

---

# The modulation of the flash-lag effect by voluntary attention

---

Janaina Namba, Marcus Vinícius C Baldo<sup>¶</sup>

Department of Physiology and Biophysics, Institute of Biomedical Sciences, University of São Paulo, São Paulo (SP) 05508-900, Brazil; e-mail: [baldo@fisio.icb.usp.br](mailto:baldo@fisio.icb.usp.br)

Received 28 November 2002, in revised form 26 November 2003

---

**Abstract.** In the flash-lag effect (FLE), a flashing object appears to lag behind a moving object when both happen to be physically aligned to each other. According to an earlier account of the FLE (Baldo and Klein 1995 *Nature* **378** 565–566), this perceptual phenomenon would result from differential delays in the perceptual processing of moving and flashing stimuli, presumably involving attentional mechanisms. Here, we have attempted to demonstrate in a more convincing way the participation of voluntary attention as a major component of the FLE. In experiment 1 the observer's attentional set was induced by the spatial probability structure of the visual stimulus. A flashing dot (relative to which the location of a moving dot should be judged) was presented, in separate blocks, at fixed, alternating, or randomly chosen locations. The two former conditions, providing a higher spatial predictability, yielded a smaller FLE than the latter condition, which provided a lower spatial predictability of the flashing dot. In experiment 2 we employed a standard cueing procedure, in which a participant was instructed to shift covertly his/her attentional focus according to a symbolic cue. The cue indicated, with a validity of 80%, the visual hemifield at which the flashing dot would be presented. As predicted by our conceptual model, the mean magnitude of the FLE in the valid trials was significantly smaller than that found in the invalid ones. Therefore, both experiments provided strong evidence supporting the participation of voluntary attention in the FLE. Attentional mechanisms should be seen not as the primary cause of the FLE, but rather as an important modulatory component of a broader process whose spatiotemporal dynamics engenders the FLE and possibly other related phenomena. Even though we elected an account based on the influence of attention on perceptual latencies, our empirical findings are compatible with other theoretical models embraced by the current flash-lag controversy and should be accommodated by every attempt to explain this perceptual phenomenon.

## 1 Introduction

If observers have to compare the position of a moving stimulus to the position of a brief, stationary flash, they usually perceive the moving stimulus as being advanced relative to the position of the flashed stimulus when, in fact, both stimuli happen to be physically aligned to each other in space and time (Mackay 1958; Nijhawan 1994). This is the so called flash-lag effect (FLE), which has received a variety of explanations over the last 10 years (Nijhawan 1994; Baldo and Klein 1995; Khurana and Nijhawan 1995; Lappe and Krekelberg 1998; Purushothaman et al 1998; Whitney and Murakami 1998; Brenner and Smeets 2000; Eagleman and Sejnowski 2000; Krekelberg and Lappe 2000; Sheth et al 2000; Bachmann and Pöder 2001; Watanabe et al 2001; Baldo et al 2002; for recent reviews, see Krekelberg and Lappe 2001; Nijhawan 2002; Schlag and Schlag-Rey 2002; Whitney 2002). According to an earlier version of the attentional explanation (Baldo and Klein 1995), the FLE would result from the time "... required to bring the flashing dots to a sufficiently high level of sensory awareness for a 'snapshot' of the moving dots to be taken. Such a time delay would be related to the abrupt onset of the flashing dots and might involve attentional mechanisms, either in capturing attention or in shifting the focus of attention from one place to another across the visual field". While retaining the original perceptual-latency explanation as the most

<sup>¶</sup> Author to whom all correspondence should be sent.

---

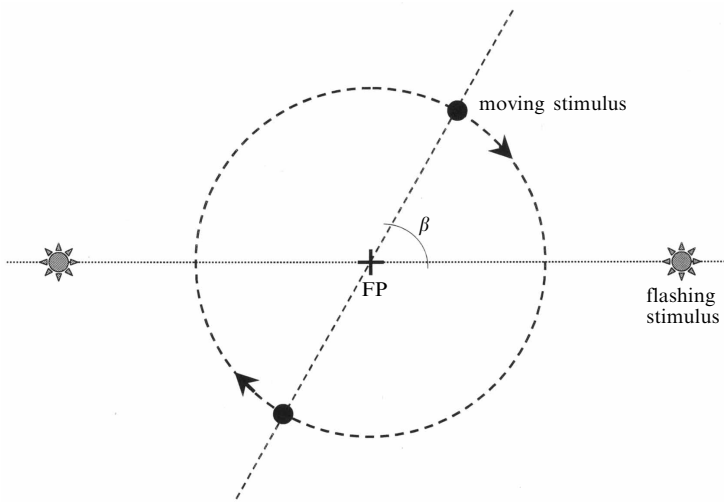
likely root for the FLE, a more recent account (Baldo et al 2002) does not regard capture or movements of the attentional focus as causal elements, but proposes that the observer's attentional set contributes to the modulation of perceptual latencies involved in that alignment task. In fact, there is empirical evidence suggesting that attentional mechanisms would also be involved in the Fröhlich effect (Müsseler and Aschersleben 1998; Kirschfeld and Kammer 1999) and the representational momentum (Hayes and Freyd 2002; Kerzel 2003), as well as in the FLE itself [Krekelberg et al 2000 (Eagleman and Sejnowski's reply); Baldo et al 2002; Baldo and Namba 2002], which seem to be perceptual phenomena possibly sharing a common underlying mechanism (Müsseler et al 2002).

The purpose of the present work was to advance the analysis of the role of voluntary attention in shaping the FLE, attempting to fulfill some significant gaps left uncovered by previous works (Baldo and Klein 1995; Baldo et al 2000; Khurana et al 2000; Baldo and Namba 2002; Baldo et al 2002). In experiment 1, we expanded and refined our previously employed methodological procedure to examine the effect of spatial predictability on the FLE (Baldo et al 2002; Baldo and Namba 2002). In experiment 2, by means of a standard cueing procedure (Posner 1980; Posner et al 1980), we measured the magnitude of the FLE under different conditions of attentional focusing. The utilisation of these distinct procedures allowed the comparison between the influence, on the FLE, of different schemes of attentional manipulation.

## 2 Experiment 1

In experiment 1 we compared three experimental conditions differing mainly with respect to the spatial predictability of the location of the flashing stimulus. A highly predictable condition (fixed condition), in which the flashing stimulus was presented at the same location throughout the experimental session, could be compared with a less predictable condition (random condition), in which, from trial to trial, the location of the flashing stimulus was randomly chosen from two possibilities. The benefits of advance information about stimuli have been termed *perceptual set effects* (Pashler 1998), and the manipulation of the spatial probability structure of the visual environment can also be used to guide the prior knowledge about stimulus location (Sperling and Doshier 1986). Therefore, an implicit assumption underlying experiment 1 is the existence of a monotonic relationship between the spatial probability of the flashing stimulus and the attentional set of the observer.

However, higher and lower probability locations are not comparable to each other with respect to the possibility of a sensory facilitation. Because repeated presentation of the flashing stimulus occurs more often at higher-probability locations, it would be possible that a temporally local facilitation, such as position priming, could occur (Sperling and Doshier 1986; Ciaramitaro et al 2001). Therefore, we attempted to uncouple spatial predictability (assumed also as a monotonic increasing function of spatial probability) and spatial recurrence, while holding constant the remaining psychophysical features of the flashing stimuli. This was achieved by introducing a third condition of stimulus presentation (alternate condition), in which the flashing stimulus was predictably presented at one of two regularly alternating locations throughout an experimental session. Whereas fixed and alternate conditions possessed identical spatial predictabilities, but different spatial and temporal features, the random condition exhibited, on average, the same spatial and temporal features assigned to the alternate condition, but a lower spatial predictability than either fixed or alternate conditions.



**Figure 1.** The visual stimuli utilised in experiment 1. Two rotating dots, 2 deg apart in the visual field, diametrically opposed to each other, rotate clockwise at  $36 \text{ rev min}^{-1}$  ( $216 \text{ deg s}^{-1}$ ) about the fixation point (FP). Another dot was flashed at either the right or the left hemifield, at an eccentricity of  $2.2^\circ$ . The rotating and flashing dots subtended 0.1 deg and 0.2 deg of visual angle, respectively. The luminance of all dots was  $20 \text{ cd m}^{-2}$ , displayed on a dark background. The observer's task was to report the perceived angle  $\beta$  as a lead ( $\beta > 0$ ) or a lag ( $\beta < 0$ ) of the rotating dots in relation to the flashing dot at the moment the latter was presented.

## 2.1 Methods

**2.1.1 Stimuli and apparatus.** The stimulus (figure 1) was a pair of dots, 2 deg apart in the visual field, rotating clockwise at  $36 \text{ rev min}^{-1}$  ( $216 \text{ deg s}^{-1}$ ) about the fixation point (FP). Another dot was flashed at either the right or the left visual hemifield, at an eccentricity of  $2.2^\circ$ . The rotating and flashing dots subtended a visual angle of 0.1 deg and 0.2 deg, respectively. The luminance of all dots was  $20 \text{ cd m}^{-2}$ , displayed on a dark background. Stimuli were generated on a 486-based PC and rendered on a Sony Multi-scan 19 sf II monitor with a 60 Hz vertical refresh rate. A chin-rest was used to maintain a constant binocular viewing distance of 57 cm. The experiments were conducted in a dimly lit room with eye movements being monitored by a video camera.

**2.1.2 Design and procedure.** After initiating a trial by pressing a key on the keyboard, participants fixated on the FP (centre of the display), and the moving dots started rotating about the FP. The whole experiment was composed of four blocks of randomly ordered sessions, in which the design differed by only the spatial presentation of the flashing dot. Only one condition (fixed, alternate, or random) was represented in each block.

- (i) Fixed condition (two blocks): The flashing dot was always presented at the right hemifield throughout one block of trials and at the left hemifield throughout another block.
- (ii) Alternate condition (one block): The location of the flashing dot predictably alternated between right and left hemifields from trial to trial.
- (iii) Random condition (one block): The location of the flashing dot (either right or left hemifield) was randomly chosen from trial to trial.

The task, in all three conditions, was to judge the location of the rotating dots in relation to the imaginary line connecting the flashing dot and the FP, at the moment the dot was flashed. By pressing one of two designated keys on the computer keyboard, this judgment was reported as a perceptual lag or lead of the rotating dots in relation to the flashing dot. A misalignment angle (between the imaginary lines

connecting the FP to the flashing and rotating dots) of either  $+21.6$  deg ( $+100$  ms) or  $-21.6$  deg ( $-100$  ms) was randomly chosen for presentation on the first trial. The next trial was started immediately after a response key had been pressed, with each successive presentation angle chosen by means of an adaptive method, namely, the PEST algorithm (Taylor and Creelman 1967). The run was ended when it reached a minimum of 15 reversals and the step size had decreased below  $7.2$  deg ( $33.3$  ms). The choice of an adaptive method was intended to confirm and extend previous findings in which we employed the method of constant stimuli to assess the modulation of the FLE by an identical manipulation of the spatial probability structure of the visual environment (Baldo and Namba 2002).

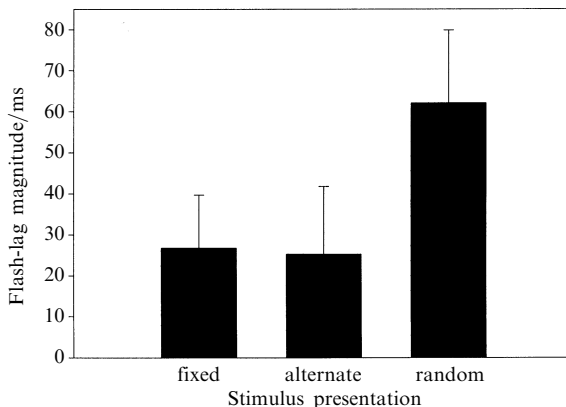
**2.1.3 Participants.** Fifteen students from University of São Paulo, naïve with respect to the particular hypothesis being tested, and one of the authors (JN), participated as volunteers in all experimental sessions. All participants, with ages between 20 and 33 years, reported normal or corrected-to-normal vision. The experimental procedure was reviewed and approved by the Human Subjects Research Committee, Institute of Biomedical Sciences, University of São Paulo.

**2.1.4 Data analysis.** The threshold (the angle of perceptual misalignment) was computed for every participant and each condition separately. A perceptual lead (lag) of the moving stimulus in relation to the flashing stimulus was converted to a temporal measure and conventionally expressed as positive (negative) values. These measures were entered into a one-way repeated-measures analysis of variance (ANOVA) with stimulus presentation (fixed, alternate, or random) as the only factor, followed by pairwise comparisons (Tukey's HSD test). The significance level was set at 5%.

## 2.2 Results and preliminary discussion

Figure 2 displays the mean magnitude of the FLE obtained in all three conditions of experiment 1. Since no statistically significant difference was found in the fixed condition, between right and left sides of presentation of the flashing dot ( $p = 0.475$ ), a grand mean for this condition was calculated by averaging over the two situations. Repeated measures (ANOVA) revealed a main effect for the stimulus presentation factor ( $F_{2,30} = 4.60$ ,  $p = 0.018$ ). Pairwise comparisons showed that the magnitude of the FLE observed in the random condition was significantly greater than the magnitudes found in both fixed and alternate conditions ( $p = 0.039$  and  $p = 0.030$ , respectively). No significant difference was found between the FLE magnitudes observed in the fixed and alternate conditions ( $p = 0.993$ ).

According to our main assumption, the spatial predictability of the flashing dot is related to the observer's attentional set. Therefore, under the condition of lower predictability (random condition) observers could not attend to the location of appearance



**Figure 2.** The flash-lag magnitude obtained in experiment 1 under the three conditions of stimulus presentation (fixed, alternate, and random). A perceptual lead (lag) of the moving stimulus in relation to the flashing stimulus was converted to a temporal measure and expressed, in ms, as a positive (negative) value.

of the flashing dot in a manner as efficient as that allowed by the conditions of higher predictability (fixed and alternate conditions). If the effect brought about by the higher spatial predictability of the flashing dot were, in fact, the result of a mere sensory facilitation, we should expect that the alternate condition (leading to a statistical distribution of presentation times identical to that obeyed by the random condition) would yield an FLE magnitude significantly greater than that observed in the fixed condition. However, we found no significant difference between the results of fixed and alternate conditions, in agreement with the fact that both conditions share the same degree of spatial predictability. These findings support the view according to which the manipulation of the observer's prior knowledge of the spatial probability structure allowed a reallocation of spatial attention, thus modulating the perceptual sensitivity related to this alignment task.

However, the three conditions in experiment 1 were run in separate blocks, possibly leading to differences regarding the cognitive effort demanded by each condition. For instance, volunteers reported that the alignment judgment was an easier task during the fixed condition in comparison with the alternate condition, in which the observer's attentional 'focus' had to alternate back and forth, throughout the entire session, between the two locations of appearance of the flashing dot. Moreover, changes in expectancies might induce not only a corresponding change in the observer's attentional set, but also a change in decisional criteria (Sperling and Doshier 1986). Therefore, to assure that we were dealing with an attentional manifestation, we turned to a standard cueing procedure, in which the effects of valid and invalid cues were intermingled throughout the same block of trials (experiment 2).

### 3 Experiment 2

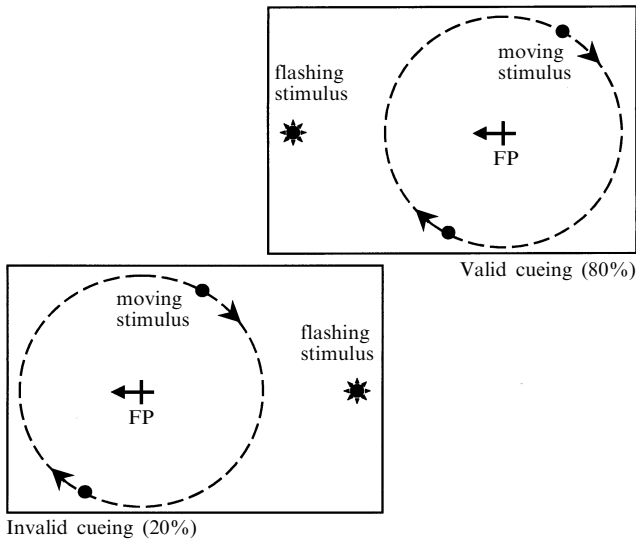
Experiment 2 assessed the magnitude of the FLE under an explicit manipulation of voluntary attention. By means of a cueing procedure (Posner 1980; Posner et al 1980), participants were instructed to attend to the visual hemifield indicated by a symbolic cue (a small arrow close to the FP). The cued location was the most likely site for the presentation of the flashing dot, whose location was the reference to which the relative position of the moving dots had to be judged (figure 3). Throughout every session in experiment 2, the perceptual task was performed under a homogeneous cognitive set, with the observer required to shift covertly his or her attention on every trial, according to the respective symbolic cue.

#### 3.1 Methods

3.1.1 *Stimuli and apparatus.* The experimental apparatus and visual stimulation were identical to those employed in experiment 1. The only difference was the use of a cueing procedure in directing attention (instead of the spatial probability structure of the visual environment) by means of a small arrow presented close to the FP (figure 3).

3.1.2 *Design and procedure.* Every trial was initiated with the appearance of the FP at the centre of the display along with an arrow pointing either to the right or to the left hemifield (figure 3). Participants were instructed to fixate their gaze on the FP, orient their attention to the hemifield indicated by the arrow, and, by pressing a key on the keyboard, allow the moving dots to start rotating about the FP (with the arrow then removed from the visual field). In 80% of the trials, the arrow indicated the correct location of appearance of the flashing dot (valid condition), the opposite being true in the remaining 20% of the trials (invalid condition). The flashing dot was presented between 3 and 5 s after the removal of the arrow. The presentation hemifield (either left or right) was chosen at random on each trial with equal probability.

The task was exactly the same as in experiment 1, with the next trial starting immediately after a response key had been pressed. The PEST algorithm (Taylor and



**Figure 3.** The visual stimuli utilised in experiment 2, which was identical to that in experiment 1 except for the use of a symbolic cue (small arrow) close to the fixation point (FP). In 80% of the trials, the arrow indicated the correct location of appearance of the flashing dot (valid condition), the opposite being true in the remaining 20% of the trials (invalid condition). In each trial the flashing dot was randomly presented at either the right or the left hemifield with equal probability.

Creelman 1967) was again employed with the same parameters previously used in experiment 1. Two interleaved staircases, one for each cueing condition separately, were run in parallel throughout each experimental session. The run was ended when, for both staircases, a minimum of 15 reversals were reached, and the step size decreased below 7.2 deg (33.3 ms). The whole experiment was composed of two identical sessions, run on different days, with the first session being used only for training purposes and not included in the statistical analysis.

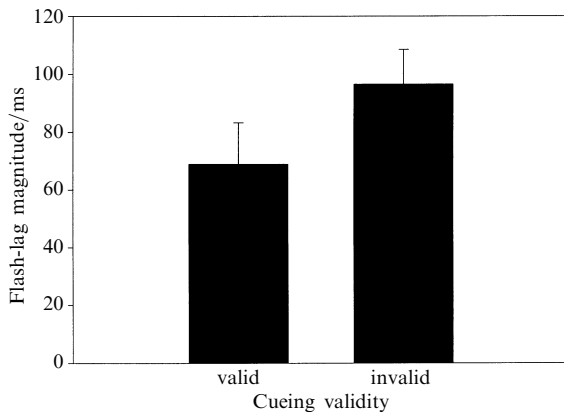
**3.1.3 Participants.** Nine students from University of São Paulo, naïve with respect to the particular hypothesis being tested, and one of the authors (JN), participated as volunteers. All participants, with ages between 20 and 29 years, reported normal or corrected-to-normal vision. The experimental procedure was reviewed and approved by the Human Subjects Research Committee, Institute of Biomedical Sciences, University of São Paulo.

**3.1.4 Data analysis.** The threshold was computed for every participant and each cueing condition separately. A perceptual lead or lag of the moving stimulus in relation to the flashing stimulus was again converted to a temporal measure and expressed as positive or negative values, respectively. The results obtained under both cueing conditions were compared by the Student *t*-test. The significance level was set at 5%.

### 3.2 Results and preliminary discussion

Figure 4 shows the mean FLE magnitude obtained under both valid and invalid cueing conditions. A statistically significant difference was found between these conditions ( $p = 0.001$ ), in the direction predicted by an account based on the attentional modulation of the FLE (Baldo and Klein 1995; Baldo et al 2000; Baldo et al 2002; Baldo and Namba 2002).

The present results are in disagreement with those previously reported by Khurana and colleagues (2000), in which a similar cueing procedure was employed to manipulate visual attention. Those authors did not observe any attentional effect on the magnitude of the FLE. Conceivable sources for these conflicting results include at least two possibilities.



**Figure 4.** The flash-lag magnitude obtained in experiment 2 under the two conditions of cueing validity (valid and invalid). A perceptual lead (lag) of the moving stimulus in relation to the flashing stimulus was converted to a temporal measure and expressed, in ms, as a positive (negative) value.

First, in their experiment 2 (Khurana et al 2000) attention was cued by means of an arrow presented 100 ms prior to the flash; yet, a stimulus onset asynchrony as short as 100 ms between a valid central cue and a target stimulus has been shown to be virtually ineffective (Müller and Rabbitt 1989; Egeth and Yantis 1997; Riggio and Kirsner 1997). In the present study (experiment 2), we employed a stimulus onset asynchrony between 3 and 5 s. Since sustained attention is generally fully present by about 400 ms after the presentation of the cue, remaining for as long as the observer maintains concentration (or until a new stimulus appears in the visual field), the procedure adopted in experiment 2 constitutes an adequate way to assess the modulatory effect of voluntary attention on the magnitude of the FLE (Müller and Rabbitt 1989; Egeth and Yantis 1997; Riggio and Kirsner 1997).

Second, Khurana et al (2000) could not find, in their experiment 3, a significant shift in the psychometric function measuring the FLE whereas a concurrent reduction in reaction times (RTs) was taken as evidence of an effective attentional cueing; however, several dissociations have been reported between RTs and discrimination tasks, such as temporal-order judgments (TOJs), with RTs being more sensitive than TOJs to several psychophysical features, including attentional allocation (Tappe et al 1994; Jaskowski 1996; Jaskowski and Verleger 2000). Such a dissociation may offer a likely explanation for their failure in observing an attentional influence on the FLE in a psychophysical procedure confounding RTs and spatial-localisation tasks.

#### 4 General discussion

In the standard FLE, a moving stimulus is perceived as leading a briefly flashed stimulus when both stimuli happen to be mutually aligned in space and time. Nijhawan, who rediscovered this perceptual phenomenon (Nijhawan 1994), conjectured that the visual system would use the predictability inherent in the trajectory of a moving stimulus to extrapolate its future location. This perceptual extrapolation would thus compensate for the spatial lag introduced by processing latencies throughout the visual pathways. Since then, several alternative models have been proposed in order to account for the FLE (Baldo and Klein 1995; Khurana and Nijhawan 1995; Lappe and Krekelberg 1998; Purushothaman et al 1998; Whitney and Murakami 1998; Brenner and Smeets 2000; Eagleman and Sejnowski 2000; Krekelberg and Lappe 2000; Sheth et al 2000; Whitney et al 2000; Bachmann and Pöder 2001; Krekelberg and Lappe 2001; Watanabe et al 2001; Baldo et al 2002).

In the present work, we have extended empirical findings which show the influence of voluntary attention on the FLE magnitude, by means of two different experimental procedures: altering the probability structure of a visual stimulus (experiment 1) and employing a cueing procedure (experiment 2).

---

In experiment 1, we manipulated the spatial probability structure of the visual environment (Sperling and Doshier 1986), with the flashing stimulus being presented under two different levels of spatial predictability: high predictability (fixed and alternate conditions) and lower predictability (random condition). The alternate condition was introduced in order to evaluate the possibility of a temporally local facilitation, such as position priming, brought about by a greater presentation frequency in the situation of higher spatial probability. Since no significant difference was found between the outcomes of the fixed and alternate conditions, despite their structural difference regarding the average presentation time of the flashing stimulus, we are led to believe that a temporally local facilitation is not a significant factor underlying the present findings. Moreover, the FLE magnitudes obtained under both fixed and alternate conditions were significantly smaller than that observed in the random condition, which obeys the same statistical distribution of presentation times for the flashing dot as that assigned to the alternate condition. We interpret these findings as a modulatory effect of the observer's attentional set on the delays related to the perceptual processing of the flashing dot. It has been widely shown, in both humans and nonhuman primates, that the accuracy and the speed involved in evaluating a visual stimulus can be influenced by prior knowledge about its probable location of appearance (Posner 1978; Posner et al 1980; Hawkins et al 1990; Luck et al 1994; Witte et al 1996; Carrasco and McElree 2001; Ciaramitaro et al 2001). In fact, our findings only confirm and extend the modulatory participation of voluntary attention to the realm of the FLE.

However, since experiment 1 in the present work dealt with the spatial probability structure of the visual stimulus in a blocked design, a potential criticism could be stated as to the possibility of changes in the observer's decisional criteria, rather than a genuine modulation of the observer's attentional set. For that reason, we set up experiment 2, in which the manipulation of voluntary attention was achieved by means of a standard cueing procedure (Posner 1980; Posner et al 1980). With a validity of 80%, a symbolic cue indicated the location of appearance of the flashing dot. Valid and invalid trials were intermingled throughout the same experimental session, thus demanding exactly the same perceptual task on each and every trial. Decisional criteria were most likely kept invariant in this procedure, in contrast to that employed in experiment 1. However, consistently with experiment 1, in experiment 2 we also identified a significant effect of cueing validity on the magnitude of the FLE, which we interpreted as clear evidence of the modulatory influence of voluntary attention on the FLE.

Therefore, attentional mechanisms should be seen not as the primary cause of the FLE, but rather as an important component of a broader process whose spatiotemporal dynamics engenders the FLE and possibly other related phenomena. According to this view, the FLE should not disappear even when attention is firmly focused on the target stimulus since the fundamental reasons for the production of this perceptual effect are rooted in the basic spatiotemporal features of sensory processing, which would still be in action. The modulatory influence of attention on these temporal features is possibly also relevant to other perceptual phenomena related to the FLE, such as the Fröhlich effect and the representational momentum (Müsseler and Aschersleben 1998; Kirschfeld and Kammer 1999; Eagleman and Sejnowski 2000; Krekelberg et al 2000; Hayes and Freyd 2002; Müsseler et al 2002; Whitney 2002; Kerzel 2003) which could be thought of as a set of phenomena sharing at least some basic underlying mechanisms.

In spite of the fact that the present results are in disagreement with those experimentally observed by Khurana and colleagues (2000), our findings do not counter their theoretical proposal, namely the motion-extrapolation hypothesis. Actually, the influence of attentional constraints on the FLE, a *modulating* rather than *the causing* factor, is an empirical observation that should be accommodated by any account attempting



---

to explain the perceptual mechanisms leading to the FLE. In this sense, the present results do not offer, *per se*, elements either to strengthen or to disprove any competing mechanism currently invoked to explain this perceptual effect, such as motion extrapolation, differential latencies, temporal averaging, or postdiction (Nijhawan 1994; Khurana and Nijhawan 1995; Purushothaman et al 1998; Whitney and Murakami 1998; Eagleman and Sejnowski 2000; Krekelberg and Lappe 2000).

If we look carefully to the physiological basis of sensory processing, we find that perceptual latencies may depend, at least, on two components: a *transmission* latency (the time taken by afferent signals to travel along vertical sensory pathways) and an *activation* latency (the time required for a given circuitry to reach a given threshold of neural activity). According to this view, a preceding, subthreshold, facilitation of visual neurons provided by top-down projections could bring a given circuitry closer to its activation threshold, thus contributing to a shortening of the overall perceptual latency (for instance, the latency involved in the perception of a highly predictable stimulus—a flash—taking part in a spatial-localisation task). A previous top-down facilitation of sensory neurons would thus correspond to the allocation of attentional resources to a given region of the visual field. This view is consistent with psychophysical and electrophysiological findings concerning the focusing of voluntary attention (Posner et al 1980; Hawkins et al 1990; Luck et al 1994; Witte et al 1996; Carrasco and McElree 2001; Ciaramitaro et al 2001).

Whereas such a mechanism may account for the observed attentional modulation of the FLE, the very origin of the FLE cannot be explained on the basis of attentional processes (Khurana and Nijhawan 1995; Khurana et al 2000) and calls for other physiological roots. A likely candidate would be the spatial and temporal interactions carried out by lateral connections: a moving stimulus would trigger a coherent spatiotemporal summation along a row of neurons corresponding to the motion pathway (Berry et al 1999). The action of facilitatory lateral connections between successive layers in a given network would thus lead to a shortening of activation latencies involved in the perception of motion. This mechanism may explain not only the standard FLE, in which a flash is presented adjacent to an object in continuous motion, but also the flash-initiated cycle, in which both flashed and moving stimuli are simultaneously presented (Khurana and Nijhawan 1995). Accordingly, although the moving stimulus also comes on abruptly at an unpredictable time, a spatiotemporal summation carried out by the recruitment of neurons along the path of motion would be induced soon after the movement initiation. This spatiotemporal facilitation would shorten the time delay in building up a neural activation corresponding to the perception of the moving stimulus (in comparison with the perception of the flash), thus leading to the FLE.

It is worth noting that the above description closely resembles the extrapolation account originally proposed by Nijhawan (1994). According to his explanation, the visual system compensates for neural delays 'spatially' on the basis of past input from the moving item (Nijhawan 1994; Khurana and Nijhawan 1995; Khurana et al 2000). In this sense, the motion extrapolation and differential latencies accounts would differ from each other solely in minor semantic aspects (Nijhawan 2002). It is quite conceivable and indeed desirable that, as experimental results are accumulated and conceptual models become refined, competing theories may eventually either merge or disappear.

## 5 Conclusion

The present results show a manifest modulatory influence of visual attention on the magnitude of the FLE. Even though we opted for an account based on the influence of attention on perceptual latencies, our empirical findings are not committed to any current theoretical explanation of the FLE and should be accommodated by every attempt to spell out this perceptual phenomenon.

**Acknowledgments.** We thank Ronald Ranvaud and Luiz Ribeiro-do-Valle for previous comments; Roberto Vieira for technical assistance; and two anonymous reviewers for valuable suggestions. A preliminary report of this work was presented at the *Visual Localization in Space-Time* Conference (VLST-2002), University of Sussex, Falmer, UK.

## References

- Bachmann T, Pöder E, 2001 "Change in feature space is not necessary for the flash-lag effect" *Vision Research* **41** 1103–1106
- Baldo M V C, Kihara A H, Klein S A, 2000 "Lagging behind because of sensory and attentional delays" *Investigative Ophthalmology & Visual Science* **41**(4) S420 (abstract)
- Baldo M V C, Kihara A H, Namba J, Klein S A, 2002 "Evidence for an attentional component of the perceptual misalignment between moving and flashing stimuli" *Perception* **31** 17–30
- Baldo M V C, Klein S A, 1995 "Extrapolation or attention shift?" *Nature* **378** 565–566
- Baldo M V C, Namba J, 2002 "The attentional modulation of the flash-lag effect" *Brazilian Journal of Medical and Biological Research* **35** 969–972
- Berry II M J, Brivanlou I H, Jordan T A, Meister M, 1999 "Anticipation of moving stimuli by the retina" *Nature* **398** 334–338
- Brenner E, Smeets J B J, 2000 "Motion extrapolation is not responsible for the flash-lag effect" *Vision Research* **40** 1645–1648
- Carrasco M, McElree B, 2001 "Covert attention accelerates the rate of visual information processing" *Proceedings of the National Academy of Sciences of the USA* **98** 5363–5367
- Ciaramitaro V M, Cameron E L, Glimcher P W, 2001 "Stimulus probability directs spatial attention: an enhancement of sensitivity in humans and monkeys" *Vision Research* **41** 57–75
- Eagleman D M, Sejnowski T J, 2000 "Motion integration and postdiction in visual awareness" *Science* **287** 2036–2038
- Egeth H E, Yantis S, 1997 "Visual attention: control, representation, and time course" *Annual Review of Psychology* **48** 269–297
- Hawkins H L, Hillyard S A, Luck S J, Mouloua M, Downing C J, Woodward D P, 1990 "Visual attention modulates signal detectability" *Journal of Experimental Psychology: Human Perception and Performance* **16** 802–811
- Hayes A E, Freyd J J, 2002 "Representational momentum when attention is divided" *Visual Cognition* **9** 8–27
- Jaskowski P, 1996 "Simple reaction time and perception of temporal order: dissociations and hypotheses" *Perceptual and Motor Skills* **82** 707–730
- Jaskowski P, Verleger R, 2000 "Attentional bias toward low-intensity stimuli: an explanation for the intensity dissociation between reaction time and temporal order judgment?" *Consciousness and Cognition* **9** 435–456
- Kerzel D, 2003 "Attention maintains mental extrapolation of target position: irrelevant distractors eliminate forward displacement after implied motion" *Cognition* **88** 109–131
- Khurana B, Nijhawan R, 1995 "Extrapolation or attention shift?" (reply to Baldo and Klein) *Nature* **378** 565–566
- Khurana B, Watanabe K, Nijhawan R, 2000 "The role of attention in motion extrapolation: Are moving objects 'corrected' or flashed objects attentionally delayed?" *Perception* **29** 675–692
- Kirschfeld K, Kammer T, 1999 "The Fröhlich effect: a consequence of the interaction of visual focal attention and metacontrast" *Vision Research* **39** 3702–3709
- Krekelberg B, Lappe M, 2000 "A model of the perceived relative positions of moving objects based upon a slow averaging process" *Vision Research* **40** 201–215
- Krekelberg B, Lappe M, 2001 "Neuronal latencies and the position of moving objects" *Trends in Neurosciences* **24** 335–339
- Krekelberg B, Lappe M, Whitney D, Cavanagh P, Eagleman D M, Sejnowski T J, 2000 "The position of moving objects" *Science* **289** 1107 (abstract)
- Lappe M, Krekelberg B, 1998 "The position of moving objects" *Perception* **27** 1437–1449
- Luck S J, Hillyard S A, Mouloua M, Woldorff M G, Clark V P, Hawkins H L, 1994 "Effects of spatial cueing on luminance detectability: Psychophysical and electrophysiological evidence for early selection" *Journal of Experimental Psychology: Human Perception and Performance* **20** 887–904
- Mackay D M, 1958 "Perceptual stability of a stroboscopically lit visual field containing self-luminous objects" *Nature* **181** 507–508
- Müller H J, Rabbitt P M A, 1989 "Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption" *Journal of Experimental Psychology: Human Perception and Performance* **15** 315–333

- 
- Müsseler J, Aschersleben G, 1998 "Localizing the first position of a moving stimulus: The Fröhlich effect and attention-shifting explanation" *Perception & Psychophysics* **60** 683–695
- Müsseler J, Stork S, Kerzel D, 2002 "Comparing mislocalizations with moving stimuli: The Fröhlich effect, the flash-lag effect and representational momentum" *Visual Cognition* **9**(1/2) 120–138
- Nijhawan R, 1994 "Motion extrapolation in catching" *Nature* **370** 256–257
- Nijhawan R, 2002 "Neural delays, visual motion and the flash-lag effect" *Trends in Cognitive Sciences* **6** 387–393
- Pashler H E, 1998 *The Psychology of Attention* (Cambridge, MA: MIT Press)
- Posner M I, 1978 *Chronometric Exploration of Mind* (Hillsdale, NJ: Lawrence Erlbaum Associates)
- Posner M I, 1980 "Orienting of attention" *Quarterly Journal of Experimental Psychology* **32** 3–25
- Posner M I, Snyder C R R, Davidson B, 1980 "Attention and the detection of signals" *Journal of Experimental Psychology: General* **109** 160–174
- Purushothaman G, Patel S S, Bedell H E, Ogmen H, 1998 "Moving ahead through differential visual latency" *Nature* **396** 424
- Riggio L, Kirsner K, 1997 "The relationship between central cues and peripheral cues in covert visual orientation" *Perception & Psychophysics* **59** 885–899
- Schlag J, Schlag-Rey M, 2002 "Through the eye, slowly: delays and localization errors in the visual system" *Nature Reviews Neuroscience* **3** 191–200
- Sheth B, Nijhawan R, Shimojo S, 2000 "Changing objects lead briefly flashed ones" *Nature Neuroscience* **3** 489–495
- Sperling G, Doshier B, 1986 "Strategy and optimization in human information processing", in *Handbook of Perception and Human Performance* Eds K Boff, L Kaufman, J Thomas (New York: John Wiley) pp 1–65
- Tappe T, Niepel M, Neumann O, 1994 "A dissociation between reaction time to sinusoidal gratings and temporal-order judgment" *Perception* **23** 335–347
- Taylor M M, Creelman C D, 1967 "PEST: Efficient estimates on probability functions" *Journal of the Acoustical Society of America* **41** 782–787
- Watanabe K, Nijhawan R, Khurana B, Shimojo S, 2001 "Perceptual organization of moving stimuli modulates the flash-lag effect" *Journal of Experimental Psychology: Human Perception and Performance* **27** 879–894
- Whitney D, 2002 "The influence of visual motion on perceived position" *Trends in Cognitive Sciences* **6** 211–216
- Whitney D, Murakami I, 1998 "Latency difference, not spatial extrapolation" *Nature Neuroscience* **1** 656–657
- 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** 137–149
- Witte E A, Villareal M, Marrocco R T, 1996 "Visual orienting and alerting in rhesus monkey: comparisons with humans" *Behavioural Brain Research* **82** 103–112



ISSN 0301-0066 (print)

ISSN 1468-4233 (electronic)

# PERCEPTION

VOLUME 33 2004

[www.perceptionweb.com](http://www.perceptionweb.com)

**Conditions of use.** This article may be downloaded from the Perception website for personal research by members of subscribing organisations. Authors are entitled to distribute their own article (in printed form or by e-mail) to up to 50 people. This PDF may not be placed on any website (or other online distribution system) without permission of the publisher.