected-to-normal vision. All gave informed consent prior to participating in the experiment and were reimbursed for their time. The experiment was approved by the local ethics committee of the Melbourne School of Psychological Sciences and

conducted in accordance with the guidelines expressed in the Declaration of Helsinki.

Stimuli

Stimuli were presented on an ASUS ROG PG258 monitor (ASUS, Taipei, Taiwan) with a resolution of $1,920 \times 1,080$ running at 100 Hz. The monitor was controlled by a HP EliteDesk 800 PC (Hewlett-Packard, Palo Alto, CA) running MATLAB R2017b (MathWorks, Natick, MA) with PsychToolbox 3.0.14 extensions (Brainard, 1997). Observers viewed the stimulus from a headrest at a distance of 50 cm.

The stimulus consisted of a linearly moving grayscale texture presented within a circular annulus around a central fixation point on a uniform 50% gray background. The texture was generated from two 1/f noise patterns, which were blurred and thresholded to yield sparse clusters of contiguous pixels. The two patterns were given opposite polarity and summed to generate a texture similar to that used by Tse, Whitney, Anstis, and Cavanagh (2011), but with less regular contours. The annulus had inner and outer radii of 6.4 and 15.7 degrees of visual angle (dva) respectively, with edges softened using a raised cosine with a width of 1.3 dva. The target stimulus was a red disc with a radius of 1.6 dva, which was flashed superimposed on the moving pattern at a random polar angle on an imaginary circle at 9.6 dva from fixation (Figure 1). In this way, the eccentricity of the target was held constant, without making the position of the target predictable.

Procedure

At the start of each trial, observers fixated the fixation point, and the annulus with the moving texture inside appeared. The texture moved at a speed of 10.5, 21, or 42 degrees of visual angle per second (dva/s), in a randomly chosen direction. After a variable interval (either 600, 750, 900, or 1,050 ms), the target was presented for a single frame (10 ms). After target presentation, the texture continued moving in one of four possible directions: it either continued on its original motion path, reversed, or moved in one of the two orthogonal directions (i.e., a direction change of 0°, 180°, 90°, or 270°, respectively). This second motion sequence was presented for either 400 or 500 ms. At the end of the trial, the texture disappeared and observers were asked to use the mouse to indicate where they perceived the target red disc. The cursor was replaced by an identical red disc to facilitate this report. Each observer viewed four repeats of each combination of conditions (4 repeats \times 3 speeds \times 4 first-motion-durations \times 4 direction changes \times 2 second-motion-durations) for a total of

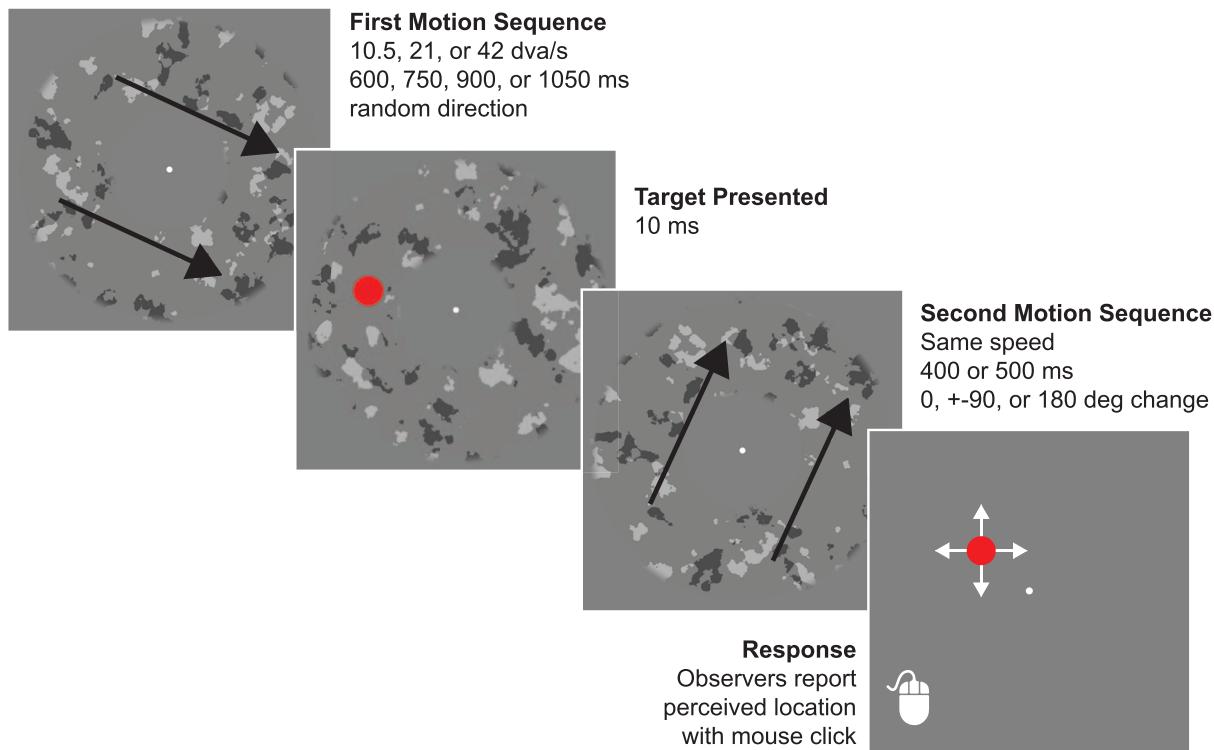


Figure 1. Stimuli and Procedure. The stimulus consisted of a moving texture pattern presented within an annulus around fixation, moving at one of three speeds in a randomly determined direction. After a variable duration, the target was flashed at a random location on the annulus. Following target presentation, the texture continued moving in one of four possible directions: continuing on the original trajectory, reversing direction, or moving in one of the two orthogonal directions (an orthogonal trial is shown). Following the second motion sequence, observers indicated the perceived position of the target using a mouse-click.

384 trials per block. Each observer completed a total of four blocks.

Results

Trials were collapsed across all first-motion durations and rotated to align all first-motion directions. Two-dimensional reported positions were averaged within observers. Two observers were removed from subsequent analysis because they had a mean within-condition response variability greater than 1 dva. Mean responses in all conditions from the remaining eight observers (all with variability <0.8 dva) were then analyzed as a function of speed and second motion sequence direction.

Results are shown in Figure 2, with responses rotated as if all first motion directions were rightward. To test whether the first and/or second motion directions significantly affected reported location, the reported locations were fitted with a multiple linear regression. The first and second velocity vectors in each trial formed the two regressors (i.e., Reported Position = $\beta_1 \times$ First Motion Vector + $\beta_2 \times$ Second Motion Vector + Error). The model fit the data almost perfectly ($R^2 = 0.992$, $F = 1266.7$, $p < 10^{-21}$; see open markers in

Figure 2). Importantly, both the first ($t = 4.5$, $p = 0.0002$) and the second ($t = 50.13$, $p < 10^{-22}$) motion vector significantly affected the reported position (regression weights -0.0056 and 0.0483 dva per dva/s). The effect of the second motion vector was a factor 11 times greater than the effect of the first motion vector, and in the opposite direction: the perceived location of the target was shifted in the same direction as the second motion vector, whereas it was shifted in the opposite direction to the first motion vector. Finally, the two effects combined linearly to determine the perceived location of the target.

In an additional analysis, we explored the effect of the motion-change transient per se, since the 90°, 180°, and 270° motion change conditions involved a sudden change in the background motion that the 0° condition did not. To do so, we added an additional regressor to the model: the velocity vector of the moving background in the 0° condition. If the pattern of results in this condition differed meaningfully from the other three conditions in any way due to the absence of the transient, then that difference would be captured by this regressor. However, this regressor did not contribute significantly to the fit of the model ($t = 1.3$, $p = 0.20$), indicating that the results revealed no evidence for an effect of the transient per se.

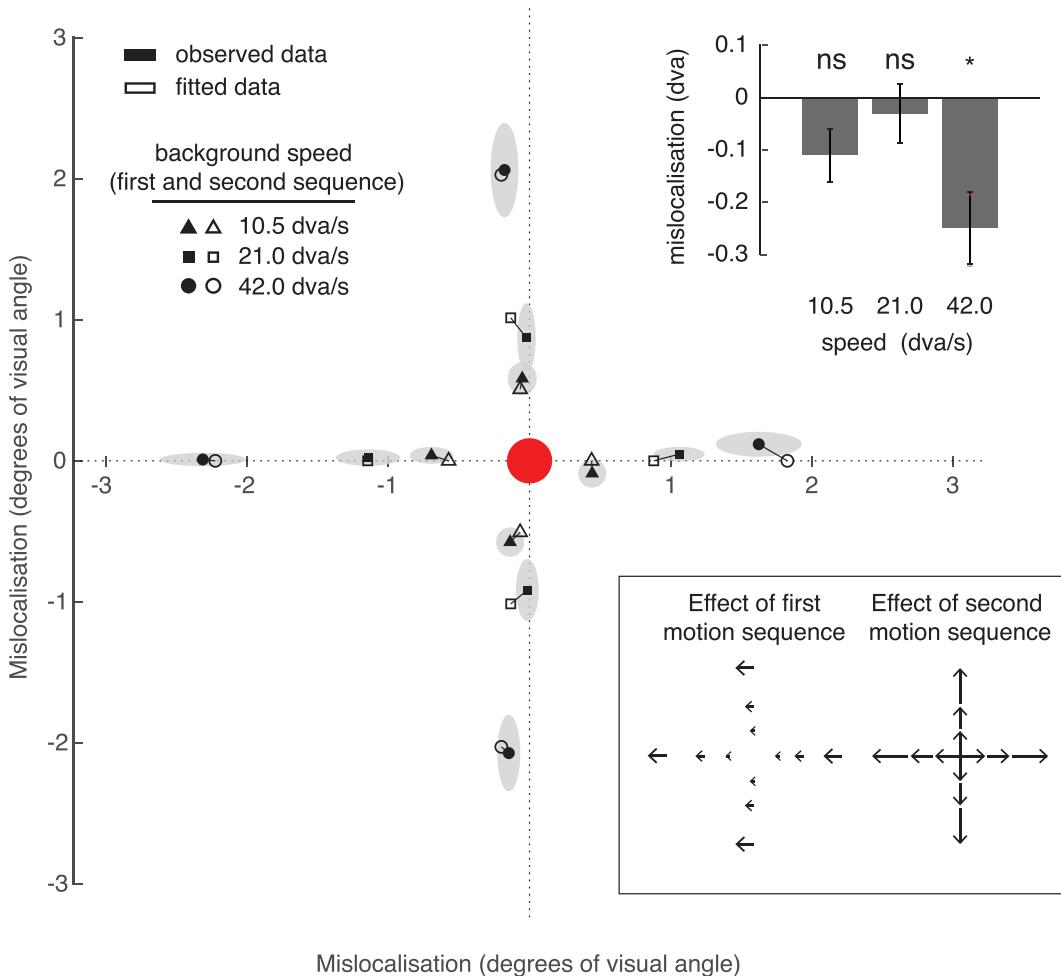


Figure 2. Results of Experiment 1. Filled markers indicate mean reported position across all observers, with all trials realigned as if the first motion was rightwards and the target was presented at the origin as indicated. Different marker shapes indicate different speed conditions and shaded regions indicate standard errors of the mean. A model based on a linear combination of velocity vectors before and after the target was fitted to the data. Filled markers indicate observed data, and connected open markers indicate model predictions. The model provides a near-perfect fit to the data, explaining 98.7% of variance in observer reports. Modeled effects of the first and second motion vectors are illustrated in the bottom-right inset. Top right inset: Mean mislocalization along the axis of the first motion sequence as a function of stimulus speed. Error bars indicate standard errors of the means across all observers. On average, the target was mislocalized in the direction opposite to the first motion direction (i.e., leftward in the main diagram), with the strongest effect at the highest speed. Two-tailed one-sample t tests revealed the effect to be significantly different from zero in the 42 dva/s condition [$*p < 0.05$ after Holm-Bonferroni correction for three comparisons (Holm, 1979)].

Consistent with previous studies of the flash-grab effect (Cavanagh & Anstis, 2013; Hogendoorn et al., 2015; van Heusden et al., 2019; van Heusden et al., 2018), the perceived position of the target was strongly mislocalized in the direction in which the background moved *after* presentation of the target. Furthermore, this effect scaled with speed, consistent with previous findings (Cavanagh & Anstis, 2013).

Interestingly, the analysis revealed that the target position was additionally shifted in the direction opposite to the direction of the moving background *before* the target was presented. This is consistent with the correction-for-extrapolation hypothesis proposed by Shi and Nijhawan (2012). The correction-for-

extrapolation effect showed some indication of scaling with the speed of the first motion sequence (Figure 2, top-right inset), but with just three speed conditions this was difficult to establish on the basis of the present data. Therefore, we carried out a second experiment to directly examine the effect of the speed of the first motion sequence on the illusion.

Experiment 2

In Experiment 2, we examined the effect of the speed of the first motion sequence on perceived mislocaliza-

tion in the flash-grab effect. To do so, we adapted the paradigm from Experiment 1, with the following changes: (1) we tested six different speeds of the first motion sequence, (2) the speed of the second motion sequence was constant across all conditions, and (3) the experiment was run in two new groups of observers.

Methods

Experimental methods were identical to Experiment 1, with the following exceptions:

Observers

Two groups of observers participated in Experiment 2. One group of 11 observers viewed trials in which the texture motion direction changed by either 90° or -90°. A second group of 10 new observers viewed trials in which the background motion direction either remained the same or reversed. This was done to limit the duration of the experiment for individual observers, so as to avoid potential training effects. All observers had normal or corrected-to-normal vision. All gave informed consent prior to participating in the experiment and were reimbursed for their time.

Stimuli

Stimuli were identical to Experiment 1, with the exception that in the first motion sequence, the texture could move at either 10.5, 14.8, 21.0, 29.7, 42, or 59.4 dva/s, and that the second motion sequence always moved at a speed of 21.0 dva/s. Again, observers viewed four repeats of each combination of conditions per block, for a total of 384 trials per block. Each observer completed a total of four blocks.

Results

As for Experiment 1, we collapsed across all first-motion durations, trials were rotated to align all first-motion directions, and reported positions were averaged within observers. One observer from the first group was removed from further analysis because of a within-condition response variability greater than 1.0 dva, leaving 10 observers in each group. Mean responses were analyzed as a function of the speed of the first motion sequence and the direction of the second motion sequence.

Results are shown in Figure 3, with responses rotated as if the first motion sequence was rightward. As for Experiment 1, the reported locations were fitted with a multiple linear regression, separately for each of the two groups. To start with, the first and second

velocity vectors in each trial again formed the two regressors (i.e., Reported Position = $\beta_1 \times$ First Motion Vector + $\beta_2 \times$ Second Motion Vector + Error). However, because a stepwise analysis showed that the regression required a non-zero x-intercept, we expanded the regression to include an x-intercept such that the regression equation became: Reported Position = $\beta_{0x} + \beta_1 \times$ First Motion Vector + $\beta_2 \times$ Second Motion Vector + Error. The effect of the first-motion vector scaled poorly with speed (incremental $t = 1.1$, $p = 0.296$), so the First Motion Vector was removed from the model, such that the final regression equation became: Reported Position = $\beta_{0x} + \beta_2 \times$ Second Motion Vector + Error.

As for Experiment 1, the overall fit of this model was excellent, explaining 97.2% of the variance in observer reports ($R^2 = 0.972$, $F = 800.8$, $p < 10^{-34}$). As before, the model was dominated by the Second Motion Vector ($t = 39.9$, $p < 10^{-36}$, regression weight $\beta_2 = 0.044$ dva per dva/s). However, the pattern of mislocalization relative to the first motion direction was best described by a constant offset in the direction opposite to the first motion direction (i.e., the x-intercept in the multiple regression; incremental $t = 2.9$, $p = 0.006$, regression weight $\beta_{0x} = -0.095$ dva). This suggested that the correction-for-extrapolation effect did not scale with speed, but rather was constant across the tested speeds.

To further investigate this, we directly investigated mislocalization along the axis of the first motion direction after accounting for the effect of the second motion sequence. To do this, we fitted the data with only the second-motion vector and projected the residual error vectors on the first motion vector. This yields a measure that simply shows how much, on average, all responses in a given condition were shifted along this axis. This is shown in Figure 3, top-right inset. The pattern of results shows a constant shift in perceived position opposite the direction of the first motion sequence across all but the highest speed we tested (59.4 dva/s). Follow-up two-tailed t tests showed that this mislocalization was significantly different from zero in all but the fastest condition, even after Holm-Bonferroni correction for six comparisons with a family-wise error rate of 0.05 (Holm, 1979). These five conditions did not significantly differ from each other (two-tailed paired-samples t tests, uncorrected; all $p > 0.61$).

Discussion

Previous accounts explaining motion-induced position shifts in terms of extrapolation mechanisms have posited a correction-for-extrapolation mechanism to explain why mislocalization is usually not observed at

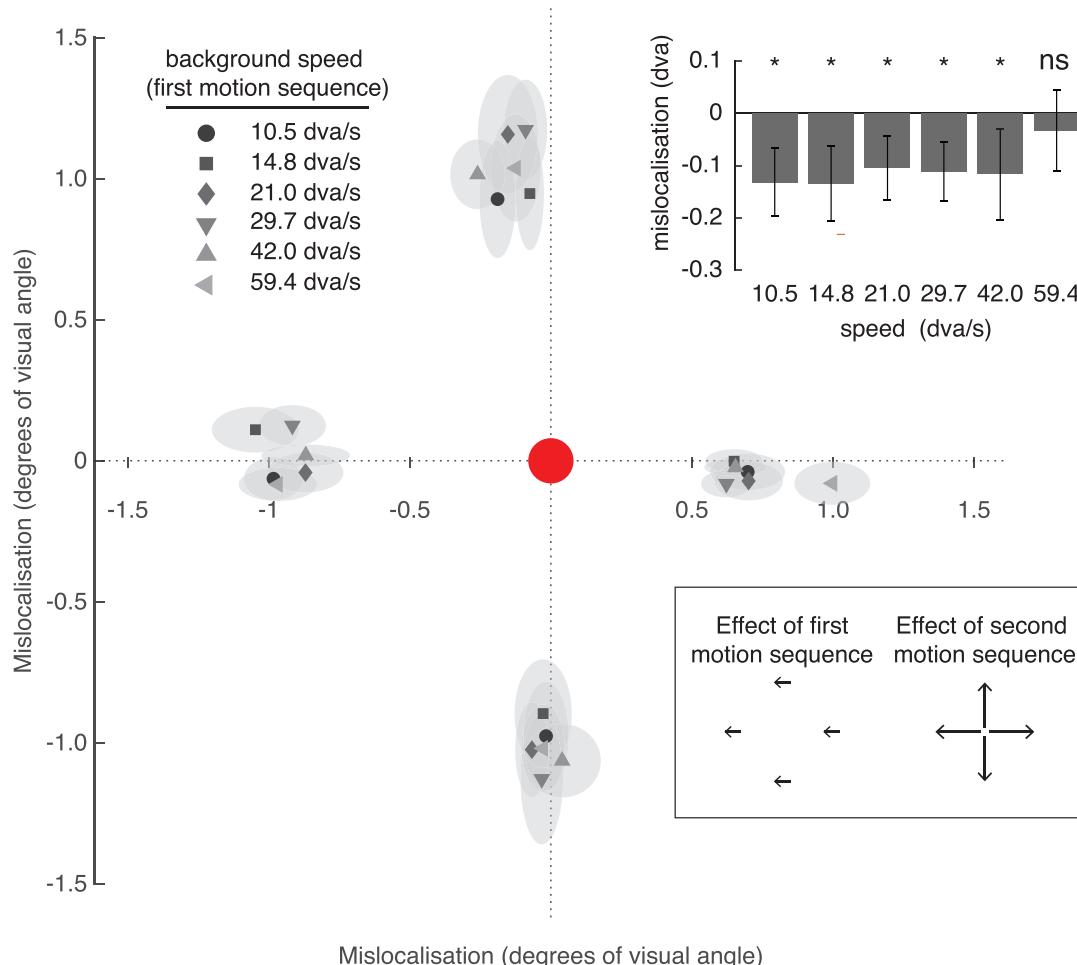


Figure 3. Results of Experiment 2. Markers indicated the mean reported position across all observers, with all trials realigned as if the first motion was rightwards and the target was presented at the origin. Different marker shapes indicate different speeds of the first motion sequence. Shaded regions indicate standard errors of the mean. For clarity, identical markers are used for each of the four possible second motion directions, but these are readily separable due to their clustering along the four cardinal directions in the plot. Modeled data are not shown, but the effects of the first and second motion vectors are illustrated in the bottom-right inset. Most importantly, mislocalization did not consistently scale with the speed of the first motion sequence. Top-right inset: Mean mislocalization along the axis of the first motion sequence as a function of the speed of the first motion sequence. Error bars indicate standard errors of the means across all observers. The target was significantly mislocalized in the direction opposite to the first motion direction for all but the fastest stimulus speed (* indicates two-tailed one-sample t tests with $p < 0.05$ after Holm-Bonferroni correction).

the end of motion trajectories. Such a mechanism would be triggered by visual transients, and work to correct motion trajectories that were anticipated, but ultimately not observed. Although extrapolation models cannot account for empirical data without this mechanism, it has never been directly demonstrated. Here, we use a two-dimensional version of the flash-grab effect to dissociate the relative contributions of the first and second motion sequence that make up the illusion. We show that, consistent with previous findings, the illusion is mainly driven by motion after the target. Importantly, however, we show that the perceived position of the target is also consistently shifted in the direction opposite to the first motion

sequence. This provides a direct psychophysical demonstration of a correction-for-extrapolation mechanism in human vision.

The results are consistent with previous reports of correction for failed extrapolation in the retinae of salamanders, mice, and rabbits (Holy, 2007; Schwartz et al., 2007). In these studies, the population activity of retinal ganglion cells briefly continued to extrapolate the position of a moving object even after that object reversed direction. When the reversal was detected, a spike of neural activity accompanied a rapid shift in the represented position of the object as the neural population “caught up” with the object. Although speculative, this brief, rapid shift in the represented

position would be expected to appear to downstream neurons as a brief spike in velocity, in the direction opposite to the first motion sequence. This brief velocity signal might then interact with any other visual information at that same position, such as the flashed target in the current paradigm, in the same way as the velocity signal ordinarily interacts with position information to extrapolate the current position of a moving object (Eagleman, 2008; Nijhawan, 2008). Since the position of the flashed target had not actually been extrapolated, it is therefore wrongly corrected, and mislocalized in the direction opposite to the initial motion signal.

Such motion-position interactions are also consistent with a recently proposed Bayesian model of unified visual motion and position estimation (Kwon et al., 2015). Although the authors of this study make no reference to the flash-lag effect or related illusions, or to delay compensation generally, they demonstrate convincingly that optimal Bayesian inference of position makes use of motion and vice versa, and that these interactions between motion and position qualitatively and quantitatively explain a number of other illusions. Our data add to the growing body of evidence showing that position and motion signals interact bi-directionally (e.g., Kwon et al., 2015), and demonstrate that they do so both predictively (i.e., shifting the target in the direction of the second motion sequence) and retrospectively (i.e., shifting the target backward along the initially predicted motion trajectory when that prediction was violated). Note that in the current paradigm, the duration of the first motion sequence was always greater than the duration of the second motion sequence. Due to this temporal asymmetry, the first motion sequence might be thought to have a stronger weighting in the integration. However, since the widest window of integration ever reported in motion-position illusions is ~500 ms (Krekelberg & Lappe, 1999, 2001), and our second motion sequence lasted either 400 or 500 ms, we do not believe the duration asymmetry biased the current results.

A surprising finding in Experiment 2 was that the correction-for-extrapolation effect did not scale with speed, instead staying constant at all but the highest speed tested. This demonstrates that the interaction of the target's position with the preceding motion vector is qualitatively different from the interaction with the subsequent motion vector, which scales very clearly with speed in our Experiment 1 as well as in previous experiments (Cavanagh & Anstis, 2013). Additionally, in our data the correction-for-extrapolation effect tapered off at the highest velocity. Again, this differs from the speed-dependence of the flash-grab effect as reported by Cavanagh and Anstis (2013), who observed that the effect saturated at maximum velocities. Since their effect was (like ours) presumably dominated by

the impact of the second motion sequence, rather than the first, this underscores that the two motion sequences interact with perceived position in a qualitatively different way. Whether the first motion sequence truly has an upper velocity limit for interacting with perceived position is an intriguing question for further study.

Additionally, the correction-for-extrapolation effect was quite weak compared to the impact of the motion-sequence following presentation of the target. Being more than an order of magnitude weaker, it cannot simply reflect an inversion of the same mechanisms that might be argued to explain mislocalization caused by motion after the target. As such, although the mere existence of the effect is consistent with the extrapolation account proposed by Nijhawan and colleagues (Maus & Nijhawan, 2006; Nijhawan, 2002, 2008; Shi & Nijhawan, 2012), the fact that the effect of subsequent motion is so much stronger than the effect of prior motion also supports the model put forth by Eagleman and Sejnowski (2007), in which transients are argued to reset the motion integration window. Our data are consistent with both models if we consider that this reset might be imperfect, such that some fraction of the correction-for-extrapolation signal survives to influence the perceived position of the flash.

Other models that have been put forth to explain the flash-lag effect, however, fail to capture the pattern of results observed in the current paradigm. For instance, explanations in differential latency (Whitney & Murakami, 1998) only predict mislocalization of static objects relative to moving objects, whereas in our data the (static) flash is mislocalized in absolute coordinates. Similarly, slow temporal averaging of object position (Krekelberg & Lappe, 2000) would only affect the perceived position of moving objects, and even if it would be averaging the motion vectors of the background, it would not predict a shift *against* the original motion direction. The pattern of results is therefore most consistent with an explanation in a correction for earlier extrapolation, as proposed by van Heusden et al. (2019) elsewhere in this issue.

In sum, this study provides a direct psychophysical demonstration of a correction-for-extrapolation mechanism that has been proposed as part of an extrapolation account. Although this is the first direct evidence for the existence of this mechanism, further research will be required to answer such questions as how predictive and corrective processes interact, on what time course(s), and to what degree they are produced by shared neural mechanisms.

Keywords: motion perception, visual cognition, spatial vision, temporal vision

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References

- Anstis, S. M. (1989). Kinetic edges become displaced, segregated, and invisible. In D. Lam (Ed.), *Neural mechanisms of visual perception* (Vol. 2, pp. 247–260). Houston, TX: Gulf Publishing.
- Baldo, M. V. C., & Klein, S. A. (1995, December 7). Extrapolation or attention shift? *Nature*, 378(6557), 565–566, <https://doi.org/10.1038/378565a0>.
- Berry, M. J., Brivanlou, I. H., Jordan, T. A., & Meister, M. (1999, March 25). Anticipation of moving stimuli by the retina. *Nature*, 398(6725), 334–338, <https://doi.org/10.1038/18678>.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4), 433–436. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9176952>
- Brenner, E., & Smeets, J. B. (2000). Motion extrapolation is not responsible for the flash-lag effect. *Vision Research*, 40(13), 1645–1648. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10814752>
- Cai, R. H., & Schlag, J. (2001). Asynchronous feature binding and the flash-lag illusion. *Investigative Ophthalmology and Visual Science*, 42: S711.
- Cavanagh, P., & Anstis, S. M. (2013). The flash grab effect. *Vision Research*, 91, 8–20, <https://doi.org/10.1016/j.visres.2013.07.007>.
- Chappell, M., & Hine, T. J. (2004). Events before the flash Do influence the flash-lag magnitude. *Vision Research*, 44(3), 235–239, <https://doi.org/10.1016/j.visres.2003.09.021>.
- Chen, E. Y., Chou, J., Park, J., Schwartz, G., & Berry, M. J. (2014). The neural circuit mechanisms underlying the retinal response to motion reversal. *Journal of Neuroscience*, 34(47): 15557–15575, <https://doi.org/10.1523/JNEUROSCI.1460-13.2014>.
- De Valois, R. L., & De Valois, K. K. (1991). Vernier acuity with stationary moving Gabors. *Vision Research*, 31(9), 1619–1626, [https://doi.org/10.1016/0042-6989\(91\)90138-U](https://doi.org/10.1016/0042-6989(91)90138-U).
- Durant, S., & Johnston, A. (2004). Temporal dependence of local motion induced shifts in perceived position. *Vision Research*, 44(4), 357–366, <https://doi.org/10.1016/j.visres.2003.09.022>.
- Eagleman, D. M. (2008). Prediction and postdiction: Two frameworks with the goal of delay compensation. *Behavioral and Brain Sciences*, 31(2): 205–206, <https://doi.org/10.1017/S0140525X08003889>.
- Eagleman, D. M., & Sejnowski, T. J. (2000, March 17). Motion integration and postdiction in visual awareness. *Science (New York, N.Y.)*, 287(5460), 2036–2038. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10720334>
- Eagleman, D. M., & Sejnowski, T. J. (2002). Untangling spatial from temporal illusions. *Trends in Neurosciences*, 25(6), 293; author reply 294. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/12086745>
- Eagleman, D. M., & Sejnowski, T. J. (2007). Motion signals bias localization judgments: A unified explanation for the flash-lag, flash-drag, flash-jump, and Fröhlich illusions. *Journal of Vision*, 7(4):3, 1–12, <https://doi.org/10.1167/7.4.3>. [PubMed] [Article].
- Fröhlich, F. W. (1924). Über die Messung der Empfindungszeit. *Pflügers Archiv Für Die Gesamte Physiologie Des Menschen Und Der Tiere*, 202(1), 566–572, <https://doi.org/10.1007/BF01723521>.
- Hogendoorn, H., & Burkitt, A. N. (2018a). Predictive coding of visual object position ahead of moving objects revealed by time-resolved EEG decoding. *NeuroImage*, 171, 55–61, <https://doi.org/10.1016/j.neuroimage.2017.12.063>.
- Hogendoorn, H., & Burkitt, A. N. (2018b). Predictive coding with neural transmission delays: A real-time temporal alignment hypothesis. *BioRxiv*, <https://doi.org/10.1101/453183>.
- Hogendoorn, H., Verstraten, F. A. J., & Cavanagh, P. (2015). Strikingly rapid neural basis of motion-induced position shifts revealed by high temporal-resolution EEG pattern classification. *Vision Research*, 113, 1–10, <https://doi.org/10.1016/j.visres.2015.05.005>.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure a simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6(6), 65–70, <https://doi.org/10.2307/4615733>.
- Holy, T. E. (2007). A public confession: The retina trumpets its failed predictions. *Neuron*, 55(6), 831–832, <https://doi.org/10.1016/j.neuron.2007.09.002>.

- Jancke, D., Erlhagen, W., Schöner, G., & Dinse, H. R. (2004). Shorter latencies for motion trajectories than for flashes in population responses of cat primary visual cortex. *Journal of Physiology*, 556(3), 971–982, <https://doi.org/10.1113/jphysiol.2003.058941>.
- Khurana, B., Watanabe, K., & Nijhawan, R. (2000). The role of attention in motion extrapolation: Are moving objects ‘corrected’ or flashed objects attentionally delayed? *Perception*, 29(6), 675–692, <https://doi.org/10.1068/p3066>.
- Kirschfeld, K., & Kammer, T. (1999). The Fröhlich effect: A consequence of the interaction of visual focal attention and metacontrast. *Vision Research*, 39(22), 3702–3709. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10746140>
- Krekelberg, B., & Lappe, M. (1999). Temporal recruitment along the trajectory of moving objects and the perception of position. *Vision Research*, 39(16), 2669–2679. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10492829>
- Krekelberg, B., & Lappe, M. (2000). A model of the perceived relative positions of moving objects based upon a slow averaging process. *Vision Research*, 40(2), 201–215, [https://doi.org/10.1016/S0042-6989\(99\)00168-6](https://doi.org/10.1016/S0042-6989(99)00168-6).
- Krekelberg, B., & Lappe, M. (2001). Neuronal latencies and the position of moving objects. *Trends in Neurosciences*, 24(6), 335–339, [https://doi.org/10.1016/S0166-2236\(00\)01795-1](https://doi.org/10.1016/S0166-2236(00)01795-1).
- Kwon, O.-S., Tadin, D., & Knill, D. C. (2015). Unifying account of visual motion and position perception. *Proceedings of the National Academy of Sciences, USA*, 112(26), 8142–8147, <https://doi.org/10.1073/pnas.1500361112>.
- Maus, G. W., Fischer, J., & Whitney, D. (2013). Motion-dependent representation of space in area MT+. *Neuron*, 78(3), 554–562, <https://doi.org/10.1016/j.neuron.2013.03.010>.
- Maus, G. W., & Nijhawan, R. (2006). Forward displacements of fading objects in motion: The role of transient signals in perceiving position. *Vision Research*, 46(26), 4375–4381, <https://doi.org/10.1016/J.VISRES.2006.08.028>.
- Maus, G. W., & Nijhawan, R. (2009). Going, going, gone: Localizing abrupt offsets of moving objects. *Journal of Experimental Psychology: Human Perception and Performance*, 35, 611–626, <https://doi.org/10.1037/a0012317.suppl>.
- Murai, Y., & Murakami, I. (2016). The flash-lag effect and the flash-drag effect in the same display. *Journal of Vision*, 16(11):31, 1–14, <https://doi.org/10.1167/16.11.31>. [PubMed] [Article].
- Müsseler, J., Stork, S., & Kerzel, D. (2002). Comparing mislocalizations with moving stimuli: The Fröhlich effect, the flash-lag, and representational momentum. *Visual Cognition*, 9(1–2), 120–138, <https://doi.org/10.1080/13506280143000359>.
- Nijhawan, R. (1994, July 28). Motion extrapolation in catching. *Nature*, 370, 256–257, <https://doi.org/10.1038/370256b0>.
- Nijhawan, R. (2002). Neural delays, visual motion and the flash-lag effect. *Trends in Cognitive Sciences*, 6(9), 387. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/12200181>
- Nijhawan, R. (2008). Visual prediction: Psychophysics and neurophysiology of compensation for time delays. *Behavioral and Brain Sciences*, 31(2), 179–239, <https://doi.org/10.1017/S0140525X08003804>.
- Patel, S. S., Ogom, H., Bedell, H. E., & Sampath, V. (2000, November 10). Flash-lag effect: Differential latency, not postdiction. *Science (New York, N.Y.)*, 290(5494), 1051. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/11184992>
- Quinet, J., & Goffart, L. (2015). Does the brain extrapolate the position of a transient moving target? *Journal of Neuroscience*, 35(34), 11780–11790, <https://doi.org/10.1523/JNEUROSCI.1212-15.2015>.
- Ramachandran, V. S., & Anstis, S. M. (1990). Illusory displacement of equiluminous kinetic edges. *Perception*, 19(5), 611–616, <https://doi.org/10.1086/p190611>.
- Rao, R. P. N., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, 2(1), 79–87, <https://doi.org/10.1038/4580>.
- Roach, N. W., & McGraw, P. V. (2009). Dynamics of spatial distortions reveal multiple time scales of motion adaptation. *Journal of Neurophysiology*, 102(6), 3619–3626, <https://doi.org/10.1152/jn.00548.2009>.
- Roulston, B. W., Self, M. W., & Zeki, S. (2006). Perceptual compression of space through position integration. *Proceedings. Biological Sciences*, 273(1600), 2507–2512, <https://doi.org/10.1098/rspb.2006.3616>.
- Schwartz, G., Taylor, S., Fisher, C., Harris, R., Berry, M. J. 2nd. (2007). Synchronized firing among retinal ganglion cells signals motion reversal. *Neuron*, 55(6), 958–969, <https://doi.org/10.1016/j.neuron.2007.07.042>.
- Shi, Z., & Nijhawan, R. (2012). Motion extrapolation in the central fovea. *PLoS One*, 7(3), 33651, <https://doi.org/10.1371/journal.pone.0033651>.

- Sillito, A. M., Jones, H. E., Gerstein, G. L., & West, D. C. (1994, June 9). Feature-linked synchronization of thalamic relay cell firing induced by feedback from the visual cortex. *Nature*, 369(6480), 479–482, <https://doi.org/10.1038/369479a0>.
- Sundberg, K. A., Fallah, M., & Reynolds, J. H. (2006). A motion-dependent distortion of retinotopy in area V4. *Neuron*, 49(3), 447–457, <https://doi.org/10.1016/j.neuron.2005.12.023>.
- Tse, P. U., Whitney, D., Anstis, S., & Cavanagh, P. (2011). Voluntary attention modulates motion-induced mislocalization. *Journal of Vision*, 11(3):12, 1–6, <https://doi.org/10.1167/11.3.12>. [PubMed] [Article].
- van Heusden, E., Harris, A. M., Garrido, M. I., & Hogendoorn, H. (2019). Predictive coding of visual motion in both monocular and binocular human visual processing. *Journal of Vision*, 19(1):3, 1–12, <https://doi.org/10.1167/19.1.3>. [PubMed] [Article].
- van Heusden, E., Rolfs, M., Cavanagh, P., & Hogendoorn, H. (2018). Motion extrapolation for eye movements predicts perceived motion-induced position shifts. *The Journal of Neuroscience*, 38(38), 8243–8250, <https://doi.org/10.1523/JNEUROSCI.0736-18.2018>.
- Whitney, D. (2002). The influence of visual motion on perceived position. *Trends in Cognitive Sciences*, 6(5), 211–216, [https://doi.org/10.1016/S1364-6613\(02\)01887-9](https://doi.org/10.1016/S1364-6613(02)01887-9).
- Whitney, D., & Cavanagh, P. (2000a). Motion distorts visual space: Shifting the perceived position of remote stationary objects. *Nature Neuroscience*, 3(9), 954–959, <https://doi.org/10.1038/78878>.
- Whitney, D., & Cavanagh, P. (2000b, August 18). The position of moving objects. *Science*, 289(5482), 1107a–1107, <https://doi.org/10.1126/science.289.5482.1107a>.
- Whitney, D., & Murakami, I. (1998). Latency difference, not spatial extrapolation. *Nature Neuroscience*, 1(8), 656–657, <https://doi.org/10.1038/3659>.
- Whitney, D., Murakami, I., & Cavanagh, P. (2000). Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flashed stimuli. *Vision Research*, 40(2), 137–149. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10793892>