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## Effect of motion smoothness on the flash-lag illusion

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### ABSTRACT

Two flash-lag experiments were performed in which the moving object was flashed in a succession of locations creating apparent motion and the inter-stimulus distance (ISD) between those locations was varied. In the first ( $n = 10$ ), the size of the flash-lag illusion was a declining non-linear function of the ISD and the largest reduction in its magnitude corresponded closely to the value where observers judged the continuity of optimal apparent motion to be lost. In the second ( $n = 11$ ) with large ISDs, we found the largest illusions when the flash initiated the movement, and no effect was observed when the flash terminated the movement. The data support motion position biasing or temporal integration accounts of the illusion with processing predominantly based on motion after the flash.

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### 1. Introduction

A moving object appears to spatially lead a flashed object when both are displayed in physical alignment. For over a decade, this flash-lag illusion (FLI) has received considerable attention from researchers who have proposed at least five theories in explanation (see reviews by Eagleman & Sejnowski, 2007; Krekelberg & Lappe, 2001; Nijhawan, 2008; Schlag & Schlag-Rey, 2002; Whitney, 2002; Ögmen, Patel, Bedell, & Camuz, 2004). Virtually all research into the flash-lag illusion has required observers to compare the position of a stationary, briefly presented stimulus to the position of a moving object that may well be reversing or changing velocity, but whose movement otherwise appears smooth. The moving object typically differs from the flash in two ways: duration of visibility and motion. Surprisingly, few experiments have manipulated these properties specifically to explore the separate effects of motion and motion perception on the flash-lag illusion. Recently, Cantor and Schor (2007) did vary the duration of flashed and moving stimuli and concluded that the magnitude of the flash-lag illusion reaches a ceiling when the moving stimulus has appeared for at least 120 ms, but the illusion disappears for ‘flashes’ lasting 80 ms or more.

In research most closely related to the experiments reported here, Vreven and Vergheze (2005) used ‘strobed’ motion (that is, sampled in space and time) to separate the effects of motion signal strength and predictability on the magnitude of the FLI. In one condition, they presented the flash alongside a moving object that was actually flashed for one frame (13 ms) in a sequence of positions, or ‘stations’, separated by 200 ms and more than 4° along its trajec-

tory (the *interstimulus distance* or ‘ISD’). The magnitude of the flash-lag illusion was reduced to nearly zero. Eagleman and Sejnowski (2007) have also used sampled motion in a different experimental paradigm – that used to measure the Fröhlich illusion (Kirschfeld & Kammer, 1999; Müsseler, Stork, & Kerzel, 2002; Whitney & Cavanagh, 2002). They measured the perceived misalignment between the location of the appearance of a ‘moving’ object and the location of a stationary landmark that appeared at the same time as the moving object and remained visible for the duration of movement. When the ‘moving’ object was flashed at just two positions with a stimulus onset asynchrony of 67 ms and separated by at least 1°, greater misalignment was reported than when the moving object occupied five positions within that same spatio-temporal span. Thus, unlike Vreven and Vergheze (2005), Eagleman and Sejnowski (2007) found that increasing the ISD increased the illusion size. Our current research also varied ISD, but over a greater number of values and compared the illusion magnitude at each of these values with the percept of motion ‘smoothness’. No previous research has investigated the nature of this relationship, as there has been no systematic manipulation of either spatial and/or temporal parameters contributing to this percept of motion continuity/smoothness (Boring, 1942; Burr, Ross, & Morrone, 1986; Ekroll, Faul, & Golz, 2008; Fahle, Biester, & Morrone, 2001; Morgan & Turnbull, 1978; Tyler, 1973) in the flash-lag paradigm.

The perceptual transition from smooth to sampled motion is important for models of human motion processing. The spatial and temporal values obtained for this discrimination circumscribe the parameters of the first stage of motion processing: initial sampling by an array of oriented, spatial- and temporal frequency-tuned filters (Adelson & Bergen, 1985; Fahle et al., 2001; Watson & Ahumada, 1985). As opposed to physically continuous motion,

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the visibility of sampled motion is determined by whether the spatio-temporal frequency combinations of sampled motion are outside a “window of visibility” and hence the sampling goes undetected (Adelson & Bergen, 1985; Watson & Ahumada, 1985). This low-level motion processing has been identified with the ‘short-range’ process in apparent motion (Braddick, 1980). In the case of these short-range processes, it has been shown that the discrimination (where feedback was given) of smooth from sampled motion occurs for ISDs less than  $0.3^\circ$ , for stimuli and velocities ( $12^\circ \text{ s}^{-1}$ ) similar to that used in the current research (Fahle et al., 2001). We tested ISDs smaller and greater than this value.

However, there are ‘long-range’ processes beyond these short-range processes that determine the criterion of smoothness of the perceived motion (Braddick, 1974; Braddick, 1980), especially in apparent motion displays. Wertheimer’s (1912/1961) original description of apparent motion noted that a unified moving percept arises from successive, discrete events given certain timings and station locations. This *optimal apparent motion* occurs when the movement generated discretely in time and space is indistinguishable from real motion (the latter is infinitely smoothly differentiable over time and space; Kolers, 1972). In this case, a single moving object is seen to traverse the entire distance between physical stimulus stations (Ekroll et al., 2008). On the other hand, a ‘pure’ apparent movement percept (Steinman, Pizlo, & Pizlo, 2000) occurs just when there is a percept of directional displacement between locations, for example, left-to-right or right-to-left, rather than stimuli just flashing in separate locations.

Operationalisation of apparent motion percepts has been in dispute since Wertheimer’s original observations (Steinman et al., 2000). It is beyond the scope of this paper to engage in this debate, but for descriptive purposes, we note that a range of perceptual states has been recently proposed by Ekroll et al. (2008) as a result of their observations where timings were varied in apparent motion using just two stimuli separated by  $2.3^\circ$ . In addition to the optimal apparent motion percept described above, these researchers also describe a *part* motion percept. Stimuli are perceived at each of the stations, and they have a perception of ‘jerky’ motion as each moves some way towards the next station.

In the current study, we have altered the percept of motion smoothness by varying the one parameter – ISD – while keeping velocity constant. We measured the magnitude of the flash-lag illusion as a function of this parameter, and to confirm that motion smoothness was indeed altered, participants judged the smoothness of the motion percept using the optimal/part motion (smooth or jerky) dichotomy described above. As the ISD was increased, the optimal apparent motion percept was lost, and we expected the magnitude of the FLI to follow if the processes which support this percept contribute to the FLI. Indeed, the magnitude may diminish most dramatically just as the smoothness of the motion percept disintegrates. On the other hand, following Eagleman and Sejnowski (2007), there may still be a significant flash-lag effect when there is no optimum motion percept at all, rather, just part motion alone. Eagleman and Sejnowski’s theory would attribute this to a motion signal associated with the part motion percept spatially biasing the location of these stimulus stations.

## 2. Experiment 1: FLI with optimal and ‘part’ motion

### 2.1. Methods

#### 2.1.1. Observers

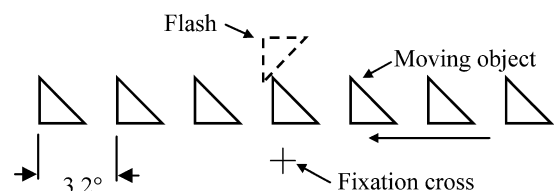
Ten observers comprising five males and five females (two authors and eight naïve participants, mean age 29.3 years) took part in the experiment. All had normal or corrected-to-normal visual acuity. Half of the naïve observers were volunteers and the

other half received course credit or reimbursement for their participation. One male observer did not complete the optimal motion perception condition (see below), due to slight physical discomfort and his incomplete data set was excluded from the analysis of this condition.

#### 2.1.2. Stimuli

Stimuli were presented on a 14 in. colour monitor with a vertical refresh rate of 72 Hz and a  $640 \times 480$  pixel resolution. It was located 57.3 cm from the observer’s eyes, where the viewing distance was kept constant with the aid of a chin rest. All stimuli were white (around  $75 \text{ cd m}^{-2}$ ) displayed on a black background ( $1.1 \text{ cd m}^{-2}$ ) in dim ambient lighting (around  $3 \text{ cd m}^{-2}$  on average). All luminance measures were recorded with a Tektronix J18  $1^\circ$  luminance probe. Fig. 1 illustrates the stimuli used in the flash-lag condition. The flashed and ‘moving’ objects were right-angled triangles measuring  $2.0^\circ$  in both height and width, with the flashed triangle spatially inverted with respect to the moving triangle. At its nearest approach, the base of the horizontally moving triangle was located  $1.5^\circ$  above the centre of a white fixation cross which subtended  $1.0^\circ$  on each arm. The lower vertex of the flashed triangle was located  $3.0^\circ$  above the centre of the cross, thus creating a potential  $0.5^\circ$  overlap between the upper vertex of the moving triangle and the lower vertex of the flashed triangle (see Fig. 1). The motion of the moving triangle was sampled in both time (determined by ‘frames’ of vertical refresh of the monitor) and space (determined by location in pixels on the screen). It was, in effect, a number of discrete stimuli, each of one frame’s duration ( $\sim 14 \text{ ms}$ ), and presented at different successive horizontal locations on the screen only on certain frames, before re-appearing at the next location.

In all conditions, a key press by the observer initiated the trial and the ‘moving’ triangle appeared after a 1.5 s delay, located approximately  $12^\circ$  either to the left or right of the fixation cross, whereupon it was displaced horizontally across the screen at the equivalent of  $12^\circ \text{ s}^{-1}$  for two seconds. The spatial difference between the sample locations was the ISD and assumed values of  $0.1^\circ$  (smoothest movement),  $0.4^\circ$ ,  $0.8^\circ$ ,  $1.6^\circ$ , or  $3.2^\circ$ . The sampling was of just seven locations across the entire screen in the latter case (see Fig. 1). Concomitant with this discrete spatial presentation was discrete temporal presentation: the stimuli appearing in every frame, every second frame, fourth, ninth or nineteenth frame, respectively. This spatial and temporal sampling maintained a constant velocity equivalent to  $12^\circ \text{ s}^{-1}$ . In the flash-lag conditions (see below), a second, inverted triangle was displayed for one frame above the moving triangle at a random location within a  $2^\circ$  horizontal ‘window’ that was adjacent to the fixation cross near the centre of the screen. The frame in which the flashed triangle appeared was always a frame in which the sampled moving triangle appeared (see Fig. 1) and was the *critical station* for the FLI comparison.



**Fig. 1.** Schematic of a flash-lag trial stimulus for an ISD of  $3.2^\circ$ . The triangular stimulus undergoing sampled motion from right-to-left (trajectory indicated by arrow) occupied the positions indicated by the solid triangles in succession for just one vertical refresh frame at a time and every 19th frame (that is, frame number 19, 38, etc.). The flashed triangle, indicated by a broken line, always appeared within frames in which the moving stimulus also appeared. The shapes of all stimuli were mirror-reversed in left-to-right motion trials.

### 2.1.3. Procedure

All observers' viewing of stimuli was binocular and the presentation of trials was self-paced. The experiment consisted of two different types of conditions: five flash-lag conditions in which the flash stimulus appeared and the moving stimulus was presented at one of the five ISDs, and one optimal motion perception condition that measured observers' perception of motion smoothness for the sampled motion stimulus. In the latter condition, the moving stimuli were generated in a similar way to the flash-lag conditions, however, there was no flashed triangle.

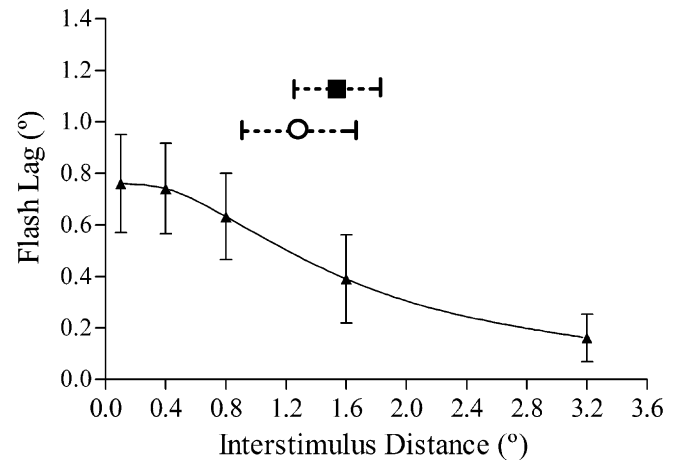
In the flash-lag conditions, observers indicated by pressing one of two keys on a keyboard whether the vertical edge of the flashed triangle was seen to the left or to the right of the vertical edge of the moving triangle. This 2AFC judgement enabled an individual's point of subjective alignment (PSA) to be estimated in the following way using an adaptive method of constant stimuli. We adopted a preliminary set of nine moving-flashed triangle alignment offsets around the estimated PSA for each ISD. After approximately every nine trials for each of the five conditions, a logistic regression (Finney, 1971) was automatically performed for each participant-condition. This enabled a new PSA to be computed for each condition, and the set of nine offsets were automatically moved if necessary so as to be centred on this new estimate.

In the separate optimal motion perception condition, the moving triangle was displayed by itself and the ISD was varied between trials. Observers were asked to indicate via a 2AFC task whether they perceived a single triangle smoothly moving across the screen, or whether there was a breakdown in such continuity and the percept was of a series of discrete stimuli successively occupying different locations on the screen in a 'jerky' fashion (Morgan & Turnbull, 1978; Tyler, 1973). Initially, nine fixed ISDs spanning the anticipated range of a change in percept from smooth motion to discrete displacements were used for these trials. The ISD at which the observer was equally likely to report either smoothness in movement or discrete stimuli was obtained by an adaptive method of constant stimuli procedure – the set of nine ISDs was shifted in a similar method to that described above to best span this critical ISD.

Each observer sat through one pilot session and one experimental session conducted on different days but normally within one week of each other. The pilot session lasted about 30 min and was used to familiarise the observer with the tasks as well as providing estimates of PSAs in the flash-lag task and critical ISDs in the optimal motion condition. The experimental session lasted approximately one hour, with breaks. The flash-lag conditions were presented in two blocks, each consisting of 270 trials. Each block consisted of three repeated presentations of each of the five ISDs at nine moving-flashed triangle alignment offsets for each of left-to-right and right-to-left motions. The optimum motion perception condition was presented in a separate block of 72 trials with four repeated presentations in each motion direction for nine ISDs. Trials were timed out after 1.5 s, but this was a very rare occurrence. Conditions were fully randomized within each block.

### 2.2. Results

Data collected during the pilot session are not presented here, and the data from the two blocks of the flash-lag conditions in the experimental sessions were combined. A sigmoidal psychophysical function was fitted via logistic regression to these data and to the optimum motion perception data, to find participants' PSA in each condition. Finney's (1971) methods were used to calculate 95% confidence intervals. A within-subjects ANOVA was conducted on the flash-lag data (Fig. 2) and with the metric set to reflect the uneven spacing of levels of the ISD, significant linear ( $F(1, 9) = 81.3, p < 0.001$ ) and cubic ( $F(1, 9) = 21.4, p = 0.001$ ) trends



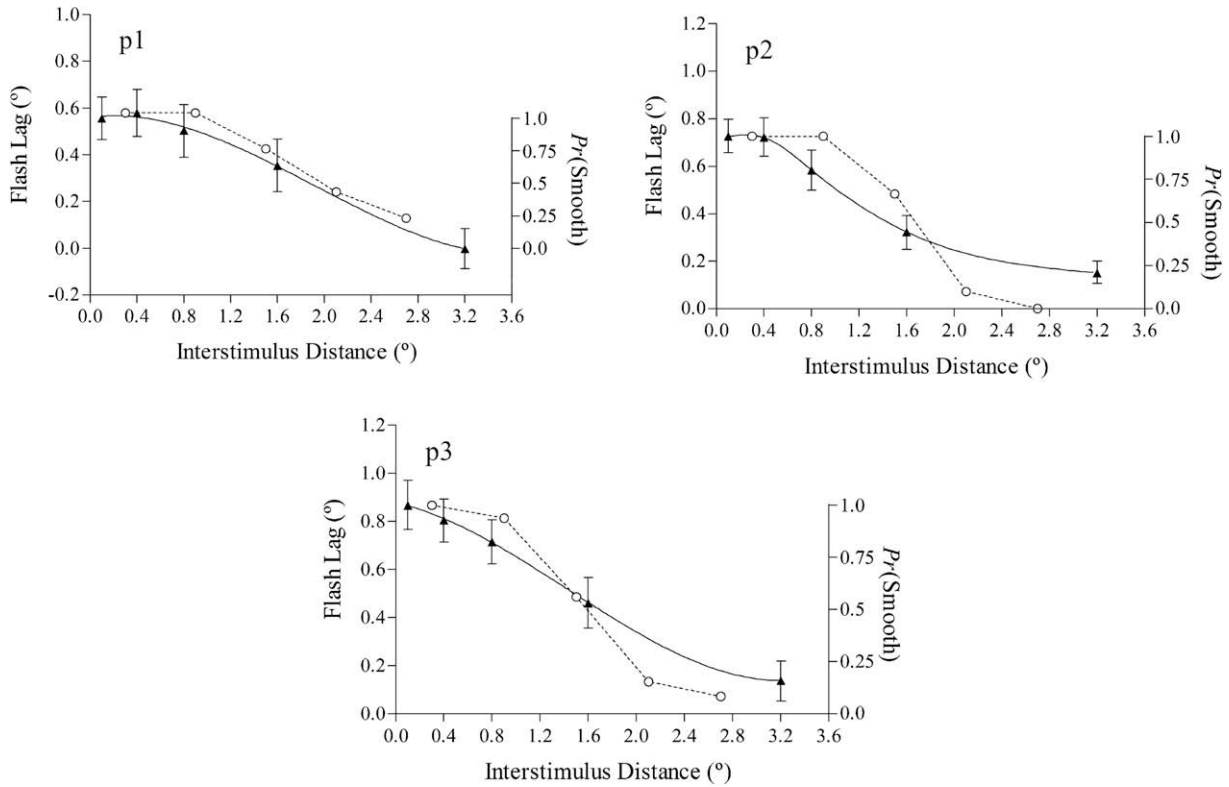
**Fig. 2.** Average magnitude of the flash-lag illusion for ten participants displayed as a function of the ISDs (triangular symbols). The curve fitted to these means is a best-fit cubic spline. The open circle symbol is the average ( $n = 9$ ) critical ISD from the optimum motion perception condition and represents the ISD where the percept changed from continuous smooth motion to discrete steps. For comparison, the closed square symbol is the average ISD corresponding to the steepest slope on a best-fitting cubic polynomial conducted on each observer's flash-lag data (see text for more details). All error bars on both axes are 95% confidence intervals.

resulted. The difference between illusions at ISD = 0.1 and 0.4° was not significant ( $p = 0.25$ ), but all other paired comparisons between successive means were (0.4° vs. 0.8°, etc.,  $p < 0.005$ ). The illusion magnitude was significantly different from zero at all ISDs as indicated by the confidence intervals on Fig. 2 (four smallest ISDs,  $ps < 0.001$ , at the largest ISD of 3.2° ( $t(9) = 3.2, p = 0.01$ )).

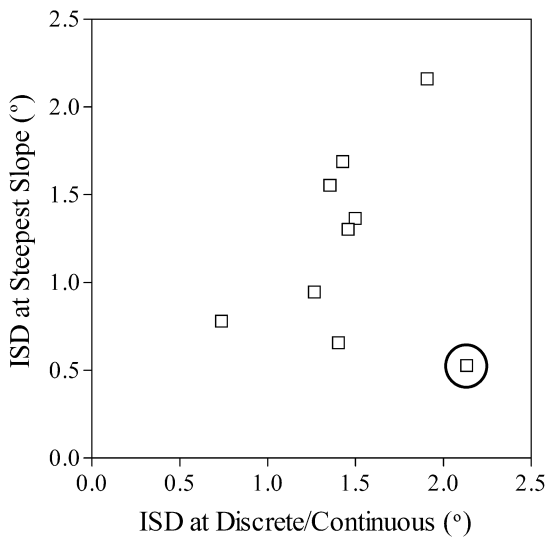
To determine at what ISD the change in the magnitude of the flash-lag illusion was greatest, flash-lag data from the nine observers completing the optimum motion perception condition were each separately fitted with a cubic polynomial. With these individual ISD data weighted according to size of confidence intervals, the best-fitting polynomial was computed and the inflexion point ( $d^2(FL)/d(ISD)^2 = 0$ ) was calculated. The average of these inflexion points is shown in Fig. 2. This is the point on the curve where the magnitude of the flash-lag illusion is decreasing most rapidly.

These data can then be compared to the results from the optimum motion perception condition. The critical ISD where observers report ( $prob. = 0.5$ ) either smooth motion or discrete steps was averaged and also graphed on Fig. 2. A  $t$ -test revealed that there was no difference between the inflexion points and the critical ISDs: ( $t(8) = 1.2, p = 0.26$ , effect size  $d = 0.4$ ). This congruence between the magnitude of the FLI and the frequency of reporting of the percept of optimum motion as a function of ISD is further illustrated in data from three observers chosen at random (Fig. 3). Because of the difference in ISD values actually tested in the smooth motion condition among the three observers that was produced by the adaptive method of constant stimuli procedure, ISD values have been binned as follows: 0.0 to 0.6° (middle = 0.3), 0.6–1.2° (middle = 0.9), 1.2–1.8° (middle = 1.5), 1.8–2.4° (middle = 2.1) and 2.4–3.0° (middle = 2.7).

Fig. 4 shows this relationship in another way where the ISD at which smooth motion failed and the ISD corresponding to the greatest decrease in the magnitude of the flash-lag illusion is plotted for each of the nine observers. It can be argued that one participant is an outlier (circled, Mahalanobis distance = 3.06) and if this observer's datum is excluded, the correlation becomes significant ( $r = 0.73, p = 0.02$ , one-tailed). The evidence strongly suggests that the greatest diminution in the magnitude of the FLE occurred just where observers were reporting the smooth motion percept changing into discrete steps.



**Fig. 3.** Individual flash-lag and optimal motion data, as a function of ISD, for three participants. Flash-lag data is displayed with respect to the left-hand y-axis as closed triangular symbols, joined by a solid line which represents the individual cubic spline best-fit similar to Fig. 1. Error bars are individual 95% confidence intervals. The open symbols joined by a broken line refer to the right-hand y-axis and represent the proportion of responses of ‘smooth’ movement vs ‘jerky’ for five bins of ISD values (see text for details).



**Fig. 4.** Scattergram ( $n = 9$ ): ISD corresponding to the steepest slope (maximum change) in the flash-lag data, for each individual (y-axis), compared against the critical ISD in the optimum motion perception task. The outlier is circled.

2.3. Discussion

As expected, the magnitude of the flash-lag illusion decreased as ISD increased. (A comparison with previous related studies is deferred to the General Discussion, 4.1, as Experiment 2 also contributes relevant data.) Further, the transition from a perception of smooth motion to one of ‘jerky’ motion coincided with a substantial lessening of the flash-lag illusion. On average, our *Ps* were los-

ing the percept of smooth motion at an ISD of around 1.2°. However, as was also found by Ekroll et al. (2008), there was considerable variation in this value among *Ps* probably due to differences in the criteria used to make the judgement. For example, the outlier (Fig. 4) may have adopted a different criterion of smooth perceived motion than the other participants (Braddick, 1980). However, the results lend support to the notion that whatever detectors and processes alter the perception of smooth motion also change the magnitude of the FLI.

Further, at the smaller ISDs, there was a significant diminution in the FLI’s magnitude, but only when an ISD was clearly outside the range of the short-range motion processes (Fahle et al., 2001, compare 0.4° vs. 0.8 ISD). There was no reduction in FLI magnitude for ISDs within this range of these processes (no difference between 0.1° and 0.4°). Whilst short-range processes may contribute to the magnitude of the flash-lag illusion, their activation is clearly not a necessary condition for the existence of a FLI. This is evidenced by the unexpected significant flash-lag effect at our larger ISDs, where in the extreme case the ‘moving’ object was seen just to occupy a series of seven locations across the screen, each separated by 3.2° and 267 ms. Vreven and Verghese (2005) interpreted their results as being due to the predictability in the ‘moving’ object, as opposed to the uncertainty of the timing and location of a static flash. They claim that this predictability allows the moving object to be both processed and hence localised faster, and this would yield the spatial illusion given the assumption that the temporal advantage is converted to a spatial offset.

Of course, in Experiment 1, even at our largest ISD, once the motion has commenced the rest of the trajectory is quite predictable. To test for the contribution of predictability, we therefore produced a trajectory for which there were no stations before the frame in which the flash occurred (the critical station), hence elim-

inating the contribution of predictability at least from before the flash. Indeed, such *Onset trajectories*, together with their counterpart *Offset trajectories* (where the moving stimulus disappears with the flash) have been used extensively to test between theories that claim motion before the flash contributes to the illusion (Nijhawan, 1994; Nijhawan, 2008) and those that claim that only motion after the flash contributes (Eagleman & Sejnowski, 2000; Eagleman & Sejnowski, 2007). In general, substantial illusions have resulted with the former trajectory, and null illusions with the latter (reviewed in Chappell, Hine, Acworth, & Hardwick, 2006).

A careful comparison of these trajectories has not been tested with sampled motion, so we ran a second experiment using just the largest ISDs of 1.6° and 3.2° with Onset and Offset trajectories in addition to the Continuous trajectory used in Experiment 1.<sup>1</sup> It is crucial to note that in the Onset, ‘flash-initiated’ trajectory, at the time the flash and the first station of the ‘moving’ object are simultaneously displayed, the observer had no cues as to whether the next flashed station of the moving object would be to the left or right, or whether it would appear 133 or 267 ms later. If predictability (up to the time of the flash) underlies our illusion with large ISDs, we would predict a null illusion with the Onset trajectory, and a non-zero illusion with the Offset trajectory.

For the Onset trajectory the displacements eventually do become predictable after the flash. This predictability could ultimately affect the perception of the position of the first station, in a ‘postdictive’ fashion, thus producing an illusion even with an Onset trajectory. However, if motion processing from before the flash also contributes to the illusion, then a Continuous trajectory would contain more information on which to base prediction, and so one might expect a larger illusion resulting from it than from an Onset trajectory. On the other hand, if predictable movement before the flash does not contribute, one might expect illusions of similar magnitude with Onset and Continuous trajectories. All of these hypotheses were tested in Experiment 2.

### 3. Experiment 2: flash initiated and flash terminated conditions

#### 3.1. Methods

##### 3.1.1. Observers

Eleven naïve observers comprising five males and six females took part in the experiment. All had normal or corrected-to-normal visual acuity and all received reimbursement for their participation.

##### 3.1.2. Stimuli

Stimuli were generated using a Cambridge Research Systems VSG 2/3F and displayed on a Sony 21 in. colour monitor with a vertical refresh rate of 120 Hz and a 640 × 479 pixel resolution. It was located 103 cm from the observer’s eyes, where the viewing distance was kept constant with the aid of a chin rest. All stimuli (including the fixation mark) were white (107 cd m<sup>-2</sup>) and displayed on a black background (1.1 cd m<sup>-2</sup>) in dim ambient lighting (0.6 cd m<sup>-2</sup> on average). All luminance measures were recorded with a Minolta CS-100A chromameter with a 1° measurement angle.

The stimuli used in this experiment were similar to those in the first experiment with a few important differences. The flashed and ‘moving’ objects were each isosceles triangles (rather than the right-angled triangles of the previous experiment) measuring 2.0° in height and 1.6° in width, with the flashed triangle spatially inverted (apex down) with respect to the horizontally moving tri-

angle (apex up). The top vertex of the moving triangle was located 3.5° above the centre of a broken white fixation line that subtended a total length of 1.0° with a central gap of 0.4°. The lower vertex of the flashed triangle was located so that the minimum vertical separation between it and the moving triangle was 0.3°. The new symmetrical shape of the stimulus was chosen after piloting for this experiment indicated a very small but consistent spatial bias (~0.04°) in participants’ judgments as measured with a Control condition as described below. The direction of the bias was such that illusion magnitudes would tend to be underestimated. The bias was eliminated by making the triangles symmetrical, and by testing in a region symmetrically distributed above the fixation point. So, compared to the previous experiment, the apices of the two stimuli being compared were the same vertical distance above the fixation mark but were closer to this mark measured horizontally. Across trials, the flash appeared in positions randomly and uniformly distributed within a window 1.0° wide, centred above fixation.

For the smooth motion condition, the moving stimulus was displaced horizontally across the screen at a speed of 12° s<sup>-1</sup>. Following Experiment 1, two ISDs were used: 1.6° and 3.2°, and in these conditions the equivalent velocity of the ‘moving’ stimulus was also 12° s<sup>-1</sup>. In all conditions, the flashed and sampled moving stimulus appeared at any one location for just one frame (~8 ms) and the flashed triangle always appeared within frames in which the moving stimulus also appeared.

##### 3.1.3. Procedure

Experiment 2 comprised eight conditions in all. For each of the two ISDs in the sampled motion conditions, Onset, Continuous and Offset trajectories were tested. ‘Continuous’ trajectories were as per Experiment 1. For the Onset trajectory, the appearance (first location) of the moving stimulus occurred in the same frame as the flash. For the Offset trajectory, the disappearance (last location) of the moving stimulus occurred in the same frame as the flash. There was also a ‘Control’ condition, where the ‘moving’ stimulus actually remained in the same location in the centre of the screen and flashed at the same temporal rate as the 1.6° ISD conditions (7.5 Hz). Finally, there was a ‘Smooth’ condition, where the moving stimulus appeared in every frame. In the Onset condition, the moving object first appeared near the centre of the screen and moved either to the left or right edge of the screen (about 12°) for 1.0 s. In the Offset condition, the moving object first appeared either at the left or right edge of the screen and moved for 1.0 s towards the centre. In the Continuous and Smooth conditions, movement was across the entire screen, starting either at the left or right edge, and lasting for 2.0 s.

Observers indicated by pressing one of two keys on a keyboard whether the apex of the flashed triangle was seen to the left or to the right of the apex of the moving triangle, where responses were timed out after 1.25 s. Offsets to be tested between the two stimuli were derived using an adaptive method of constant stimuli similar to that described above, but more efficient. In this case, the range of offsets that was estimated (via logistic regression) to most reduce the magnitude of the confidence interval of the PSA was continually being computed and tested.

Conditions were fully randomised within a single block as were the directions of movement (leftwards or rightwards) where applicable. Starting estimates of each PSA were obtained for five Ps from pilot results, and one session proved sufficient to reliably measure most participants’ PSA for each condition. We adopted a reliability criterion of a maximum confidence interval width of 0.7° for each PSA. One P was invited back for a second session and only these data are reported here, as the first session’s data failed to meet this criterion and exhibited significant bias in alignment judgements in the Control condition.

<sup>1</sup> We thank anonymous reviewers for suggesting the need for an experiment testing predictability.

### 3.2. Results

Data from the pilot work referred to above were very similar to the experimental data and are not presented here. PSAs for each condition were averaged across participants and are plotted in Fig. 5. The Control condition (no motion) result indicates that there was no bias in alignment judgments on average, and in fact no individual  $P$  exhibited any significant bias. The 95% confidence intervals indicate that all other conditions, apart from the Offset conditions, yielded significant illusions. Paired-sample  $t$ -tests (two-tailed) were performed on differences of interest and the following differences were found to be significant. Onset  $1.6^\circ$  was larger than Onset  $3.2^\circ$ :  $t(10) = 4.45$ ,  $p = 0.001$ , Continuous  $1.6^\circ$  was larger than Continuous  $3.2^\circ$ :  $t(10) = 3.71$ ,  $p = 0.004$ , and Smooth was larger than Continuous  $1.6^\circ$ :  $t(10) = 3.70$ ,  $p = 0.004$ . Onset  $1.6^\circ$  was larger than Continuous  $1.6^\circ$ :  $t(10) = 4.22$ ,  $p = 0.002$ , which in turn was larger than Offset  $1.6^\circ$ :  $t(10) = 4.36$ ,  $p = 0.001$ . The comparison between Onset  $3.2^\circ$  and Continuous  $3.2^\circ$  yielded  $t(10) = 2.68$ ,  $p = 0.023$  (this test was the only one whose significance would be affected by any family-wise control for Type I error due to multiple pair-wise comparisons), whilst the difference between Continuous  $3.2^\circ$  and Offset  $3.2^\circ$  was not significant. Each of the Onset  $3.2^\circ$  and Continuous  $3.2^\circ$  averages were different from zero (one-sample tests,  $t(10) = 3.24$ ,  $p = 0.009$  and  $t(10) = 2.645$ ,  $p = 0.025$ , respectively) reproducing the result from Experiment 1.

### 3.3. Discussion

The absolute size of the FLI for the Continuous conditions was smaller on average than the corresponding condition in the first Experiment. This could have been due in part to the different refresh rates used in the two experiments. In Experiment 2, stimuli were potentially visible for a shorter 8 ms (one refresh) as opposed 14 ms in Experiment 1. This would effectively increase the temporal interstimulus intervals (ISI) between stations in Experiment 2 compared to Experiment 1. Ekroll et al. (2008) have shown that increasing the ISI produces less reporting of optimal motion vs part motion. So, even though the ISDs were similar, the faster, 'crisper' display in Experiment 2 probably yielded a less smooth percept, and as the results of Experiment 1 have shown, this diminishes the magnitude of the FLI. Most probably, however, the effects of these differences would be subtle, and other differences in the geometry of the stimuli between the two Experiments also contributed to the difference in effects.

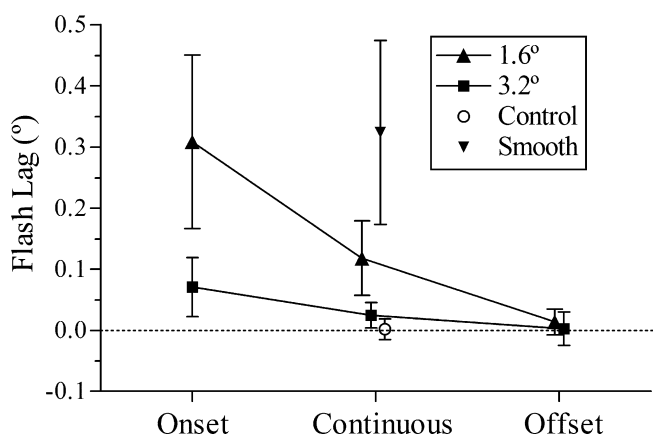


Fig. 5. Average magnitude of the FLI for the Onset, Continuous and Offset conditions of Experiment 2 ( $n = 11$ ), as well as the two control conditions. Error bars are 95% confidence intervals and have been slightly offset along the x-axis in some cases for ease of reading.

The Onset trajectory results clearly demonstrate that the illusions with the larger ISDs in Experiment 1 were not the result of predictability from the trajectory before the flash (cf. Eagleman & Sejnowski, 2007). In fact, we obtained significantly larger effects in the unpredictable Onset conditions than we did in the Continuous conditions, similar to what has been found previously with a smoothly moving object (Chappell et al., 2006; Eagleman & Sejnowski, 2000; Müsseler et al., 2002; Ögmen et al., 2004). This result is surprising, given that, for  $ISD = 1.6^\circ$  conditions, the first station of the apparent motion is  $1.6^\circ$  and 133 ms from the second, and for this reason we would have expected  $P$ s to more accurately localise the point of appearance of the moving stimulus with respect to the flash in this sampled condition than when the motion was smooth. It is also notable that perception of the position of the first station of the  $ISD = 3.2^\circ$  Onset trajectory is also being affected, albeit in a small way, by the appearance of the second station 267 ms later. In our previous work with smooth motion (Chappell et al., 2006), we found the FLI with an Onset trajectory to be 33% bigger than with a Continuous trajectory. The proportional difference here of a much larger 260% is even more surprising. This ratio was greater than 200% for 7 out of 11  $P$ s in Experiment 2.<sup>2</sup>

Predictability of trajectory after the time of the flash also does not seem important. As noted above, if it were an important contributor to the illusion, Continuous and Onset trajectories should produce illusions of similar magnitude, whereas the former was found to be less than half the magnitude of the latter. If predictability both before and after contribute, then a continuous trajectory should yield a larger illusion than an Onset trajectory – the opposite of what was found.

Onset conditions are a problem for Nijhawan's predictive theory. His recent explanation (Nijhawan, 2008) relies on the fact that with a motion-onset stimulus, the moving stimulus will undergo a significant shift across several photoreceptors while the flash is being processed. He specifies that this happens within 0.9 ms of the moving stimulus appearing, so that there is some motion information in the pathway capable (later) of a directionally selective response. In our case, this cannot occur within such a time-window. At the critical station, all that is displayed is two flashes, one above the other, with no shift on the retina. In the  $1.6^\circ$  ISD condition, no event occurs for another 133 ms, and during that interval it is not known whether movement will be to the left or right, or whether there will be no movement at all (Control condition). Yet the FLI is still substantial.

The null illusions with an Offset trajectory are in agreement with other previous work for stimuli centrally located and possessing sharp edges (Chappell et al., 2006; Eagleman & Sejnowski, 2000; Kerzel, 2000; Kerzel, Jordan, & Musseler, 2001). Nijhawan (2008) has argued that the overshoot is not perceived because the sudden disappearance of the moving stimulus causes a substantial transient in the visual system, which has the effect of very quickly terminating the predictive process claimed by him to underlie the FLI. Our null results provide a further challenge to this predictive account as there is nothing different, in terms of stimulus presentation, about the last station of our Offset trajectory, compared to all other stations – at each station the stimulus is just flashed once and so each is a 'transient' of equal potency.

Our combined results with the various trajectories also pose a challenge to the temporal integration theory of Krekelberg and Lappe (Krekelberg & Lappe, 1999; Krekelberg & Lappe, 2000; Lappe & Krekelberg, 1998), in which a range of positions the moving object occupies over time are averaged to determine its instantana-

<sup>2</sup> As noted by a reviewer, the confidence interval is quite large for the Onset  $1.6^\circ$  ISD condition. However, our pilot experiment with eight  $P$ s, including four not in the experiment reported above, found this proportion to be 230%. This suggests that this large proportional increase is reliable.

neous position. Most generally, each position is assumed to be weighted by a function which varies smoothly, generally decreasing from the time and place the moving object occupied at the time of the flash.

We found no illusion for the offset trajectory, suggesting that no moving object positions prior to the terminal station contribute to the temporal integration. Parsimony suggests the same should be true for other trajectories. We need only consider weights for the discrete positions at which our stations occurred. However, the resulting linear combination of weights and positions will then be identical for both the Continuous and Onset trajectories, so temporal integration must predict the same illusion magnitude. In fact, of course, we found the illusion magnitude with Onset trajectory to be more than twice as large as that with the Continuous trajectory. Hence, without additional assumptions, temporal integration cannot fit our data.

Assuming temporal integration can be revised, our data provide additional constraints for the temporal window in this model. Lappe and Krekelberg (1998) and Krekelberg and Lappe (2000) proposed a window size of about 500 ms. In a later review (Krekelberg & Lappe, 2001, p. 336) they said: “Brenner and Smeets report 150 ms, Eagleman and Sejnowski argue for an 80 ms window, and Whitney et al. suggest an even shorter 50 ms window (albeit in combination with differential latencies)”: other’s research was indicating a substantially smaller window than their earlier simulations indicated. Our significant effects with  $ISD = 3.2^\circ$  would constrain the window to extend at least 267 ms after the flash.

#### 4. General discussion

The magnitude of the FLI declined as both the frequency of the motion sampling, and with it the perception of motion smoothness, was reduced. However, the illusion was not eliminated even with our largest ISD. Finally, predictability of the moving stimulus before the time of the flash does not seem to play any part in the illusion, and predictability at any stage is not helpful in explaining the pattern of our results. We have discussed the latter result above and the two other main results emerging from our research will now be discussed in turn.

##### 4.1. Effect of ISD and sampled motion

In both experiments as ISD increased, the FLI was significantly reduced as Vreven and Verghese (2005) found. This effect was even larger with the Onset trajectories in Experiment 2, which more closely resembles the experimental methodology used in Eagleman and Sejnowski’s (2007) paper. Although we have not eliminated all of the methodological differences, trajectory type is clearly not one that can be used to explain why Eagleman and Sejnowski found illusion magnitude to increase with ISD. We note that the average size of the FLI for an ISD of  $1.6^\circ$  for the Onset trajectory was similar to the value for Eagleman and Sejnowski’s two station condition with similar spatial separation and movement velocity.

Our results can also be compared with Murakami’s (2001b) randomly jumping stimulus (with no predictability at all) that did produce a flash-lag effect with a temporal equivalent of 70 ms. His stimulus occupied stations within a  $2.5^\circ$  horizontal range, with a uniform distribution across this range. To compare this with our ISDs, we generated two uniform random distributions of 1000 observations within his range to represent successive jumps. Our Monte Carlo simulation indicated that the absolute distance displaced had a triangular distribution, skewed towards small moves, with a mean of  $0.83^\circ$ , and a median of  $0.73^\circ$ . These ISD values are within the range of our values for reliable smooth movement perception, but are considerably smaller than our largest ISD.

We have found clear evidence of a relationship between absence of smooth motion and a decrement in the magnitude of the illusion. Does it necessarily follow that engagement of the processes underlying optimal smooth motion is causing the flash-lag illusion? In Murakami’s (2001a) descriptive account of the flash-lag illusion that does not invoke any specific motion processes, spatio-temporal correlations between the perceived locations of ‘moving’ and flashed objects are well accounted for by a Gaussian distribution of differential latencies in processing between the two stimuli, with the ‘dynamic’ stimulus (be it smoothly moving or randomly jumping) having a temporal advantage. The mean of this distribution of differential latencies is always estimated at around 60–80 ms (Murakami, 2001a; Murakami, 2001b). We predict that Murakami’s analysis applied to our data would reveal a substantial reduction in the mean differential latency as the ISD is increased above  $0.8^\circ$ .

Kanai, Sheth, and Shimojo (2007) have proposed that the reason for the moving objects’ processing advantage could be that a smoothly moving object rapidly forms a single ‘representation’, or gestalt, integrated over space and time. This will not occur if the object is seen to occupy a number of separate positions at different times and is thus not processed as efficiently. This could be the reason for the trend down in flash-lag illusion size with increasing ISD and decreasing motion smoothness (Fig. 2).

##### 4.2. Flash-lag illusion at large ISDs

Even at our most widely-spaced locations we found a significant illusion in both experiments. However, in Experiment 2 it was quite small, and we are clearly approaching the ISD where it would disappear altogether. Vreven and Verghese’s (2005) flashed location appeared every fifth of an entire rotation corresponding to a distance of  $8.8^\circ$  of visual angle along the curved movement path. It is thus unsurprising that they found a null illusion with that ISD.

In our largest ISD from Experiment 1 and 2, in order to appear to be aligned with the ‘moving’ stimulus, the flashed stimulus actually occupied positions on the screen (at least  $0.1^\circ$  ahead on average), adjacent to locations that the moving stimulus never occupied. It could be that observers were performing some interpolation of the ‘moving’ object’s location (Fahle et al., 2001, for review, see Steinman et al., 2000) part of the way towards the next station’s location (Ekroll et al., 2008).

Alternatively, the moving object’s location might be biased forwards along the trajectory (Eagleman & Sejnowski, 2007). In support of such a process operating, Eagleman and Sejnowski found that when the colour of a white apparent motion stimulus with ISDs of  $2.1^\circ$  was changed to blue at just one of these stations, a blue coloured stimulus was observed at a later position the moving stimulus never occupied. Given the difference between our Onset condition and Continuous condition in Experiment 2, this model would need to assume that the first station of sampled motion is even more vulnerable to position biasing than the point of appearance with smooth motion. Chappell et al. (2006) have previously suggested that attentional processes associated with setting up a new object representation might contribute to larger FLIs with Onset trajectories. Incorporating these into the positional bias, or temporal integration models might allow both these models to predict these data.

Apparent motion has been reported in the classical literature with ISDs ranging up to  $18^\circ$  (De Silva, 1926; Zeeman & Roelefs, 1953) for ‘flashed’ presentations of stimuli at different locations. This implies a motion signal, albeit ‘long-range’, exists at large ISDs, and could contribute to Eagleman and Sejnowski’s (2007) biasing process. From our data we can conclude that alignment judgements are affected by events substantially distant in time (267 ms) and space ( $3.2^\circ$ ) from the critical frame and screen loca-

tion in which the flash and the moving stimulus both appeared. This temporal range is far outside the 100 ms window of integration specified by those researchers supporting theories that the FLI is due to 'motion biasing' of positional judgments (Eagleman & Sejnowski, 2000; Eagleman & Sejnowski, 2007; Roulston, Self, & Zeki, 2006). In our case, this would exclude the second station for both the 1.6° and 3.2° ISD conditions, and thus render the illusion non-existent.

#### 4.3. Conclusions

As well as revealing a relationship between the smoothness of the moving stimulus and the magnitude of the FLI, our data challenge the notion that the predictability of the moving object's trajectory is an important determinant of the flash-lag illusion, in agreement with other work with Onset and Offset trajectories, and Murakami's (2001b) with random motion. The data from Experiment 2 also challenges the validity of visual prediction theories of the flash-lag illusion, which utilize information regarding the moving stimulus' trajectory before the flash-lag flash. Of extant theories of the flash-lag illusion, the motion biasing or temporal integration accounts could fit our data, but only if they utilize information from a relatively long time after the flash, and incorporate additional assumptions to cater for the Onset trajectory. It is left to future research to precisely determine whether the spatio-temporal parameters in apparent motion which yield a percept of part motion (as opposed to 'flicker'; with no sense of motion) also produce motion biasing and hence a flash-lag illusion.

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