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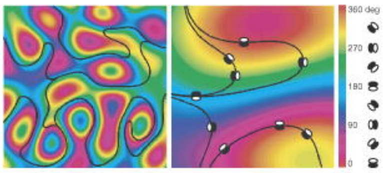

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Spatial facilitation is involved in flash-lag effect

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Abstract

The flash-lag effect (FLE) is the perceptual phenomenon in which a flash adjacent to a continuously moving object is perceived behind it. Horizontal propagation of activity could explain a shorter latency for moving than for flashed objects but, to our knowledge, no psychophysical data supporting this has been given. We show that two concurrent moving stimuli increase the FLE, presumably due to a latency decrease in movement perception. Our results support the idea that spatial facilitation along the trajectory of a moving object reduces movement perception delay and, therefore, sustains an involvement of latency differences in FLE generation.

Keywords: Motion; Flash-lag effect; Neural processing delays; Horizontal propagation; Differential latencies

1. Introduction

When a moving and a flashed stimulus are physically aligned in space and time, observers usually perceive the moving stimulus ahead of the flashed stimulus. This situation is known as the flash-lag effect (FLE) or flash-lag Illusion (Mackay, 1958; Nijhawan, 1994).

This effect may be related to a major constraint present in all sensory systems, namely, having to deal with the unavoidable delays imposed by the nature of biological processing (De Valois & De Valois, 1991). That is, sensory response to physical events must be transformed, in a time-consuming process, by different neural stages before perception and awareness emerge. How does the neural system keep up with changes that happened 10 ms in the past? Whenever things in the world move faster than processing times, the resulting delays could become life-threatening. Therefore, some sort of compensation may have evolved. We might also expect that such a mechanism would start low in the processing hierarchy and would be simple enough to avoid adding further neurocomputational processing.

A sudden uncorrelated change in the environment cannot be predicted, but a moving object present in the visual field for some time allows at least some inference about its future position. This kind of foretelling could be done by means of pre-activating adjacent areas in the visual cortex in the direction of the moving object. This facilitation along the moving object's trajectory has been postulated to explain shorter delays for moving than for flashed objects in the salamander retina (Berry, Brivanlou, Jordan, & Meister, 1999) and also in the cat primary-visual cortex (Jancke, Erlhagen, Schoner, & Dinse, 2004).

Spatial propagation of activity in the visual cortex, via the long range horizontal connections between modules processing similar characteristics of stimuli (e.g., orientation), is well established (Gilbert & Wiesel, 1989; Toth, Rao, Kim, Somers, & Sur, 1996). This connectivity and the activity spread that it carries, is thought to underlie the subthreshold synaptic integration field of the cortical neurons. This physiological entity is defined by variations

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in the subthreshold membrane potential of the cells provoked by stimuli beyond the limits of the classical (suprathreshold) receptive field. These stimuli, although not capable of driving responses, can exert robust suppressive or facilitative effects on the response to the presentation of stimuli in the classical receptive field (Allman, Miezin, & McGuinness, 1985; Fitzpatrick, 2000; Fregnac, Bringuier, & Chavane, 1996; Toth et al., 1996). The functional consequence of this subthreshold field of synaptic integration is that the discharge of the cell becomes a probabilistic conditional function of the spatial and temporal pattern of stimulation in this extended region (Bringuier, Chavane, Glaeser, & Fregnac, 1999). These are the kind of arrangements that might be involved in early stages of motion processing (Georges, Series, Fregnac, & Lorenceau, 2002; Series, Lorenceau, & Fregnac, 2003) and, for that reason, they have been postulated as a plausible explanation for perceptive phenomena such as the line-motion illusion or FLE (Jancke, Chavane, Naaman, & Grinvald, 2004).

Based on these ideas, we postulate that two moving objects that would collide (see Fig. 1) should "add" their pre-activations, resulting in an even shorter delay for perceiving the position of one of the objects in this facilitated spot. Therefore, if we compare the position of one of the moving objects with a flash, this shortening in the latency for detecting the moving target should increase the flash-lag effect. We tested this with five subjects and found that the presence of a second moving object does indeed significantly augment FLE magnitude. We show that this increase is selective to the direction toward the target, is spatially bounded and varies gradually with the contrast of the second moving object.

Some of these results have appeared previously in a congress abstract (Maiche, Budelli, Estaún, & Gómez-Sena, 2005).

2. General methods

In order to measure the FLE in a situation that allows interaction between two moving objects, we use an experimental paradigm in which the primary moving object is a ring that passes horizontally across the screen; the flash is a vertical line that appears over the ring and the second moving object is a filled circle that moves vertically. For the sake of simplicity, we refer to this second moving object as the "primer". The general dynamics of the experiments are represented in Fig. 1.

In the four experiments presented here, subjects have to point out where they perceive a flashed line with respect to the ring that moves from left to right on the screen. They have to indicate whether the line is on the right half-side of the ring or on the left side. The position at which the line was flashed was varied according to the constant stimuli method, but the values were calculated for each subject according his/her perceived central position (PCP). The PCP was determined before each experimental session by a short preliminary adjustment method procedure (see Section 2.3 for details).

2.1. Observers and apparatus

Five observers were used in these experiments, three naïve and two authors (A.M. and L.G.). All observers had normal or corrected-to-normal vision, and their age range was between 24 and 42 years. Subjects were trained in psychophysical experiments and were also specifically trained in maintaining fixation at the central cross used as a fixation point (FP), particularly during ring motion. Eye movements were monitored (ViewPoint EyeTracker; Arrington Research) in random trials during training in order to ensure that there was no pursuit.

Stimuli were displayed on a CRT 19-inch monitor (Phillips Brilliance 109P4) with a 1024×768 pixel resolution and 85 Hz refresh rate under control of a Pentium IV 3.2 GHzs running MATLAB (Mathworks Inc.) and Psychophysics Toolbox (Pelli, 1997). Observers were positioned in front of the monitor at a viewing distance of 30 cm and an adjustable chinrest (KJ-1000, INDO inc.) restricted head movement. Since, viewing was monocular and the right eye was always used, the chinrest was set to align the subject's right eye with the center of the screen.

2.2. Stimuli

Stimuli are presented on the monitor in a darkened room. Each trial begins with an FP on the central area of the screen. The FP appears at random position in each trial within the range of 1° in order to prevent the use of distance between the FP and the flash as a cue to solving the task. The ring emerges from the left border, passes horizontally across the screen at a constant speed of 35°/s and disappears through the right border. Once the ring has passed the FP, a red vertical line is flashed over the ring for one single frame (11.7 ms) in one of seven different horizontal positions.

In each experiment there were always two kinds of trials: experimental and reference. In some of them the primer appears static at the beginning of the trial and at a given moment starts to move vertically. The direction of the motion and the horizontal position depends on the experiment. In

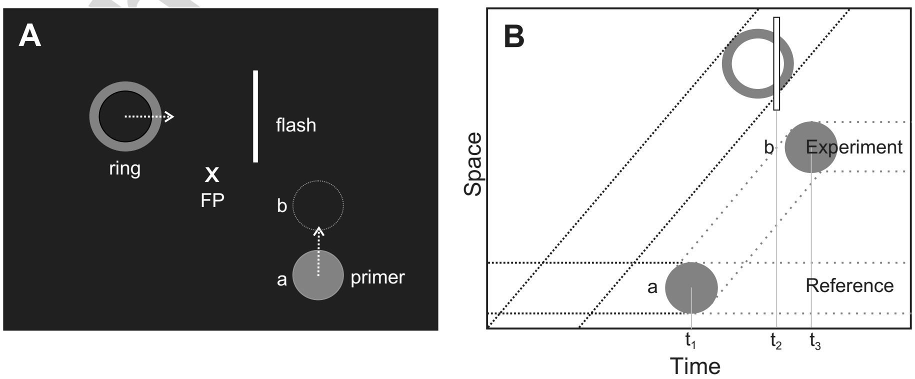

Fig. 1. Schematic representation of the two kinds of trials for the basic experimental setup. (A) Screen impression in an experimental condition trial. The primer is static at the beginning of the trial and starts moving 200 ms before the flash occurs. (B) Space and Time diagram showing the dynamics of both kinds of trials.

others, the primer remains at its initial position throughout the whole trial. The purpose of these trials is to generate a configuration that, at the beginning, is indistinguishable from those in which the primer moves, but with a primer presumably neutral in producing any change in the FLE.

Fig. 1B shows the details on the time and space relation of each object on the screen for one trial. For those trials where the primer moves, the temporal dynamics were always the same: the primer starts moving 100 ms before the flash occurs and stops 40 ms afterwards. In that time, the primer moves 5° in a vertical motion that leads to a final position always below the ring's line of motion (for cases of motion toward the ring). It is worth noting that the primer moves vertically in a trajectory at the right of the zone where the flash appears.

The external diameter of the ring is 5.8° and the width is 1°. The flashed line subtends 7.2° in length and 0.06° width. For those trials where the primer does not move it appears at its initial position and remains there until the ring disappears from the right border of the screen.

2.3. Procedure

Each session starts with a brief adjustment procedure where the subjects have to move the flash until they perceive it aligned with the center of the ring. The initial position of the flash was determined empirically by an average of the FLE obtained in previous preliminary experiments. The step of the adjustment procedure is constant at 0.036° and the experiment finishes when the subject judges the alignment as good enough. The distance in degrees from the middle of the ring to the final position of the flash in the adjustment procedure is the perceived central position (PCP). The objective of this preliminary procedure was to optimize the range of flash positions used in the constant stimuli experiments given the intersubject and intersession variability.

After this initial procedure a session of the constant stimuli experiment starts where the position of the flashed line is varied from trial to trial choosing between seven positions in the range $PCP - 0.8°$ to $PCP + 0.8°$. Each session consisted of 210 trials: 30 for each position ($30 \times 7 = 210$), in which 15 were experimental trials and the other 15 were reference. Each subject performed four sessions in each of the four experiments presented here.

In experiment 1, we compare the FLE perceived when the primer moves upward (experimental condition) with that perceived when the primer remains static at its initial position (reference condition). In this experiment, the primer's vertical line of motion is situated at approximately 5° to the right of FP (see Fig. 1A). The horizontal location of the primer in this condition is adjacent to the right of the zone where the flash appears.

In experiment 2, the experimental trials were similar to those in experiment 1, but the movement of the primer was reversed (opposite direction) so the initial position of the primer was its final position in experiment 1 (from position *b* to *a* in Fig. 1A). Thus, we compare the magnitude of FLE perceived when the primer moves downward with the FLE perceived when the primer remains static at its initial position. Note that in this case the initial position of the primer is close to the ring's line of motion (position *b* in Fig. 1A).

In experiment 3, the primer starts moving upwards at the same time as in the previous experiments but the primer's line of motion is located approximately 15° to the right of the FP. The movement of the primer therefore occurs while the ring is still far from it. Again, we compare the FLE perceived when the primer moves with the FLE perceived when the primer remains static at its initial position.

The primer always remains static at its final position after its motion finishes in order to avoid a new perceptual flash caused by its disappearance. On the other hand, the ring keeps moving throughout the whole trial.

In experiment 4, the primer starts moving upwards 100 ms before the flash occurs but the primer has a very low contrast in the experimental condition and the same contrast as in the previous experiments in the reference condition. Again, we compare the FLE perceived when the primer has low contrast with the FLE perceived when it has standard contrast.

2.4. Psychometrics and curve fitting

At the end of each experiment, responses are quantified to obtain the psychometric functions. Experimental data were fitted with the logistic function: $1/(1 + \exp(-a^*x - b))$ using the Levenberg–Marquardt algorithm to minimize the sum of squared errors; the Point of Subjective Equality (PSE) is $-b/a$. The R-square for all fits was over 0.78 and 90% of the values were over 0.9. The PSE represents the offset needed for the subject to perceive the flash as if it appeared in the middle of the ring. Fig. 2 shows the two psychometric functions (one for each condition) obtained for one subject in one session of the first experiment. Gray filled circles correspond to the reference condition while black squares show data from the experimental condition (see Section 3 for further explanation). In each experiment, one PSE was obtained for the reference condition (PSE_{ref}) and one for the experimental condition (PSE_{exp}). From these values, we defined the variable ΔPSE as ($PSE_{exp} - PSE_{ref}$) that will henceforth be used as the dependent variable (see Fig. 2 double arrow).

3. Results

Each experiment had its own internal control or reference situation. In the first three experiments this reference situation is the condition with the primer remaining steady in its initial position. This was conceived in order to obtain a neutral condition and, at the same time to avoid possible biases in the answer. In the fourth experiment the reference situation is the moving primer with the contrast used in the other experiments.

If we take the PSE of the reference situations of the first three experiments, we obtained a unimodal distribution with a mean of 39.42 ms and a standard deviation of

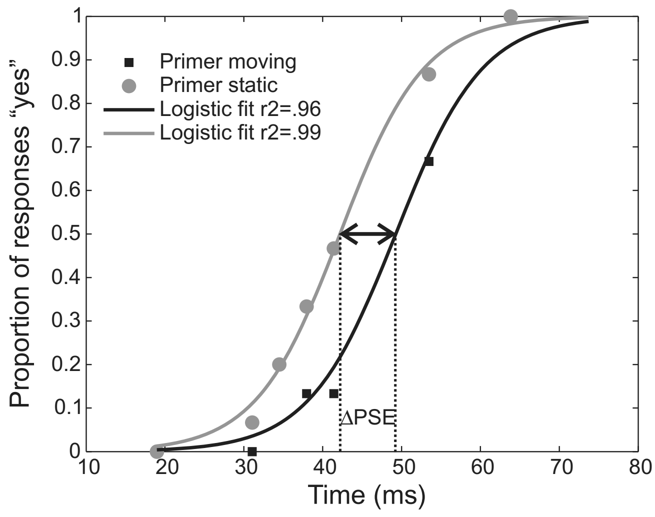

Fig. 2. Psychometric curves for a session of Subject AR for the two conditions: with the primer moving upwards and with the primer static (experimental situation and reference situation). Each point represents the proportion of answers "yes" to the question "Is the flash ahead of the half ring?" as a function of the time it will take the middle of the ring to reach the position of the flashed bar. Each group of data were fit with logistic functions to derive the PSE, which indicates the "distance" required by the subject in order to perceive the flash line exactly in the middle for each condition. Spatial offsets have been converted to time units indicating the temporal advantage of the flash in relation to the middle of the ring. Each data point is based on 15 trials (210 trials per session). Note: $\Delta PSE = (PSE\_exp - PSE\_reference)$.

5.73 ms. This value can be considered as the basal absolute value of the FLE for our setup and is comparable with results obtained in similar conditions by other authors.

3.1. Experiment 1: A second moving object increases FLE

According to our hypothesis we should locate the trajectory of the primer just ahead (to the right) of the region where the moving ring is perceived when the flash is perceived. In this way we expect to produce the maximum decrease in the latency for the perception of the moving object in this precise moment. As was previously mentioned, we finally selected a position a bit further to the right because if we put the primer coincident with the zone where the flash appears the flash would also be facilitated by the primer.

Fig. 2 shows the percentage of ''flash perceived ahead'' as a function of the time between the flash and the moment at which the center of the ring arrives at the position of the flash, for both conditions (reference and experimental). Both psychometric curves correspond to one session with subject one (naïve). The curves show that, when the primer is moving, the PSE is larger than when the primer remained static. We can therefore say that the primer's motion increases the FLE by about 7 ms for this case.

Fig. 3 shows the mean ΔPSE obtained for each subject (four sessions per subject). It indicates that this result is consistent for the five observers studied (mean: 6.13 ms, standard error: 0.57). The Wilcoxon signed-rank test for the null hypothesis of zero mean shows a significant increase of the FLE magnitude for the condition in which the primer moves ($p = .0001$). This increase in the effect remains even when relatively small changes are applied in the horizontal position, angle of the trajectory or primer phase.

This increase in the FLE is consistent with our hypothesis of pre-activation of neighboring areas ahead of motion due to excitation carried out by horizontal connectivity. This result can be explained by a ''summation'' of pre-activations and, therefore, by an additional facilitation of the moving object perception.

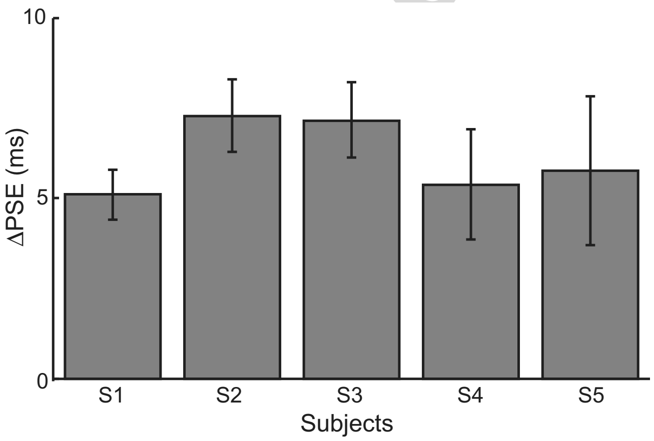

Fig. 3. Mean values of ΔPSE: variation in the point of subjective equality (ΔPSE) produced by the primer for five subjects.

The reference condition, besides being neutral, shows that the simple presence of another object (static) does not produce a similar magnification of the FLE.

It could be argued that the FLE magnification found in the experimental condition might be a postdictive consequence of the static presence of the primer at its final position after the flash occurs (Eagleman & Sejnowski, 2000). In order to rule out this possibility, we ran a further control experiment in which the primer appeared randomly at the initial or final positions and remained static throughout the whole trial. No differences between the two psychometric curves were found. Differences were not significant in terms of the Wilcoxon signed-rank test ($p > .05$). We therefore conclude that it is the movement of the primer and not its static presence that is responsible for the magnification effect of flash lag.

3.2. Experiment 2: What matters is the direction of motion

It could also be argued that motion itself might be responsible for the magnification and not the fact that both movements were concurrent. Thus, in this experiment we examined whether the direction of the primer's motion is necessary to cause FLE magnification. The primer at the beginning of the trials is now located in the same horizontal position as in the previous experiment but, vertically, its initial position is close to the ring trajectory (position *b* in left panel of Fig. 1). The primer could move downwards, i.e., away from the ring trajectory, or remain static at its initial position (close to the ring trajectory). Temporally, the primer motion was similar to that described for experiment 1, but in the opposite direction.

Fig. 4 shows the mean ΔPSE obtained for experiment 2 in comparison with the same variable measured in the remaining experiments. The first bar (from left to right) corresponds to the mean value for all subjects in experiment 1. The second bar shows the mean value for all subjects in this experiment. It shows that the ΔPSE is close to zero, which means that there is no difference in FLE between the experimental condition (primer moving away) and the reference situation with the primer static. Data are pooled for all subjects, but each of the five subjects showed similar result patterns. The Wilcoxon test for one sample (H0: mean = 0) gives a p of .073, showing that the ΔPSEs are not significantly different from 0. Therefore there is no magnification effect when the primer moves away from the ring trajectory. Moreover, the comparison between results for Exp. 1 and 2 gives a $p = .00045$ with the Wilcoxon test.

As is shown, the opposite direction of motion in the primer object does not produce any magnification of the FLE, giving similar results when the primer is moving and static. Therefore, we could assume that the FLE is not related to the motion of the primer itself but, instead, is linked to the direction of motion. This is coherent with our hypothesis:

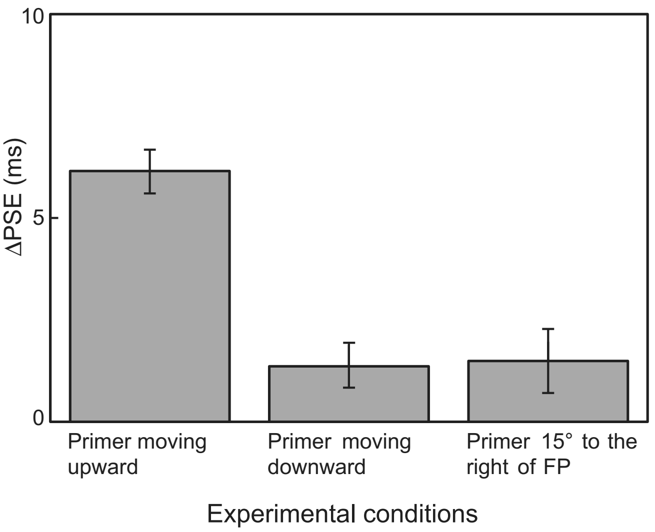

Fig. 4. Mean values of ΔPSE for different experimental conditions in five subjects (the same of those in Fig. 3). Left: conditions of experiment 1. Middle: the same conditions as in experiment 1, but the primer moves between the two extreme positions (A and B in Fig. 1) in the opposite direction. Right: the same conditions as in experiment one, but the primer was placed 10° to the right (15° to the right of the FP).

the motion of the primer should "add" its pre-activation to the ring's forthcoming positions, creating a facilitated spot roughly in the area in which they would intersect (see Section 4).

3.3. Experiment 3: The effect of the primer is spatially bounded

In order to prove that magnification is spatially bounded, as predicted by the mechanism that we are postulating, we ran another experiment analogous to experiment 1 but, in this case, the primer was situated at approximately 15° in advance of the FP (10° to the right of the position of the primer in experiment 1). As the temporal dynamics of the trial were identical to those applied in experiment 1, we obtained a situation in which the primer starts moving when the ring is still far from it.

The third bar from the left in Fig. 4 represents the pooled ΔPSE for the five subjects in this experiment. Each of the five subjects showed similar patterns of results. The Wilcoxon test for one sample (H0 mean = 0, $p = .14$) does not give ΔPSEs significantly different from 0: there is no magnification effect when the primer moves upwards if this motion occurs away from the ring's forthcoming positions at the moment of the flash (Fig. 4). This was another prediction concerning the underlying mechanism we postulate for the FLE magnification by a second moving object.

3.4. Experiment 4: The effect of the primer depends on its contrast

An alternative explanation to the observed phenomenon could be that the increased FLE is not caused by augmented facilitation but related to the fact that the two moving objects are expected to collide. The time and location of the collision are easy to predict by the observers. This could affect the FLE because the observers could pay attention to the expected collision location, which will 'pull' the perceived location of the moving objects towards the expected collision point and therefore further on in their trajectory. Even though the mechanism we postulate could be a low level embodiment of this higher level mechanism of anticipation, we designed another experiment where this expectancy is kept constant and the other variable, plausibly related to the facilitation mechanism, is changed. Experiment 4 is basically equal to the experiment 1 but the primer moves upward in every trial. The contrast of the primer was varied at random in each trial between two values; one with very low contrast, barely discernible from the background, and the other with the same contrast used in the previous experiments. The PSE was obtained for both contrast conditions and the difference between them (the ΔPSE) was calculated. Note that in this case neither of the two conditions is neutral and the ΔPSE will reflect whether there is a variation in the intensity of the effect between the two conditions. The resulting mean effect is 1.82 ms significantly different from 0 (Wilcoxon test for one sample with a $p = 8.14 \times 10^{-5}$) and similar for the five subjects. This means that the effect with the primer with low contrast is approximately 2 ms less than the effect obtained with the contrast used in the other experiments. If we take as a reference the magnification of the FLE obtained in experiment 1 the low contrast primer would produce a magnification 30% smaller.

4. Discussion

The FLE shows that our Visual System is unable to accurately localize a continuously visible moving object with respect to another that appears intermittently. This inability brings up the puzzling problem of how we can maintain a "real time" relation with moving objects in the world in spite of the potentially relatively long neural delays involved in the process. The FLE illusion reveals—and allows us to investigate—part of the neuronal machinery involved in dealing with that problem.

The extensive description of the phenomenon and the relations between the numerous variables involved, has led to many explanations and fruitful hypotheses since Nijhawan's paper (1994). Most of them (prediction, postdiction, attentional) imply high level mechanisms of psychological nature. Others at a lower level (differential latencies) invoke neural mechanisms, but do not propose specific neural properties. It is worth noting that explanations at different levels usually are not contradictory: the low level explanation may be the basic embodiment of the high level ones.

The existence of a general facilitation along the trajectory of motion, like the one shown by Berry et al. (1999) in retina and Jancke et al. (2004), Jancke, Erlhagen et al.

(2004) in cat cortex can be part of the basic explanation for a shorter latency in movement perception, and consequently for the different latencies explanation of the FLE. The results we show in this work give further support to this line of reasoning. Our hypothesis assumes: (1) the participation of this facilitation mechanism in the genesis of FLE; (2) the facilitation waves of two movements should add together (not necessarily in a linear manner). Even though we do not have physiological data supporting the second assumption, it seems a reasonable supposition since the alternative possibility would be that pre-activation is highly specific. If this kind of pre-activation of neighboring areas is involved in movement perception and is perturbed in the above-mentioned way, it would modify perception. More precisely, if facilitation of the two moving objects adds together, the consequence would be a supplementary facilitation, an even shorter perceptual delay, and—because of that—an increase in lag for the flashed object. Since the overall result for the operation of this mechanism would be a shorter perceptual delay for the moving object, it provides a substrate for the "differential latencies" type of explanation. Finally, this mechanism although simple, can embody in cell connections and response properties the spatio-temporal statistics of the natural world, allowing efficient tuning with perceptually meaningful targets (Vinje & Gallant, 2002).

The extrapolation explanation for this illusion (Nijhawan, 1994) postulates that the moving target is spatially projected by the visual system to a predicted position so as to partially compensate for processing delays. As a lateral effect of extrapolation, a flash seems to lag behind a moving object, even if they are physically aligned. The main point that differentiates our explanation from extrapolation is that there would be no response (and therefore no perception) unless there is actual stimulation at the facilitated spot. Our proposal, retaining the appealing anticipatory aspect of extrapolation, accounts for the absence of overshoot that seriously jeopardizes the plausibility of the spatial extrapolation explanation (Whitney & Murakami, 1998). The anticipation is done in a probabilistic way, thus, relating our hypothesis with the Bayesian framework for vision (Kersten & Yuille, 2003) and more particularly for speed perception (Stocker & Simoncelli, 2006). Facilitatory signals could be considered as giving the prior probability distribution for a given direction of movement in the cortical map and the actual stimulation would be the likelihood distribution. Given these two distributions an optimal observer could estimate the best movement direction according to the Bayes rule.

An alternative explanation for the effect we present here would be that attention is captured by the second moving object, in some way delaying the process of comparison and as a result giving the increase in FLE magnitude (Baldo & Klein, 1995). Even though we cannot completely rule out attention participation, it is difficult to explain why this effect would be selective for the convergent movement (experiment 1) yet absent when the object moves away (experiment 2). Another possible explanation could be that the expectation of collision somehow accelerates movement perception leading to the observed FLE increase. Experiment 4 shows that, keeping the expectation of collision constant, the effect can be modulated by changing primer contrast. This gradual change of the effect is to be expected from the facilitation hypothesis we propose. It should be noted that the small effect of changing the contrast of the primer points to a strong non linearity, either in the first stages of the visual pathways or at high levels, as for example different cortical areas. These alternatives can be tested by neurophysiological experiments.

Visual perception is a complex process in which bottom–up and top–down fluxes of information interact in producing actual perception. Consequently, it is difficult to dismiss the possibility that attention (Baldo & Klein, 1995) or "internal model updating" (Eagleman & Sejnowski, 2000) may be involved in the production of the illusion. It is also as difficult to discard early processing differences in the production of the phenomenon. The spatio-temporal properties of ganglionic, geniculate and cortical cells' receptive fields (RF) account for different responses, depending on the spatio-temporal history of the stimulus. Sub-threshold facilitation carried by the horizontal spreading of activation has been shown to be involved in phenomena such as illusory contours, filling-in or the line-motion illusion; this involvement has now also been shown for FLE.

References

Allman, J., Miezin, F., & McGuinness, E. (1985). Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local–global comparisons in visual neurons. *Annual Review of Neuroscience, 8*, 407–430.

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

Berry, M. J., 2nd, Brivanlou, I. H., Jordan, T. A., & Meister, M. (1999). Anticipation of moving stimuli by the retina. *Nature, 398*(6725), 334–338.

Bringuier, V., Chavane, F., Glaeser, L., & Fregnac, Y. (1999). Horizontal propagation of visual activity in the synaptic integration field of area 17 neurons. *Science, 283*(5402), 695–699.

De Valois, R. L., & De Valois, K. K. (1991). Vernier acuity with stationary moving Gabors. *Vision Research, 31*(9), 1619–1626.

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

Fitzpatrick, D. (2000). Seeing beyond the receptive field in primary visual cortex. *Current Opinion in Neurobiology, 10*(4), 438–443.

Fregnac, Y., Bringuier, V., & Chavane, F. (1996). Synaptic integration fields and associative plasticity of visual cortical cells in vivo. *Journal of Physiology Paris, 90*(5-6), 367–372.

Georges, S., Series, P., Fregnac, Y., & Lorenceau, J. (2002). Orientation dependent modulation of apparent speed: Psychophysical evidence. *Vision Research, 42*(25), 2757–2772.

Gilbert, C. D., & Wiesel, T. N. (1989). Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. *Journal of Neuroscience, 9*(7), 2432–2442.

Jancke, D., Chavane, F., Naaman, S., & Grinvald, A. (2004). Imaging cortical correlates of illusion in early visual cortex. *Nature, 428*(6981), 423–426.

Jancke, D., Erlhagen, W., Schoner, G., & Dinse, H. R. (2004). Shorter latencies for motion trajectories than for flashes in population responses of cat primary visual cortex. *Journal of Physiology, 556*(Pt 3), 971–982.

Kersten, D., & Yuille, A. (2003). Bayesian models of object perception. *Current Opinion in Neurobiology, 13*(2), 150–158.

Mackay, D. M. (1958). Perceptual stability of a stroboscopically lit visual field containing self-luminous objects. *Nature, 181*(4607), 507–508.

Maiche, A., Budelli, R., Estaún, S., & Gómez-Sena, L. (2005). Contextual dependence of flash-lag illusion magnitude. *Perception, 34*(Suppl.), 160–161.

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

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Series, P., Lorenceau, J., & Fregnac, Y. (2003). The "silent" surround of V1 receptive fields: Theory and experiments. *Journal of Physiology Paris, 97*(4-6), 453–474.

Stocker, A. A., & Simoncelli, E. P. (2006). Noise characteristics and prior expectations in human visual speed perception. *Nature Neuroscience, 9*(4), 578–585.

Toth, L. J., Rao, S. C., Kim, D. S., Somers, D., & Sur, M. (1996). Subthreshold facilitation and suppression in primary visual cortex revealed by intrinsic signal imaging. *Proceedings of the National Academic Sciences of the United States of America, 93*(18), 9869–9874.

Vinje, W. E., & Gallant, J. L. (2002). Natural stimulation of the nonclassical receptive field increases information transmission efficiency in V1. *Journal of Neuroscience, 22*(7), 2904–2915.

Whitney, D., & Murakami, I. (1998). Latency difference, not spatial extrapolation. *Nature Neuroscience, 1*(8), 656–657.