Vision Research 48 (2008) 1584–1591

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Comparison of flashed and moving probes in the flash-lag effect: Evidence for misbinding of abrupt and continuous changes

Angélique Gauch, Dirk Kerzel *

Faculté de Psychologie et des Sciences de l'Éducation, Université de Genève, 40 Boulevard du Pont d'Arve, 1205 Genève, Switzerland

ARTICLE INFO

Article history:
Received 18 March 2008
Received in revised form 24 April 2008

Keywords:
Flash-lag effect
Trajectory
Moving probe
Motion bias
Uncertainty
Fröhlich effect
Motion
Illusion
Binding problem

ABSTRACT

In the flash-lag effect, a flash displayed at the same position as a moving object is perceived to lag the moving object. Current accounts of the illusion make different predictions about how the size of the lag would change if participants compared the position of a moving object to the onset position of a moving probe instead of a flash. We compared the lag effect with a moving probe relative to a flashed probe at motion onset, during ongoing motion, and at motion offset. At motion onset and offset, the lag effect was larger with a moving than with a flashed probe, but there was no difference during ongoing motion. Our results are best explained by the assumption that abrupt changes are erroneously bound to continuous changes following the occurrence of the abrupt change. Typically, the abrupt onset of the flash is misbound to continuous target motion, resulting in the flash-lag effect. With moving probes, abrupt changes of the target (onset, offset) may also be misbound to continuous motion of the probe which increases the lag.

1. Introduction

The localization of a moving object relative to a flashed object has been intensively studied in the context of the flash-lag effect (Nijhawan, 1994). In a typical flash-lag paradigm, the flash is displayed along the trajectory of a moving object. This paradigm is referred to as "continuous-motion" paradigm, because motion of the moving object starts long before the occurrence of the flash and continues after the flash. In another variant, the flash is displayed at motion onset (flash-initiated cycle) or offset (flash-terminated cycle). The illusion is comparable in magnitude at motion onset (Khurana & Nijhawan, 1995), but eliminated at motion offset (Eagleman & Sejnowski, 2000; Nijhawan, 1992; Whitney, Murakami, & Cavanagh, 2000).

Different theories have been suggested in order to elucidate the mechanisms underlying the flash-lag illusion (Baldo & Klein, 1995; Brenner & Smeets, 2000; Krekelberg & Lappe, 2000; Nijhawan, 1994; Purushothaman, Patel, Bedell, & Ogmen, 1998; Whitney et al., 2000). Motion extrapolation (Khurana & Nijhawan, 1995; Nijhawan, 1994) was among the first hypotheses that have been proposed. According to this view, a mechanism of extrapolation shifts the positions of moving objects in order to enable us to perceive their true position. This mechanism is predictive, bases its computations on the past trajectory of the moving object and depends on predictable and continuous motion. Hence, extrapolation implies a spatial mechanism. Applied to the flash-lag effect, the theory postulates that the real location P_x at time t_0 is extrapolated so that we perceive it at position P_x at t_0 despite neural delays. In contrast, the flash is too short and unpredictable to initiate any extrapolation. Consequently, the abrupt onset of the flash is perceived at position P_x at time $t_{1.}$ However at time t_1 the moving bar is perceived at position P_{x+1} which causes the perceived lag.

Although motion extrapolation could explain the presence of the flash-lag effect at motion onset (Khurana & Nijhawan, 1995), it has difficulty accounting for two other phenomena. First, the absence of flash-lag effect at motion offset (Eagleman & Sejnowski, 2000; Krekelberg et al., 2000; Nijhawan, 1992) (but see Nijhawan, 2008). Second, the fact that the flash-lag effect is modulated by luminance (Purushothaman et al., 1998). On the basis of these findings, the differential latency account suggests that the flash-lag effect is due to a temporal misjudgement between the flash and the moving object (Purushothaman et al., 1998; Whitney et al., 2000). More precisely, perceptual latencies of the moving object are supposed to be shorter than perceptual latencies of the flash. Consequently, when the moving and flashed objects are displayed at position P_x at time t_0, the moving object would be perceived at time t_1 and the position of the flash at time t_2. Note that at time t_2, the moving bar is perceived at position $P_{x+1.}$ If the differential latencies account was correct, the perceived onset time of the flash

* Corresponding author. Fax: +41 (0) 22 37 99 229.
E-mail address: dirk.kerzel@pse.unige.ch (D. Kerzel).

0042-6989/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2008.04.025

relative to the position of the moving object at time t_1 would not coincide. However, it has been demonstrated that temporal order judgements of the flash relative to motion onset are correct; that is, the perceived onset time of the flash and the moving object coincided (Eagleman & Sejnowski, 2001).

Both differential latencies and motion extrapolation consider the flash as a spatio-temporal marker indicating when a position judgment has to be made (Nijhawan, 2002). In contrast to this view, postdiction theory suggests that the position of a moving object is determined as a function of what happens about 80 ms after flash onset (Eagleman & Sejnowski, 2000; for a related account see Krekelberg et al., 2000). The theory postulates that the onset of the flash resets motion integration and causes the visual system to re-estimate position. Because the object is moving during the integration interval, it perceptually leads the flash. In Eagleman and Sejnowski (2000) terms, the moving object is postdicted to the time of the flash. However, this theory is controversial (Patel, Ogmen, Bedell, & Sampath, 2000). Moreover, in addition to the three theories mentioned above, other authors suggested attention (Baldo & Klein, 1995), predictability (Vreven & Verghese, 2005), sampling (Brenner & Smeets, 2000), asynchronous feature binding (Cai & Schlag, 2001), motion biasing (Eagleman & Sejnowski, 2007) as the reason for the lag effect, but there is no agreement on any particular mechanism.

1.1. Aim of study

In this paper, we compared the localization of a moving target relative to a flash with the localization of a moving target relative to the onset position of a probe that moved in the opposite direction. Localization of the moving target was investigated at the onset and offset of target motion, as well as during ongoing target motion. Each theory makes different predictions about the localization of two moving objects relative to one another and about a moving probe relative to a flashed probe (see Table 1).

Motion extrapolation theory (Nijhawan, 1994) would predict a spatial lag that is twice larger with a moving probe than with a flash. Consider position P_x at time t_0 as the position where probe and target are aligned (see Fig. 1A). When the moving probe appears at position P_x at time $t_{0,}$ the target is correctly perceived without any delay (see Fig. 1C). However, extrapolation for the moving probe is not yet triggered at time t_0. Activation of this mechanism at time t_1 results in a shift of the perceived probe location to its actual position P_{x-1}. Similarly, the moving target would be perceived at its real position P_{x+1} at time $t_{1,}$ which produces a spatial offset twice larger than the flash-lag effect. At motion onset, the extrapolation mechanism is triggered at time t_1 for both bars, consequently the target would be perceived at position P_{x+1} and the probe at position P_{x-1}. At motion offset, the position of the target would be perceived as shifted in the direction of motion because the visual system extrapolates object position at time t_1 so that the offset of the bar is perceived at position P_{x-1}.

Table 1
Summary of predictions for the spatial lag along the trajectory and results of Experiments 1–3

Condition	Predictions			Results
	Extrapolation	Differential latencies	Postdiction	Experiments 1–3
Motion onset	Moving probe >> flash	/	moving probe >> flash	moving probe >> flash
Continuous motion	Moving probe >> flash	/	moving probe >> flash	moving probe = flash
Motion offset	Moving probe >> flash	/	moving probe > flash	moving probe > flash

The table indicates whether the lag in the moving probe condition was (expected to be) larger (">"), twice larger (">>") similar ("=") or absent ("/") relative to the spatial lag of the flash condition.

Postdiction theory considers the abrupt onset of a moving object as a trigger re-setting position integration similar to the way a flash does. At the onset of the moving probe (P_x), the temporal integration process is reset so that both the position of the continuously moving target and the probe must be estimated on the basis of the future trajectory (see Fig. 1D). This estimation is made by averaging the future positions of the object in a time window of ~80 ms. Consequently, the perceived position of both bars would be displaced in motion direction (P_{x+1} for the target, P_{x-1} for the probe), resulting in a lag effect twice as large as with a flash. At motion onset, the positions of both bars are averaged at the same time. Again, the lag effect would be twice larger than with a flash. At target offset, spatial integration for the target would end, because there are no future positions. However, the onset of the moving probe triggers position integration, and the perceived position of the moving probe would be shifted in the direction of motion. The lag effect should therefore be similar in size to the flash-lag effect.

Finally, according to the simplest version of the differential latency account, there would be no lag effect at all with a moving probe, because both the target and the probe move at the same velocity and should therefore have the same latency. Hence, the two bars would be perceived at the same position (P_x) but later in time (t_1). At time t_0 the target is perceived at its previous position P_{x-1} (see Fig. 1E). Although not explicit about this point, some advocates of the differential latency account cite the flash-initiated cycle as evidence in favor of their theory (Krekelberg et al., 2000), suggesting that the latency of moving objects is shorter than the latency of stationary objects from motion onset on. Others argue that the latency of moving objects at motion onset is indistinguishable from those of a flash, but do not provide any evidence in favor of this view (Murakami, 2001). In their computational model, Baldo and Caticha (2005) come to the conclusion that the stationary flash reaches threshold earlier, but is nonetheless spatially misaligned with the moving stimulus. In contrast, the only study aimed at measuring the latency of moving stimuli (by varying the subjective luminance) concluded that latencies are actually shorter at motion onset than during ongoing motion (Ogmen, Patel, Bedell, & Camuz, 2004). On the basis of this finding, we should find a reduced lag effect with a moving probe. The reason is that the moving probe is perceived at position P_x at time t_0, when the target is still perceived at P_{x-1}. Overall, there is little consensus on the flash-initiated cycle from the differential latency point of view.

Further, each of these theories suggests that the same process is involved at motion onset, motion offset, and along the trajectory. However, Müsseler, Stork, and Kerzel (2002) have demonstrated that the magnitude of mislocalization changes along the trajectory of a moving bar. Mislocalization was larger at motion onset than during ongoing motion and reversed at motion offset. This suggests that different mechanisms are involved along different parts of the trajectory (although, the authors did not exclude the presence of a single mechanism). On the basis of these findings, mislocalization of the moving probe could also differ when perceptual judgments must be made at different points along the trajectory of moving objects.

In the following experiments, we evaluated spatial displacement in two conditions; the "flash" and the "moving probe" condition. Observers were asked to judge the onset position of the moving or flashed probe in the lower part of screen relative to the position of the target in the upper part of the screen (see first two columns in Fig. 2). The comparison was done at the onset of target motion (Experiment 1), during ongoing target

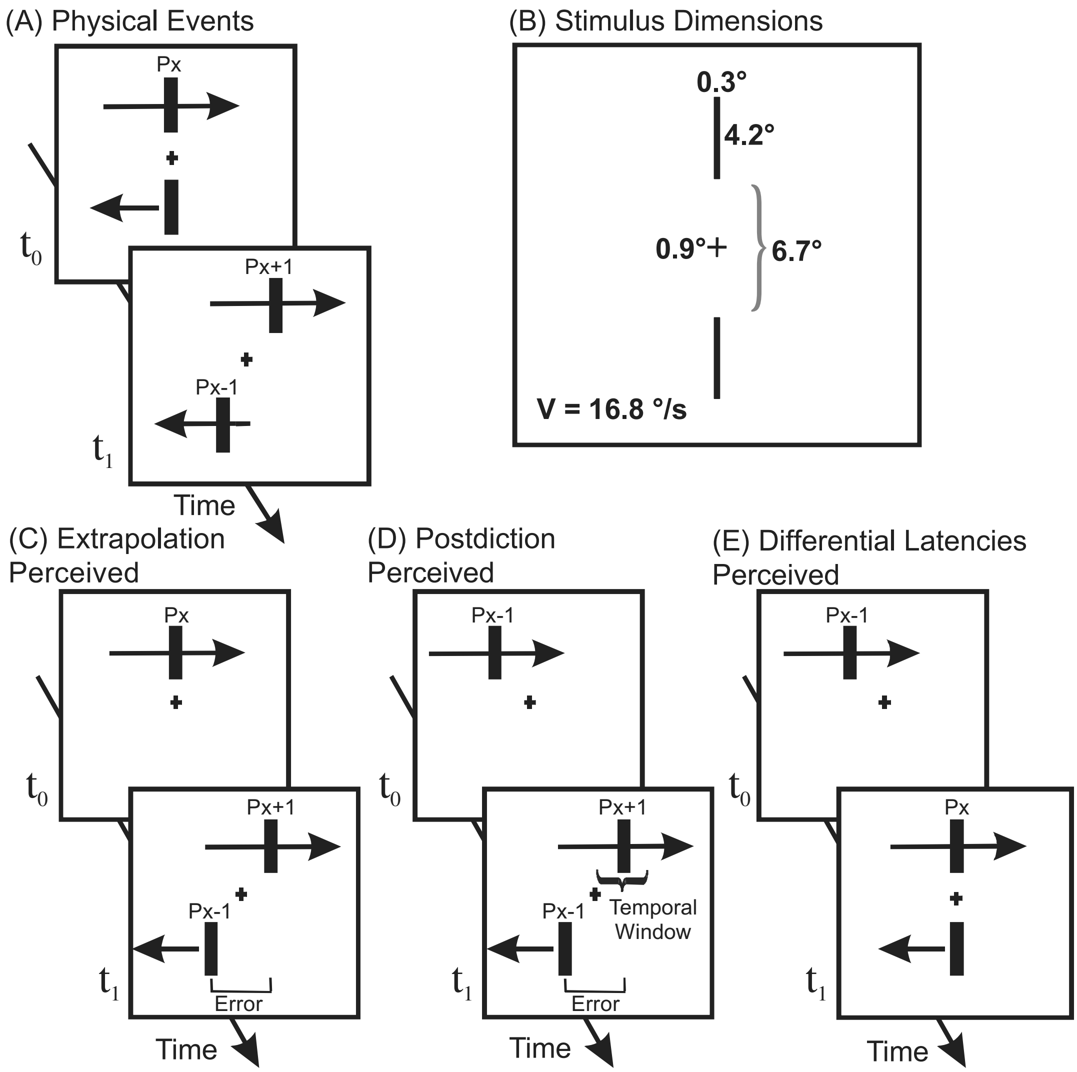

Fig. 1. Illustration of stimuli and predictions. The sequence of physical events is shown in (A), the stimulus dimensions in (B) (drawn to scale), and the predictions of the different theories in (C–E). (A) The two bars are aligned at position P_x at time t_0. At time t_1, they have moved to positions $P_{x\pm1}$. (C) Motion extrapolation would predict a lag that is twice larger with a moving probe than with a flash, because the positions of two bars are extrapolated into the future and are seen at their true position. (D) Postdiction would predict a lag that is twice larger with a moving object than with a flash, because the onset of the second moving bar resets spatial integration and consequently, the position of both bars must be estimated in a temporal window of 80 ms. (E) The simplest version of the differential latency account would predict no lag, because perceptual latencies for both objects are the same.

motion (Experiment 2), and at the offset of target motion (Experiment 3). In Experiment 4, we investigated whether the onset position of the moving probe would be displaced relative to a fixed spatial reference. If the perceived position is displaced in this condition, the localization errors in previous experiments would at least partially reflect this shift. The displacement of the perceived onset position of a moving object has been discovered by Fröhlich (1923) and it is mostly observed at very high stimulus velocities. A number of theories have been suggested but, as in the literature on the flash-lag effect, there is no agreement on the mechanism underlying the illusion (for a review see Kerzel, in press).

2. Methods

2.1. Participants

Students at the University of Geneva participated in theses experiments. They reported normal or corrected to normal visual acuity. Participants took part in only a single experiment. Thirteen students participated in Experiment 1, 24 in Experiment 2, 22 in Experiment 3, and 17 in Experiment 4.

2.2. Apparatus and stimuli

Stimuli were generated by a ViSaGe graphics adaptor (Cambridge Research Systems, Rochester, UK) and presented on a 21 in. monitor at a resolution of 1024 × 768 pixels at 100 Hz. The background was gray, CIE (1930) chromatic coordinates of ($x = 0.279$, $y = 0.303$), with a luminance of 65.52 cd/m^2. Stimuli were black bars (0.3° × 4.24°, horizontal × vertical). Bars were shown above and below central fixation at an eccentricity of 3.34° to the nearest edge (see Fig. 1B). Thus, the vertical separation of the two bars was 6.7°. A 0.9° × 0.9° fixation cross was displayed at the center of the screen. Object motion was horizontal at a velocity of 16.79°/s. Eye fixation was monitored by a High Speed Video Eyetracker (Cambridge Research Systems, Rochester, UK).

The two main conditions were the "moving probe" and the "flash" conditions that are illustrated in the first and second column of Fig. 2, respectively. In the two conditions, a bar (target) moved horizontally towards the screen center in the upper part of the screen, with exception of Experiment 4 where a stationary target was shown. The probe stimuli (flashes or moving probes) were shown in the lower part of the screen. In the "flash" condition, a flashed bar appeared for one frame, whereas in the "moving probe" condition a moving bar appeared and moved opposite to target motion. The flash/moving probe appeared either during ongoing target motion (Experiment 1), at target motion onset (Experiment 2), or at target motion offset (Experiment 3). Finally, in Experiment 4, we compared a flash to a continuously moving target, and the moving probe to a stationary

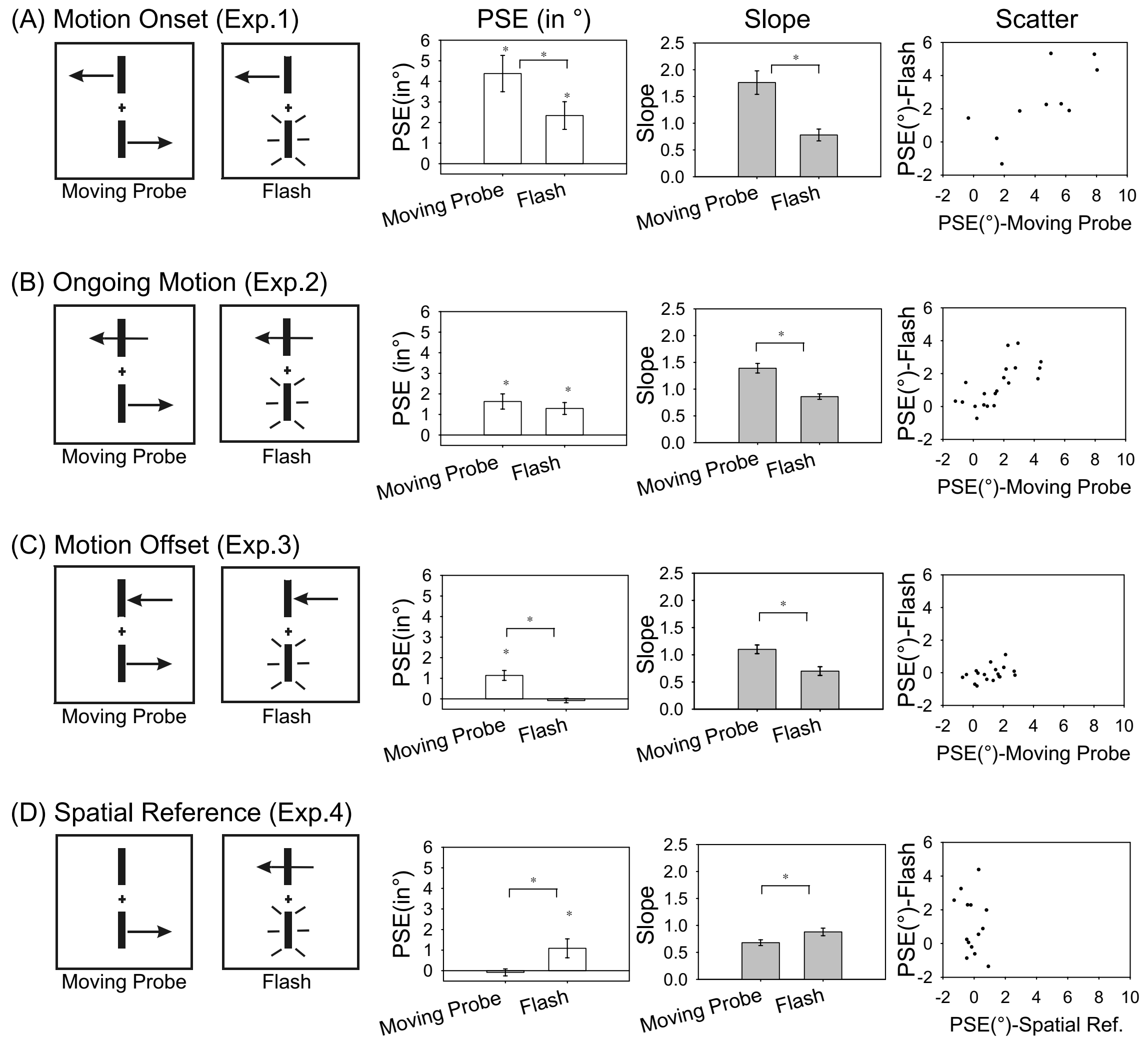

Fig. 2. Illustration of experimental conditions (columns 1–2) and results (columns 3–5). Target and probe were presented in the upper and lower hemifields, respectively. Moving (column 1) and flashed (column 2) probes were used. We varied the trajectory position where the probe was presented. (A) Moving or flashed probes at target onset. (B) Moving or flashed probes during ongoing motion. (C) Moving or flashed probes at target offset. (D) In the condition with a spatial reference (column 1), a stationary bar was presented well before the onset of the moving probe and remained on the screen. The right part of the figure shows mean points of subjective equivalence (PSEs, in degrees of visual angle, column 3), slope values (column 4) and scatter plots of individual PSEs (column 5). Error bars indicate the between-subject standard error. In most conditions, positives PSE values indicate that participants perceived the flashed/moving probe behind the moving target (i.e., the flashed/moving probe had to be presented ahead of the moving target in order to be perceived as aligned). With a stationary target (Experiment 4), positive PSE values indicate that participants perceived the moving probe ahead of the stationary target (Fröhlich effect). Large slope values indicate shallow psychometric functions and weak discrimination performance. Significant differences between conditions are indicated by an asterisk (*t*-test, $p < .05$).

target which remained visible throughout the trial. The stationary probe acted as a landmark. Most studies on the Fröhlich effect used static reference points for comparison (e.g., Fröhlich, 1923).

The relative position of the flash or moving probe was randomly varied in order to appear either before, behind or at the same position as the moving target. Negative probe positions indicated that the bar appeared behind the moving target. Positive probe positions indicated that the flash or moving probe appeared ahead of the moving bar.

Nine relative positions between moving target and flash/moving probe were selected according to the results of a pilot study. In the "flash" condition of each experiment, the positions were −2.85°, −1.18°, −0.34°, 0.50°, 1.34°, 2.18°, 3.02°, 3.86°, and 5.54°. In the "moving probe" condition, relative positions were adjusted individually for each experiment. In Experiment 1, the probe positions were evenly spaced around 4.03° from −1.34° to 9.4°. In Experiment 2, the probe positions were evenly spaced around 1.34° from −4° to 6.7°. In the "moving probe" condition of Experiment 3, the probe positions were the same as in Experiment 1. In Experiment 4, the probe positions were spaced evenly around 0.67° from −2.01° to 3.36°. Exceptionally, positive values in Experiment 4 refer to positions of the stationary target that were ahead of the moving probe. In this coding scheme, the Fröhlich effect would be reflected in positive values, which we found much more intuitive than negative values. In all Experiments, the horizontal target position at probe onset was jittered by ±2.52° around the screen center. All conditions were randomly intermixed and the direction of target motion was random.

2.3. Procedure

The experiments took place in a dimly lit room. Participants viewed the stimuli at a distance of 52 cm from the monitor. Head movements were restricted by a chin rest. Both in the "moving probe" and "flash" condition, participants pressed one of two keys to indicate whether they perceived the bar (flashed or moving) in the lower part of the screen as appearing to the left or right of the moving target in the upper part of the screen. In each experiment, the nine relative positions were paired with two directions of motion. In sum, each participant worked through 1152 trials in two sessions. In each session they performed 576 trials (2 probe conditions × 9 spatial offsets × 2 directions × 16 repetitions). The first session was considered as training and the data were discarded.

3. Results

Left/right responses were converted to ahead/behind judgments and the logistic function was fit to the relative frequencies: $y = 1/(1 + \exp(-(x - c)/a))$, where a indicates the slope of the curve, c estimates the point of subjective equality (PSE) between probe and target position, x indicates the relative positions, and y the relative frequency of "ahead" responses. Negative PSE values indicate that the position of the flash/moving probe has to be displayed behind the moving target for the two bars to appear aligned. Conversely, positive values indicate that the position of the flash/moving probe has to be displayed in front of the moving target in order to be perceived at the same position as the target. Further, we also considered the slope value, *a*. Slope values provide a measure of observers' ability to discriminate stimuli. When the just noticeable difference is large, the psychometric function will be shallow. Note that, due to the exponential, large values of *a* indicate shallow curves; that is, large slope values indicate a poor ability to discriminate.

Psychometric functions were calculated for each condition and participant. The fit of individual functions was good (R-square close to 1.00). To evaluate differences between conditions and differences from zero, *t*-tests were conducted on PSE and slope values. We also calculated Pearson's correlation between the PSE values of the different conditions across observers.

The data from 3 participants in Experiment 1, 4 in Experiment 2, 4 in Experiment 3, and 3 in Experiment 4 were excluded because the psychometrical functions were essentially flat. The poor discrimination performance was probably due to difficulties in judging a peripheral event while maintaining fixation (or misunderstanding the task). In other words, these observers found it extremely difficult to comply with the eye movement instruction and could do little more than avoid fixation errors. Thus, data from 10 students was retained in Experiment 1, 20 in Experiment 2, 18 in Experiment 3, and 14 in Experiment 4.

PSE and slope values of each experiment are depicted in Fig. 2. In Experiment 1, PSEs were determined at motion onset. A *t*-test revealed a significant lag effect with a flash (2.34°), $t(9) = 3.48$, $p = .007$, and with a moving probe (4.38°), $t(9) = 4.96$, $p = .001$. The lag effect with a moving probe was significantly larger than with a flash (difference of 2.06°), $t(9) = 3.36$, $p = .008$. Moreover, discrimination was better (i.e., slope values were smaller) with a flash than with a moving probe (0.78 vs. 1.76), $t(9) = 2.76$, $p = .004$, and PSEs in the two conditions correlated significantly, $r = .73$, $p = .02$. That is, individuals who had a large PSE with a moving probe also had a large PSE with a flashed probe.

In Experiment 2, PSEs were determined during ongoing motion. A *t*-test revealed a lag effect with a flash (1.29°), $t(19) = 4.51$, $p < .001$, and with the moving probe (1.63°), $t(19) = 4.44$, $p < .001$. The lag effect in the two conditions was of the same magnitude (difference of 0.34°), $t(19) = 1.25$, $p = .23$. Thus, the flash and the moving probe had to be presented ~1° ahead of the moving target in order to be perceived at the same position. Moreover discrimination was better with a flash than with a moving probe (0.86 vs. 1.39), $t(19) = 5.31$, $p < .001$, and correlations between PSEs of the two conditions were significant $r = .69$, $p = .001$.

In Experiment 3, PSEs were determined at the offset of motion. A *t*-test revealed no lag effect with a flash (−0.08°), $t(17) = -0.76$, $p = .46$, but a significant lag effect with a moving probe (1.14°), $t(17) = 4.77$, $p < .001$. The difference between conditions was significant (1.22°), $t(17) = 5.55$, $p < .001$. Moreover, discrimination was better with a flash than with a moving probe (0.7 vs. 1.1), $t(17) = 5.07$, $p < .001$. Correlations between PSEs of the two conditions were not significant $r = .39$, $p = .11$.

Finally in Experiment 4, we found no lag effect with a stationary target relative to the onset of a moving probe (−0.08°), $t(13) = -0.46$, $p < .65$. That is, we did not observe a Fröhlich effect with our set of stimulus parameters. The lag effect with a flash relative to a target in continuous motion was significant (1.09°), $t(13) = 2.38$, $p = .03$, and the difference between conditions was also significant (−1.17°), $t(13) = -2.23$, $p = .04$. Unlike in the previous experiments, discrimination was better with a moving probe than with a flash (0.7 vs. 0.9), $t(13) = -2.79$, $p = .02$, and correlations between PSEs of the two conditions were not significant $r = -0.24$, $p = .41$.

4. Discussion

Consistent with the literature, the spatial flash-lag was of ~1° during target motion and eliminated at target offset. The lag with a moving probe decreased from target onset to target offset (4.38°, 1.63°, and 1.14°). Similarly, the flash-lag decreased from target onset to target offset (2.39°, 1.29°, and −0.08°). Theses results are in accordance with suggestions that lag effects depend on the trajectory position that is probed (Erlhagen, 2003; Müsseler et al., 2002). The pattern of mislocalization with a moving probe is at odds with most of the theories presented in the introduction (see Table 1).

4.1. Differential latencies

The simple differential latency account which claims that the latency of moving objects is equal at motion onset and during ongoing motion is clearly refuted by the present data. In this case, the moving probe and the moving target should have been perceived at the same time, eliminating any spatial error. However, lag effects were consistently found. The alternative idea, that the latency at motion onset is similar to flashed stimuli does not account for the data, either. If the latency of a moving probe was similar to a flash, we would expect the spatial error to be the same. However, differences were observed at motion onset and offset.

More elaborate versions do not fare much better. According to the multiple-channel differential latency account (Ogmen et al., 2004; Patel et al., 2000), the position computation process reaches steady state some time after motion onset. During steady state, the latency of the position computation process is stable. Right after motion onset, however, position computation is in a transient phase and latency varies. The results of Ogmen et al. (2004) suggest that the latencies are shorter during the transient phase and progressively increase until they reach the asymptotic value of steady state computation. Moreover, the authors suggest that the first positions of the moving object during the transient state are not perceived as a result of the Fröhlich effect.

The multiple-channel differential latency account would therefore predict that the perceived position of the moving probe leads the perceived position of the continuously moving target (see p. 2116 in Ogmen et al., 2004): because the onset of the moving probe is perceived earlier than the continuously moving target, the probe needs to be presented behind the continuously moving object to be subjectively aligned with it. We observed the exact opposite, a lag of the moving probe relative to the continuously moving target. However, Ogmen et al. (2004) based their conclusions on a variation of the subjective luminance of the flashed and moving object. Because we did not measure detection thresholds, we are not able to fully evaluate their model. It may be that a bright moving probe (with short latencies) produced a lead effect.

4.2. Motion extrapolation and postdiction

Motion extrapolation and postdiction predict the lag at motion onset to be twice larger with a moving probe than with a flash. Consistent with this prediction, Experiment 1 showed that the lag at motion onset was larger with a moving probe than with a flash.

However, the lag of ~1° during ongoing target motion was of the same magnitude with moving and flashed probes. Both motion extrapolation and postdiction theories have difficulty explaining this result as both predict lags that are twice larger with a moving probe than with a flash.

Finally, at motion offset, simple motion extrapolation predicts a lag twice larger with a moving probe, whereas postdiction predicts a lag effect of the same magnitude as the flash-lag effect. Because the lag with a moving probe at motion offset in Experiment 3 was of similar size as with a moving probe along the trajectory (∼1°), the postdiction account is supported. However, it should be noted that advocates of the extrapolation account recently attributed the absence of a flash-lag effect at motion offset to masking by the target's offset. That is, the disappearance of the moving object produces a transient that is much stronger than the signal arising from extrapolation (Maus & Nijhawan, 2006; Maus & Nijhawan, in press; Nijhawan, 2008). Therefore, no lag effect is found in the flash-terminated cycle, and we would also expect the lag with a moving probe to be reduced.

Overall, motion extrapolation and postdiction can explain the pattern of displacement at motion onset, but only postdiction can easily explain the pattern of displacement at motion offset. Similar predictions can be derived for the related motion-biasing account (Eagleman & Sejnowski, 2007). Extrapolation is also capable of accommodating the offset condition if the masking-from-transients argument is accepted. However, both theories fail during ongoing motion.

4.3. Suggested explanation: Misbinding between abrupt and continuous changes

A major conclusion of the present study is that at target onset and offset, larger displacements occurred with moving than with flashed probes. In contrast, no difference between moving and flashed probes was found along the trajectory. So what is different about target onset/offset vs. ongoing motion? The most evident difference is that target onset and offset are abrupt changes, while positions along the trajectory represent continuous changes. Another way of summarizing our results would therefore be that abrupt changes of the target (onset or offset) produce larger displacements with moving probes than continuous changes of the target.

Larger lag effects with abrupt changes are consistent with previous research showing that the perception of abrupt events tends to lag the perception of continuous changes. For instance, an abrupt color change appears to lag a continuous color change (Sheth, Nijhawan, & Shimojo, 2000). The lag of abrupt events was also confirmed with changes along different perceptual dimensions (attributes): Cai and Schlag (2001) reported that an abrupt color change appears to lag a continuous position change (see also Gauch & Kerzel, in press) and proposed that the cortical representation of continuous and abrupt changes are fundamentally different. We believe that the distinction between transient and sustained channels (reviewed in Breitmeyer & Ögmen, 2006) may underlie the processing of continuous and abrupt changes. This is not the same as claiming that one attribute is processed faster than the other. Actually, there is ample (but controversial) evidence that color is processed faster than motion (e.g., Zeki & Bartels, 1998) (but see Nishida & Johnston, 2002), whereas the lag of a colored flash relative to a moving object seems to suggest the opposite. Thus, it is not the processing time of each individual attribute that is crucial, but the binding of the two. Lag effects will therefore strongly depend on the type of change, and the task at hand (Bedell, Chung, Ogmen, & Patel, 2003). In sum, the temporal binding of abrupt and continuous changes may be asynchronous, because the neural substrate and processing characteristics differ.

In contrast, Sheth et al. (2000) argued that an interaction of masking from successive target presentations, priming from previous presentations, and attention shifts to the flash may explain why abrupt changes lag continuous ones. Whatever the exact mechanism may be, for our present purposes it is sufficient to retain the principle that abrupt changes are bound to continuous changes that succeed the occurrence of the abrupt change. It should be noted, however, that the principle goes beyond stationary and moving objects, as it seems to hold regardless of the attribute under consideration.

With a moving probe, an abrupt change of the target (appearance or disappearance) may be bound to a probe position that is displaced in the direction of motion. For clarity, we will refer to the "direction" of the misbinding as "abrupt target to continuous probe", because it is an abrupt event of the target that is erroneously bound to a continuous change of the probe. In a typical flash-lag experiment, the flashed probe produces misbinding in the opposite direction, from "abrupt probe to continuous target". When probe and target represent continuous and abrupt events at the same time, as with moving probes at motion onset (see Experiment 1), the "target to probe" and "probe to target" misbindings add up. Therefore, the lag effect at motion onset is larger with a moving than with a flashed probe. In contrast, continuous target motion does not produce misbinding from "target to probe", because there is no abrupt event in the target. Therefore, the lag effect during ongoing motion does not differ between moving and flashed probes (see Experiment 2).

In other words, we assume that the onset of a moving probe represents an abrupt event that is quite similar to a flash. Therefore, moving probes initially produce the same error pattern as flashes. Additionally, a moving probe also represents a continuous change that may be erroneously bound to abrupt changes of the target. Thus, the dual nature of moving probes (at the same time abrupt and continuous) is the basis of the current explanation.

Table 2 shows the predictions of "bidirectional" misbinding. At motion onset with moving probes (cf. Experiment 1), both the "abrupt target to continuous probe" and the standard "abrupt probe to continuous target" misbindings are possible. Because the two directions of misbinding add up, the lag is larger with moving than with flashed probes. During ongoing motion (cf. Experiment 2), only abrupt changes of the probe may be misbound to continuous changes of the target. Therefore, the lag with moving probes is similar to a flash. At target offset (cf. Experiment 3), abrupt probe events cannot be misbound to continuous changes of the target, because target motion stops. Thus, no lag is observed with a flash. However, the abrupt disappearance of the target is erroneously bound to the continuous change of the probe. Therefore, a lag occurs with a moving probe.

In sum, our favored explanation is that asynchronous binding of abrupt and continuous changes produces lag effects and that more than one abrupt event can be misbound. With flashed probes, the abrupt change of the probe is erroneously bound to continuous target motion and a lag occurs. With moving probes, abrupt changes of the target may also be erroneously bound to continuous changes of the probe. Thus, a lag occurs with moving probes in the offset

Table 2
Suggested explanation

Probe	Target		
	Onset (abrupt + cont.)	Trajectory (cont.)	Offset (abrupt)
Moving probe (abrupt + continuous)	++	+	+
Flash (abrupt)	+	+	–

Target and probe stimuli in the various conditions are characterized by the presence of abrupt and/or continuous changes. Continuous changes are only considered when they follow the abrupt change. In general, abrupt changes are erroneously bound to a continuous change occurring after physical synchronicity. Because both the target and the probe may represent abrupt and continuous changes, erroneous binding of abrupt target changes to continuous changes of the probe is possible. In the table, a plus sign is added for each possible misbinding of an abrupt to a continuous change. The number of plus signs indicates the relative size of the lag effect. The predicted pattern matches our results (see rightmost column of Table 1 and third column of Fig. 2).

condition where the flash-lag effect is typically absent. Also, bidirectional misbinding of an abrupt event (onset of target and probe) to a continuous change (motion of probe and target, respectively) occurs in the onset condition, which doubles the lag.

4.4. The role of uncertainty along the trajectory

It has been demonstrated that increasing uncertainty about the moving object's position by blurring the edge of the stimulus increases the flash-lag effect (Fu, Shen, & Dan, 2001). Moreover, according to Kanai, Sheth, and Shimojo (2004) perceptual uncertainty is one of the key factors: "[...] the size of the overshoot, namely the lag effect, is dependent on perceptual uncertainty about the final position of the moving stimulus, and not the (presumably veridical) perceived location of the reference, usually flashed, stimulus." (p. 2614). Moreover, the authors suggest that, at motion offset, the position of the moving target is certain because the moving target stops after the flash, and this stop constitutes an additional marker.

In the present study, analysis of the slope values showed that, in general, the just noticeable difference between successive probe positions was lower with a flash than with a moving probe. Thus, one may argue that observers were less certain about the position of the moving probe (relative to the target) than about the flash position. In other words, the slope of the psychometric functions may be a measure of the degree of uncertainty about the relative positions of target and probe. Under this assumption, the proposal of Kanai et al. (2004) boils down to the hypothesis that a high variable error (shallow slopes) also produces a high constant error (large PSEs). Consistent with this suggestion, slopes were flatter with moving probes than with flashes and at the same time, PSE values were in general larger with moving probes than with flashes. Further, comparison between experiments shows that as the slope values decreased from motion onset to motion offset, PSEs also decreased. Finally, the between-subjects variability also confirms this point. The scatter between individual PSEs decreased from motion onset to motion offset, and the PSEs followed this trend (see Fig. 2). The only exception is Experiment 2: slopes of the psychometric functions during motion were steeper with a flash than with a moving probe (i.e., smaller slope values), but the magnitude of the perceived lag was the same. In sum, the assumed correlation between uncertainty and size of the lag effect may explain the data from the onset and offset condition, but is not entirely supported by the data from the ongoing motion condition. The failure to explain data in the ongoing motion condition is similar to the extrapolation and postdiction accounts (see above).

While these observations confirm that uncertainty differed between conditions and that this may have influenced PSEs, the substantial correlations between PSEs in the flash and the moving probe conditions indicate that the underlying processes were not fundamentally different. Inspection of the rightmost column of Fig. 2 shows that subjects who showed a large PSE in the flash condition also showed a large PSE in the moving probe condition and vice versa. Thus, our experiments suggest that participants resolved the task in the same way in both conditions, or that similar mechanisms were implied with a flash as with a moving probe.

4.5. Potential caveat: The Fröhlich effect

In the Fröhlich effect, the perceived onset of a moving object is shifted in the direction of motion (Fröhlich, 1923). Consequently, one may argue that the larger lag with a moving probe relative to a flash is due to mislocalization of the initial position of the moving probe.

The first argument against an involvement of the Fröhlich effect is that the spatial error was not always larger with a moving probe than with a flash. Remember that during ongoing motion, moving probes produced a lag of similar size as a flash. If the Fröhlich effect caused the difference between moving probe and flash, this difference should be visible at all trajectory positions.

Second, we found no Fröhlich effect when the onset of a moving probe was compared to a fixed spatial reference. This indicates that the lag effect in our experiments does not reflect a general misperception of the onset of the moving probe. Rather, the illusory shift depends on target motion. The absence of a Fröhlich effect is consistent with two previous studies that used relative judgments. For (tangential) velocities below 30°/s, no Fröhlich effect was observed in Kreegipuu and Allik (2003) and Kerzel (2002). With pointing responses, the Fröhlich effect may also be observed at slower velocities (Müsseler & Aschersleben, 1998), but post-perceptual response biases contribute heavily (Müsseler & Kerzel, 2004). Further, one may worry that the presence of a stationary reference object before motion onset may have reduced the Fröhlich effect in Experiment 4. However, when a stationary probe stimulus was presented either 1 s before motion onset (i.e., presence of a landmark), or after motion offset, the Fröhlich effect was equally absent with slow and moderate velocities, suggesting that the presence of stationary landmarks does not influence the localization error (Experiment 2 in Kerzel, 2002).

In conclusion, the flash-lag phenomenon is not restricted to a misperception of the relation between a moving and a briefly presented static object, but it generalizes to two moving objects. At motion onset and offset, postdiction or motion biasing may explain why the perceived lag in motion direction was larger with a moving probe than with a flash. During motion, however, neither motion extrapolation nor postdiction could fully explain the spatial lag with a moving probe. Further, the differential latency hypothesis is mostly incompatible with our results. We propose a simple account in terms of misbinding of abrupt and continuous changes. Abrupt changes lag continuous ones, and with moving probes, abrupt changes of the target may also be misbound to continuous changes of the probe. At target onset and offset, this increases the error.

Acknowledgment

The authors were supported by the Swiss National Foundation 10011-107768/1.

References

Baldo, M. V., & Caticha, N. (2005). Computational neurobiology of the flash-lag effect. *Vision Research, 45*(20), 2620–2630.

Baldo, M. V., & Klein, S. A. (1995). Extrapolation or attention shift? *Nature, 378*(6557), 565–566.

Bedell, H. E., Chung, S. T., Ogmen, H., & Patel, S. S. (2003). Color and motion: Which is the tortoise and which is the hare? *Vision Research, 43*(23), 2403–2412.

Breitmeyer, B., & Ögmen, H. (2006). *Visual masking: Time slices through conscious and unconscious vision*. Oxford, UK: Oxford University Press.

Brenner, E., & Smeets, J. B. (2000). Motion extrapolation is not responsible for the flash-lag effect. *Vision Research, 40*(13), 1645–1648.

Cai, R. H., & Schlag, J. (2001). A new form of illusory conjunction between color and shape [abstract]. *Journal of Vision, 1*(3), 127a.

Eagleman, D. M., & Sejnowski, T. J. (2000). Motion integration and postdiction in visual awareness. *Science, 287*(5460), 2036–2038.

Eagleman, D. M., & Sejnowski, T. J. (2001). The flash lag effect illusion is a consequence of adaptative spatial filtering. *Society of Neurosciences Abstract, 165*, 29.

Eagleman, D. M., & Sejnowski, T. J. (2007). Motion signals bias localization judgments: A unified explanation for the flash-lag, flash-drag, flash-jump, and Frohlich illusions. *Journal of Vision, 7*(4), 3.

Erlhagen, W. (2003). Internal models for visual perception. *Biological Cybernetics, 88*(5), 409–417.

Fröhlich, F. W. (1923). Über die Messung der Empfindungszeit. *Zeitschrift für Sinnesphysiologie, 54*, 58–78.

Fu, Y. X., Shen, Y., & Dan, Y. (2001). Motion-induced perceptual extrapolation of blurred visual targets. *Journal of Neuroscience, 21*(20), RC172.

Gauch, A., & Kerzel, D. (in press). Perceptual asynchronies between color and motion at the onset of motion and along the motion trajectory. Perception & Psychophysics.

Kanai, R., Sheth, B. R., & Shimojo, S. (2004). Stopping the motion and sleuthing the flash-lag effect: Spatial uncertainty is the key to perceptual mislocalization. *Vision Research, 44*(22), 2605–2619.

Kerzel, D. (2002). Different localization of motion onset with pointing and relative judgements. *Experimental Brain Research, 145*(3), 340–350.

Kerzel, D. (in press). The Fröhlich effect: Historical notes and relation to the flash-lag, current theories and reconciliation with the onset repulsion effect. In R. Nijhawan & B. Khurana (Eds.), Space and time in perception and action. Cambridge, UK: Cambridge University Press.

Khurana, B., & Nijhawan, R. (1995). Extrapolation or attention shift. *Nature, 378*(6557), 566.

Kreegipuu, K., & Allik, J. (2003). Perceived onset time and position of a moving stimulus. *Vision Research, 43*(15), 1625–1635.

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.

Krekelberg, B., Lappe, M., Whitney, D., Cavanagh, P., Eagleman, D. M., & Sejnowski, T. J. (2000). The position of moving objects [technical comments]. *Science, 289*(5482), 1107a.

Maus, G. W., & Nijhawan, R. (in press). Going, going, gone: Localizing abrupt offsets of moving objects. Journal of Experimental Psychology: Human Perception and Performance.

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.

Murakami, I. (2001). A flash-lag effect in random motion. *Vision Research, 41*(24), 3101–3119.

Müsseler, J., & Aschersleben, G. (1998). Localizing the first position of a moving stimulus: The Frohlich effect and an attention-shifting explanation. *Perception & Psychophysics, 60*(4), 683–695.

Müsseler, J., & Kerzel, D. (2004). The trial context determines adjusted localization of stimuli: Reconciling the Fröhlich and onset repulsion effects. *Vision Research, 44*(19), 2201–2206.

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.

Nijhawan, R. (1992). Misalignment of contours through the interaction of apparent and real motion systems. *Investigative Ophthalmology & Visual Science, 33*, 1415.

Nijhawan, R. (1994). Motion extrapolation in catching. *Nature, 370*(6487), 256–257.

Nijhawan, R. (2002). Neural delays, visual motion and the flash-lag effect. *Trends in Cognitive Sciences, 6*(9), 387.

Nijhawan, R. (2008). Visual prediction: Psychophysics and neurophysiology of compensation for time delays. *Behavioral and Brain Sciences, 31*(2), 179–198; discussion 198–239.

Nishida, S., & Johnston, A. (2002). Marker correspondence, not processing latency, determines temporal binding of visual attributes. *Current Biology, 12*(5), 359–368.

Ogmen, H., Patel, S. S., Bedell, H. E., & Camuz, K. (2004). Differential latencies and the dynamics of the position computation process for moving targets, assessed with the flash-lag effect. *Vision Research, 44*(18), 2109–2128.

Patel, S. S., Ogmen, H., Bedell, H. E., & Sampath, V. (2000). Flash-lag effect: Differential latency, not postdiction. *Science, 290*(5494), 1051.

Purushothaman, G., Patel, S. S., Bedell, H. E., & Ogmen, H. (1998). Moving ahead through differential visual latency. *Nature, 396*(6710), 424.

Sheth, B. R., Nijhawan, R., & Shimojo, S. (2000). Changing objects lead briefly flashed ones. *Nature Neuroscience, 3*(5), 489–495.

Vreven, D., & Verghese, P. (2005). Predictability and the dynamics of position processing in the flash-lag effect. *Perception, 34*(1), 31–44.

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.

Zeki, S., & Bartels, A. (1998). The asynchrony of consciousness. *Proceedings of the Royal Society B: Biological Sciences, 265*(1405), 1583–1585.