

Computational neurobiology of the flash-lag effect

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Abstract

In the flash-lag effect (FLE) a moving object is perceived ahead of a stationary stimulus flashed in spatial alignment. Several explanations have been proposed to account for the FLE and its dependence on a variety of psychophysical attributes. Here, we show that a simple feed-forward network reproduces the standard FLE and several related manifestations, such as its modulation by stimulus luminance, trajectory, priming, and spatial predictability. A minimal set of elements, based on plausible neuronal mechanisms, yields a unified account of these visual illusions and possibly other perceptual phenomena.

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1. Introduction

When observers are to compare the positions of a moving object and a stationary flash presented in the visual field, they usually perceive the moving stimulus as being advanced in relation to the position of the flash when, in fact, both stimuli happen to be physically aligned to each other in space-time (MacKay, 1958; Metzger, 1932; Nijhawan, 1992, 1994). This is the so-called *flash-lag effect* (FLE), which has received a variety of explanations over the last decade (Baldo & Klein, 1995; Brenner & Smeets, 2000; Eagleman & Sejnowski, 2000a, 2000b, 2000c; Kanai, Sheth, & Shimojo, 2004; Krekelberg, 2001; Krekelberg & Lappe, 2000a, 2000b, 2001; Namba & Baldo, 2004; Nijhawan, 1992, 1994, 2002; Ögmen, Patel, Bedell, & Camuz, 2004; Purushothaman, Patel, Bedell, & Ögmen, 1998; Schlag & Schlag-Rey, 2002; Whitney, 2002; Whitney & Murakami, 1998). Nijhawan, who rediscovered this perceptual effect,

hypothesized that it would arise from a spatial extrapolation of the moving object's perceptual position to compensate for processing delays along the neural pathways (Khurana & Nijhawan, 1995; Nijhawan, 1994, 1997, 2002). Since then, several other interpretations have been offered besides motion extrapolation including, among others, differential perceptual latencies between flashing and moving stimulus (Baldo & Klein, 1995; Baldo, Kihara, Namba, & Klein, 2002; Krekelberg & Lappe, 2000a; Patel, Ögmen, Bedell, & Sampath, 2000; Purushothaman et al., 1998; Whitney & Murakami, 1998; Whitney & Cavanagh, 2000; Whitney, Murakami, & Cavanagh, 2000) and sensory postdiction (Eagleman & Sejnowski, 2000a, 2000b, 2000c). Apart from any theoretical account, the magnitude of the FLE has been empirically shown to depend on psychophysical properties such as eccentricity (Baldo & Klein, 1995; Baldo et al., 2002), luminance (Patel et al., 2000; Purushothaman et al., 1998), trajectory (Eagleman & Sejnowski, 2000a; Whitney & Murakami, 1998), priming (Chappell & Hine, 2004; Whitney & Cavanagh, 2000), and spatial predictability (Baldo & Namba, 2002; Baldo et al., 2002; Eagleman & Sejnowski, 2000b; Namba & Baldo, 2004).

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Perceptual mismatches have also been reported between an abruptly changing object (a generalized “flash”) and an object in generalized “motion” (an object displaying a continuous temporal shift in any perceptual variable other than its spatial location in the visual field). Thus, the boundaries of the FLE have been enlarged by incorporating chromatic effects (Cai & Schlag, 2001; Nijhawan, 1997), “motion” in luminance and color spaces (Sheth, Nijhawan, & Shimojo, 2000), vestibular and auditory stimulation (Alais & Burr, 2003; Schlag, Cai, Dorfman, Mohempour, & Schlag-Rey, 2000), and potential consequences on motor control (Nijhawan & Kirschfeld, 2003).

The aim of this study was to obtain the primary traits of the original FLE from the simplest rules governing neuronal function and integration. Instead of translating any existing conceptual model of the FLE into a mathematical representation, we started from well-known features usually present in theoretical models of real neurons and neuronal networks (Koch, 1998). These features include, for instance, graded membrane potentials, temporal integration of excitatory and inhibitory inputs, nonlinearity, firing of action potentials, convergent and divergent synaptic connections between neuronal layers and center-surround antagonist receptive fields. Such a set of properties is by no means tailor-made for the job of reproducing the FLE and

fitting its attributes, being instead quite natural in any sensory neural model.

We have designed and studied a class of feed-forward neural networks in which the “membrane potentials” of leaky integrate-and-fire neurons vary in a graded way, integrating excitatory and inhibitory impulses, decaying exponentially, and firing when a predetermined threshold is exceeded (Koch, 1998). The essence of the model (Fig. 1) can be summarized as follows (see Section 2 for details): (i) the network consists of a feed-forward layered architecture (*input*, *hidden*, and *output* layers); (ii) these layers are linked by means of convergent and divergent interlayer connections; (iii) every neuron in a hidden layer receives input stemming from a receptive region of neurons in the input layer and projects onto a corresponding region in the output layer; and (iv) the pattern of connections reproduces center-surround antagonist receptive fields.

In the simulations of the present model, the input layer is excited by a “moving” stimulus, which sequentially excites the neurons belonging to a given row of the layer. At some point of the moving stimulus’ trajectory, an abrupt-onset stationary stimulus starts exciting a single neuron located in a parallel row of the input layer, in spatial alignment with the moving stimulus at that moment (Fig. 1).

2. Methods

The architecture employed in the leaky integrate-and-fire (LIF) network consists of an input layer, one hidden layer and an output layer connected by convergent and divergent projections. Each layer is an $M \times N$ rectangular lattice on a horizontal plane indexed by coordinates $\varepsilon = (\varepsilon_x, \varepsilon_y)$. In Fig. 1 each unit represents a LIF neuron linked to other neurons in the previous and/or next layer by means of either excitatory or inhibitory unidirectional “synaptic” connections of strength J_{ij} from neuron j in layer $K-1$ to neuron i in layer K (the connections of only one neuron belonging to the hidden layer are shown in Fig. 1).

In the neuron i at position $\varepsilon = (\varepsilon_x, \varepsilon_y)$ in layer K , the graded “membrane potential” $v_i^K(t)$ at time t evolves according to

$$v_i^K(t) = (1 - \Omega)v_i^K(t-1) + I_i(t), \quad (1)$$

the leaking voltage decays with a constant Ω kept between 0 and 1. The input current $I_i(t)$ for a given neuron i is obtained by integrating over its receptive field; the overall input $I_i(t)$ depends on both the state $v_j^{K-1}(t-1)$ of each neuron j belonging to the layer $K-1$ at the time $t-1$, and the weight of the synaptic connection J_{ij} from neuron j onto neuron i

$$I_i(t) = \sum_{j \in \text{layer}(K-1)} J_{ij} \Theta(v_j^{K-1}(t-1) - \lambda). \quad (2)$$

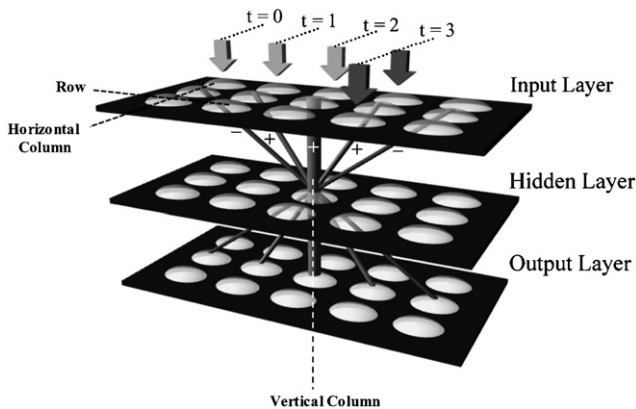


Fig. 1. The models’ basic architecture. An input layer, one hidden layer and an output layer are connected by convergent and divergent projections (lateral interactions). Each layer is composed by neurons arranged in rows and horizontal columns, linked to neurons located in other layers by means of excitatory (+) and inhibitory (–) connections (the figure shows the connections of only one selected neuron belonging to the hidden layer). A vertical column is defined by the connection between neurons located in different layers but belonging to the same row and same horizontal column. The moving stimulus consists of a spatio-temporal sequence of inputs starting at $t=0$ along a row of neurons; in another row, a stationary stimulus is applied to a single neuron located at the same horizontal column occupied by the moving stimulus at that moment ($t=3$). Light gray arrows: preceding moving inputs (from $t=0$ to $t=2$); dark gray arrows: current moving and stationary inputs presented in spatial alignment to each other at the same horizontal column ($t=3$).

The step function Θ yields zero (one) for negative (positive) arguments and implements firing above-threshold λ . The connections J_{ij} between neurons j and i were chosen as follows: $J_{ij} = J_{vc} > 0$ if j and i belong to the same *vertical column* (see Fig. 1); $J_{ij} = J_{ilc} > 0$ ($J_{ilc} < J_{vc}$) if J_{ij} is the *innermost lateral connection* and $J_{ij} = J_{olc} < 0$ if J_{ij} is the *outermost lateral connection*. The parameters adopted in the majority of our simulations were $J_{vc} = 0.4$, $J_{ilc} = 0.2$, and $J_{olc} = -0.2$ for the connections, $\lambda = 0.65$ for the threshold, and $\Omega = 0.6$ for the leaking constant. The intensities of the stationary (I_{stat}) and moving (I_{mov}) stimuli were specified in accord to the condition under study. The receptive fields were one-dimensional, in the direction of motion. Neurons in the input layer lacked a firing threshold, displaying only graded membrane potentials similarly to generator potentials in sensory receptors.

In the present simulations, comparisons between “physical” and “neural” locations of a given stimulus (either moving or stationary) were made by comparing

its position in the input layer and the corresponding neural activity generated in the output layer (a single vertical column defines the same coordinates x and y for all layers). Nonetheless, the output layer should not be taken as a decisional stage or the percept itself, but rather as a still intermediate stage where the initial stimulation pattern has been transformed according to the dynamics of neural processing. Indeed, if any mismatch between “physical” and “neural” locations is observed already in this intermediate level (output layer), a related mismatch would be likely to manifest in a later stage of sensory processing and perceptual generation as well.

3. Results and partial discussion

Besides the standard flash-lag and Fröhlich effects, the present model was also able to reproduce several other perceptual findings, reported over the last decade (see Table 1 for a summary). These findings include

Table 1
Comparison between reported and present results

Empirical findings of published psychophysical studies	Main references	Results of the present simulations
Flash-lag effect: a moving object is perceived ahead of a flashed, spatially aligned, and stimulus	Metzger (1932); MacKay (1958); Nijhawan (1992, 1994)	Figs. 2A and C
Fröhlich effect: the position of a newly moving object is perceived ahead of its starting location	Fröhlich (1923); Müsseler et al. (2002); Kerzel and Gegenfurtner (2004)	Figs. 2B and D
The FLE's magnitude depends on the relative luminance between stationary and moving stimuli (I_{stat}/I_{mov} ratio). For high enough ratios, a flash-lag may turn into a flash-lead	Purushothaman et al. (1998); Patel et al. (2000)	Fig. 3A (compare to Fig. 1C in Purushothaman et al., 1998)
Within a limited range, the magnitude of the FLE varies linearly with the speed of the moving stimulus	Nijhawan (1994)	Fig. 3B
The FLE is produced even when the moving stimulus appears simultaneously with the stationary stimulus (flash-initiated cycle, FIC). Under the FIC condition, a high-luminance stationary stimulus leads to a flash-lag instead of a flash-lead effect, which is observed under the continuous motion condition	Nijhawan (1992); Khurana and Nijhawan (1995); Patel et al. (2000)	Fig. 4A (compare to Fig. 1C in Patel et al., 2000)
If a moving stimulus either stops or reverses direction at the moment of the flash, the observed flash-lag is either nil or actually opposite to the reported in the continuous condition, respectively	Whitney and Murakami (1998); Eagleman and Sejnowski (2000a)	Fig. 4B (compare to Fig. 1 in Eagleman and Sejnowski, 2000a)
When a stimulus starts its movement and then suddenly reverses its direction of motion, the FLE depends on the time spent by the moving stimulus before reversing direction	Eagleman and Sejnowski (2000a)	Figs. 4C and D (compare to Fig. 2 in Eagleman and Sejnowski, 2000a)
When a stationary cue is presented, briefly removed and then presented again in motion, the Fröhlich effect is virtually abolished, without changing the magnitude of the FLE elicited by an adjacent flash	Whitney and Cavanagh (2000); Chappell and Hine (2004)	Fig. 5A (compare to Fig. 1B in Whitney and Cavanagh, 2000)
The FLE depends on the spatial predictability of the stationary stimulus, possibly reflecting the spatial distribution of visual attention over the visual field	Baldo and Klein (1995); Eagleman and Sejnowski (2000b); Baldo et al. (2002); Baldo and Namba (2002); Namba and Baldo (2004)	Fig. 5B (compare to Fig. 5 in Baldo et al., 2002 and Fig. 1 in Eagleman and Sejnowski, 2000b)

the dependence of the FLE on psychophysical parameters such as the luminance ratio between flashing and moving stimuli, the trajectory of the moving object, priming, and the spatial predictability of the stationary stimulus. All simulations were performed under a set of conditions that represent a significant sample of those reported in the literature. Far from an arbitrary selection, these conditions were chosen for sharing the following characteristics, which allowed their simulation by the model at its current level of complexity: restriction to only one modality of sensory processing (instead of taking into account possible crossmodal interactions); limitation to the analysis of sensory localization in space-time (instead of dealing with more elaborated perceptual tasks); recruitment of a “visual” monochannel activated by luminance only (instead of involving chro-

matic processing); and confinement to the sensory branch of neural processing (instead of taking into account potential motor effects).

In the following paragraphs, we describe the simulations implemented by means of the present neural network and their relationship to a set of experimental observations reported in the literature.

3.1. The standard flash-lag and Fröhlich effects

Our simulations show that a moving object activates the neural network in such a way that the first above-threshold activity appears, in the output layer, at a location ahead of the corresponding starting position of the moving stimulus in the input layer (Fig. 2). This is a reproduction of the well-known Fröhlich effect: the

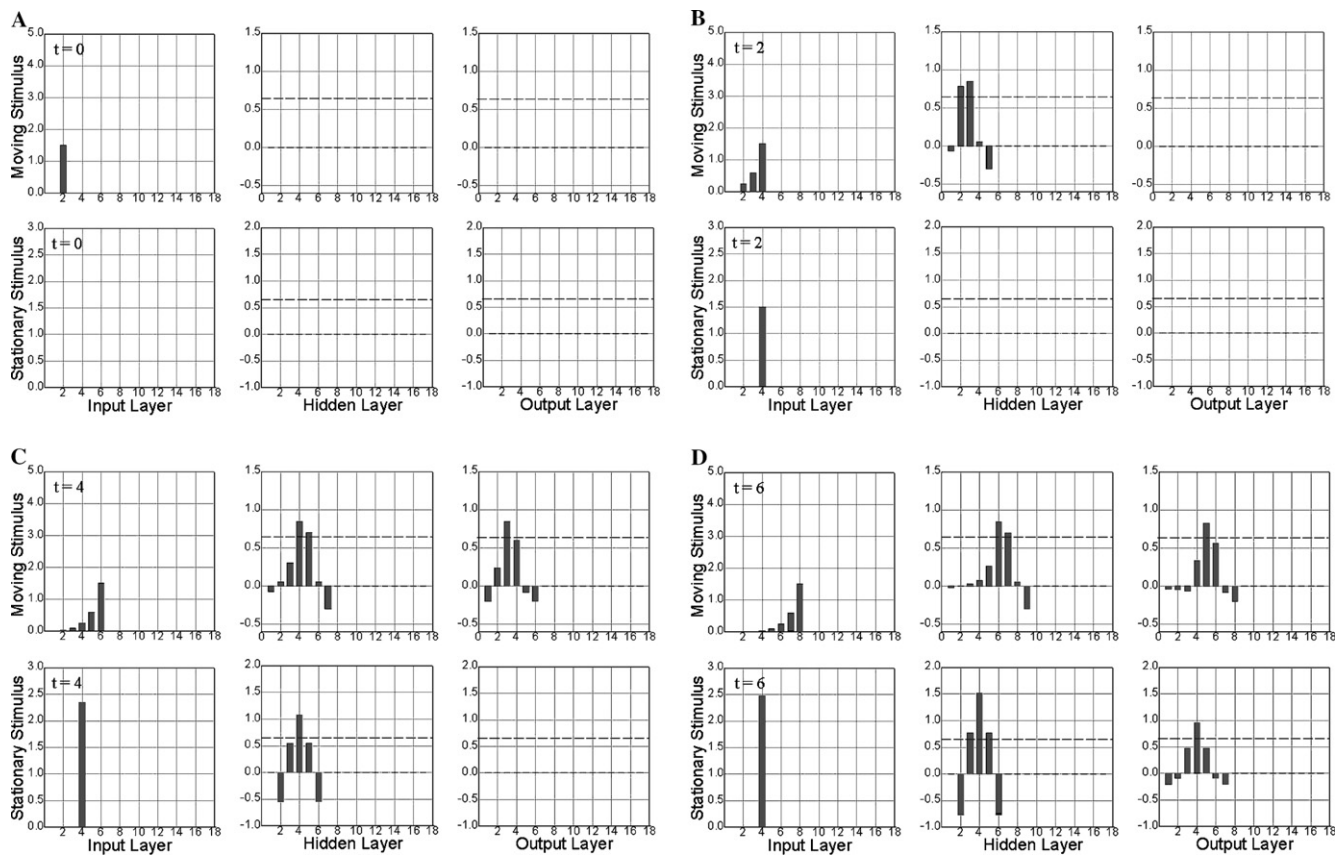


Fig. 2. Simulated behavior of the leaky LIF network. From (A) to (D) the panels show four snapshots ($t = 0, 2, 4,$ and 6 arbitrary units of time) of the neural activity taking place at the input (leftmost), hidden (middle), and output (rightmost) layers for both moving (upper panels) and stationary (lower panels) stimuli. (A) At $t = 0$ the moving stimulus initiates its movement in the input layer from horizontal column #2 (see Fig. 1 for the definition of horizontal column). (B) At $t = 2$, when the moving stimulation is now being presented at the horizontal column #4, the stationary stimulus is presented at the same horizontal column of the input layer but in a different row, in spatial alignment with the moving stimulus; we can notice in the hidden layer by this time an above-threshold activity induced by the moving stimulus (the threshold is indicated by the horizontal dashed line). (C) At $t = 4$ the activity generated by the moving stimulus first crosses the threshold (horizontal dashed line) in the output layer: the first above-threshold activity induced by the moving stimulus in the hidden layer happens at horizontal column #3 (instead of #2), a clear manifestation of the Fröhlich effect; an above-threshold activity induced by the stationary stimulus is seen in the hidden layer, but none is seen yet in the output layer. (D) At $t = 6$ the activity generated by the stationary stimulus first crosses the threshold (horizontal dashed line) in the output layer at the horizontal column #4 (the same horizontal column where it is being presented in the input layer); at this time, however, the corresponding activity of the moving stimulus is located at the horizontal column #5, a clear manifestation of the flash-lag effect. A corresponding simulation of a neural network composed of neurons described by the FitzHugh–Nagumo (FHN) model also shows a clear manifestation of the flash-lag and Fröhlich effects (see www.fisio.icb.usp.br/~vinicius/flashlag.htm).

misperception of the starting position of a newly moving object (Fröhlich, 1923; Kerzel & Gegenfurtner, 2004; Müsseler, Stork, & Kerzel, 2002), which naturally arises from the model's dynamics. Moreover, an abrupt-onset stationary stimulus presented in spatial alignment with a moving stimulus (occupying the same horizontal column in the input layer) triggers, in the output layer, an above-threshold activity that lags behind the neural activity generated by the moving stimulus: the flash-lag effect (Nijhawan, 1992, 1994).

The present model, not committed to any mechanism previously proposed to account for the FLE, actually helps us recognize the rationale possibly inspiring those explanations. For instance, divergent interactions in the neural network seem to be an important ingredient in the spatial mechanisms leading to the FLE (Berry, Bri-vanlou, Jordan, & Meister, 1999; Erlhagen, 2003; Erlhagen & Jancke, 2004; Krekelberg & Lappe, 2001). These lateral interactions can carry out an anticipation of the motion along a row of neurons, resembling the extrapolation account proposed by Nijhawan (1994) and empirically observed in electrophysiological recordings (Berry et al., 1999). In fact, we have run an additional set of simulations of the LIF model in which the lateral interactions were more deeply examined. These simulations showed that the presence of the excitatory divergent connections is a significant factor in promoting the emergence of the FLE, most likely for carrying out the spatial facilitation along the motion pathway. Removing all lateral connections and keeping only the direct (vertical) excitatory connection led to the disappearance of the flash-lag phenomenon, whereas exclusively inhibitory divergent connections (besides the excitatory direct one) could even give rise to a flash-lead effect.

3.2. Dependence of the FLE on stimulus luminance and speed

As first reported by Purushothaman et al. (1998), the FLE's magnitude depends on the luminance ratio between stationary and moving stimuli ($I_{\text{stat}}/I_{\text{mov}}$). These authors found that for high enough $I_{\text{stat}}/I_{\text{mov}}$ ratios, a

flash-lag may turn into a “flash-lead” effect. Fig. 3A shows the simulated spatial lead of the moving stimulus for a set of luminance ratios ranging from 0.8 to 2.3. The model captured not only the dependence of the FLE magnitude on the luminance ratio but also the reversal of the perceptual effect from a flash-lag to a flash-lead when the luminance ratio was set to $I_{\text{stat}}/I_{\text{mov}} = 2.3$. As discussed in greater detail below (see Section 5), changes in the luminance ratio between stationary and moving stimuli ($I_{\text{stat}}/I_{\text{mov}}$) modified the latencies of neurons belonging to the hidden and output layers: the higher (lower) the luminance ratio, the shorter (longer) the latency of neurons processing the stationary stimulus, following thus a decrease (increase) in the magnitude of the FLE.

As first reported by Nijhawan (1994), an increase in the speed of the moving stimulus leads to a corresponding increase in the magnitude of the FLE. Even though constrained by a relative narrow range of speed manipulation, the proposed model was able to capture qualitatively the influence of the moving stimulus' speed on the magnitude of the FLE. Fig. 3B shows, for $I_{\text{stat}}/I_{\text{mov}} = 0.8$, the magnitude of the FLE simulated under three different motion speeds: 0.33, 0.5, and 1.0 space unit/time unit. Not only the FLE decreased with decreasing speeds, but this dependence also portrayed a roughly linear relationship within the range of speed variation allowed by the model.

3.3. The dependence of the FLE on the trajectory of the moving stimulus

The FLE is observed even when the moving stimulus initiates its motion simultaneously with the presentation of the stationary stimulus, a condition known as “flash-initiated cycle” (FIC), in opposition to the usual “continuous motion” (CM) condition. The FIC condition and its counterpart, the flash terminated cycle (FTC) condition, were first devised by Romi Nijhawan to further explore possible explanations for the FLE (Nijhawan, 1992). Khurana and Nijhawan (1995) later employed the FIC condition as an attempt to prevent

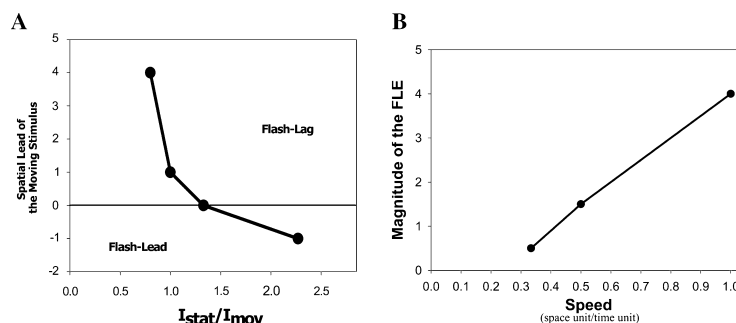


Fig. 3. Dependence of the FLE on the stimulus luminance and speed. (A) Spatial lag (positive values) or lead (negative values) of the stationary stimulus as a function of stationary-to-moving stimulus' luminance ratio ($I_{\text{stat}}/I_{\text{mov}}$). (B) Within the range allowed by the model, the magnitude of the FLE showed a linear dependence on the speed of the moving stimulus.

the potential influence of attentional shifts on the FLE. Our model was able to reproduce the FLE under the FIC condition even for a high-luminance stationary stimulus, as first reported by Patel et al. (2000). These investigators observed that under the FIC condition a high-luminance flash still yields a usual FLE, instead of turning it into a “flash-lead” effect, as observed in the CM condition (Patel et al., 2000). Accordingly, Fig. 4A shows the effect of a high-luminance ratio between stationary and moving stimuli ($I_{stat}/I_{mov} = 2.3$) under both CM and FIC conditions, as obtained by simulations of the present model. The simulation shows that, in the CM condition, a faster build-up of neural activity induced by the stationary stimulus in the output layer crosses the threshold when the activity induced by the moving stimulus is still behind the alignment

location. When both stimuli are presented at the same time (FIC condition), the stationary stimulation indeed crosses the threshold in the output layer earlier than the moving one, whose first above-threshold in the output layer happens, however, at a location ahead of the alignment location. The spatial advance of the activity generated in the output layer by the moving stimulus is due to the combination of excitatory and inhibitory connections carried out by the lateral interactions (in this case correlating the manifestations of the Fröhlich and flash-lag effects).

In relation to the CM condition, the FLE can be either nil or even reversed if the moving stimulus, respectively, stops or reverses direction at the moment of the flash (supposing both stimuli are physically aligned to each other at this point). When the moving object stops

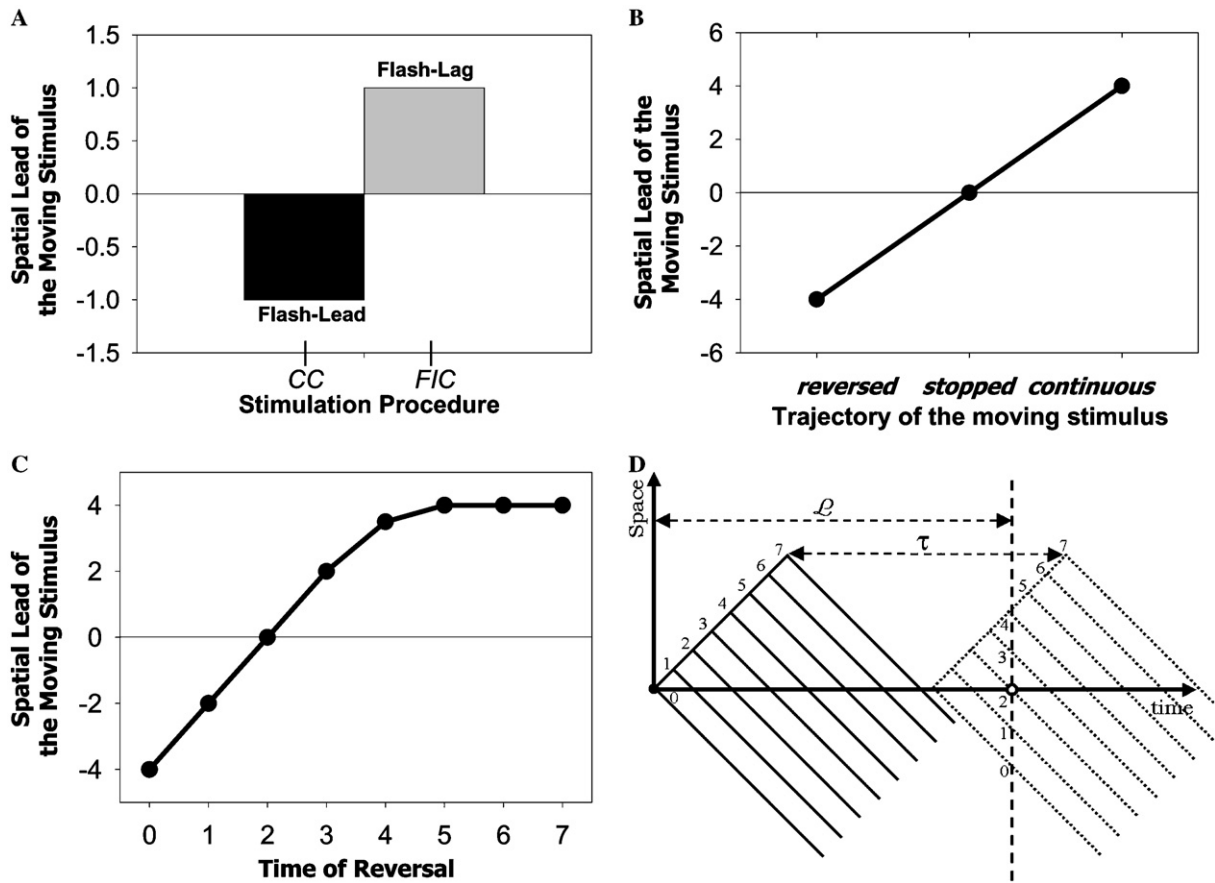


Fig. 4. Dependence of the FLE on the moving stimulus' trajectory. (A) Under continuous motion (CM), a high enough stationary-to-moving stimulus' luminance ratio ($I_{stat}/I_{mov} = 2.3$) led to a flash-lead effect; the same luminance ratio led, however, to the usual flash-lag effect when both moving and stationary stimuli were presented simultaneously (flash-initiated cycle, FIC). (B) Spatial lead of a moving stimulus that continues, stops or reverses motion at the instant a stationary stimulus is presented in spatial alignment. (C) Spatial lead of a moving stimulus that reverses direction of motion after a variable time interval (*Time of Reversal*) starting with the presentation of a spatially aligned flash. (D) Space-time diagram representing a set of possible trajectories of a moving stimulus (solid line) that starts its motion at the same time a stationary stimulus (filled circle) is presented (flash-initiated cycle condition, FIC). The moving stimulus then reverses direction after a variable time, indicated by the trajectories numbered from 0 to 7 (actually, trajectory 0 represents the absence of any forward movement and therefore no reversal at all). The number indicating a given trajectory coincides with the time of reversal shown in (C). The percept of the moving and stationary stimuli is represented by the dotted lines and empty circle, respectively; L represents the perceptual latency of the stationary stimulus and τ symbolizes the temporal shift between physical and perceptual motion. The perceptual localization of the moving stimulus, at the moment the stationary stimulus is perceived, is given by the intersection of the vertical dashed line with each possible trajectory; these intersections reproduce the saturating function exhibited in (C).

in spatial alignment (and temporal simultaneity) with the stationary stimulus (flash terminated cycle, FTC), no perceptual misalignment is usually observed, as first reported by Nijhawan (1992) and later replicated by other authors (Eagleman & Sejnowski, 2000a). Yet, if the moving stimulus reverses its direction of motion at that moment, a FLE in the reversed direction is perceived. Fig. 4B shows the magnitude of the FLE under both reversed and stopped conditions in comparison to the usual continuous motion condition, as revealed by simulations of our model. An elaboration of this experimental condition was conducted by Eagleman and Sejnowski (2000a), in which a FIC is followed, after some variable amount of time, by a direction reversal of the moving stimulus. Fig. 4C shows an accurate replication by our model of the result reported by these authors (Eagleman & Sejnowski, 2000a). This result can also be easily grasped with the help of a space-time diagram (Fig. 4D).

3.4. The dependence of the FLE on cueing and attentional deployment

If a stationary cue is briefly flashed at the initial point of the motion trajectory shortly before the presentation of a moving stimulus, the resulting Fröhlich effect is greatly reduced (Whitney & Cavanagh, 2000). Yet, the same cueing procedure has no impact on the magnitude of the FLE, observed when an abrupt stationary stimulus is added to the display under a FIC condition (Whitney & Cavanagh, 2000). An identical outcome emerged from our simulations when the moving stimulus was preceded by the presentation of a brief stationary stimulus at the first point of the trajectory (Fig. 5A): a clear decrease in the magnitude of the Fröhlich phenomenon with no effect at all on the FLE.

In simulating the cueing effects on these phenomena, we employed the same luminance level for both stationary and moving stimuli ($I_{\text{stat}}/I_{\text{mov}} = 1$). Under these circumstances we observed a FLE because at the moment the activity induced by the stationary stimulus crosses the threshold in the output layer, the moving activity is already leading the alignment location (owing to the spatial facilitation carried out by the divergent connections, as discussed above). This misalignment happens regardless of whether the Fröhlich effect is observed: when the cue is present, the activity generated by the moving stimulus is stronger in all three layers, and the moving activity crosses the threshold in the output layer closer to the alignment location, which is the starting vertical column (a lower Fröhlich effect due to the partial offsetting of the inhibitory lateral projections by the presentation of a previous cue); meanwhile, the activity generated by the stationary stimulus in the output layer is still below threshold, crossing it only one processing step later, when the moving activity is spatially advanced in relation to the alignment location (the FLE). The present simulations show that, albeit partially coupled to each other by means of the underlying mechanisms of spatial integration, the Fröhlich and flash-lag effects are distinct enough to allow their dissociation under especial manipulations (not only computationally, but empirically as well).

It has been increasingly established the modulation of the FLE by visual attention (Baldo & Klein, 1995; Baldo & Namba, 2002; Baldo et al., 2002; Eagleman & Sejnowski, 2000b; Namba & Baldo, 2004). The previous knowledge of the location of appearance of the stationary stimulus can reduce the magnitude of the FLE, in comparison to the condition wherein the stationary stimulus may appear randomly in two or more

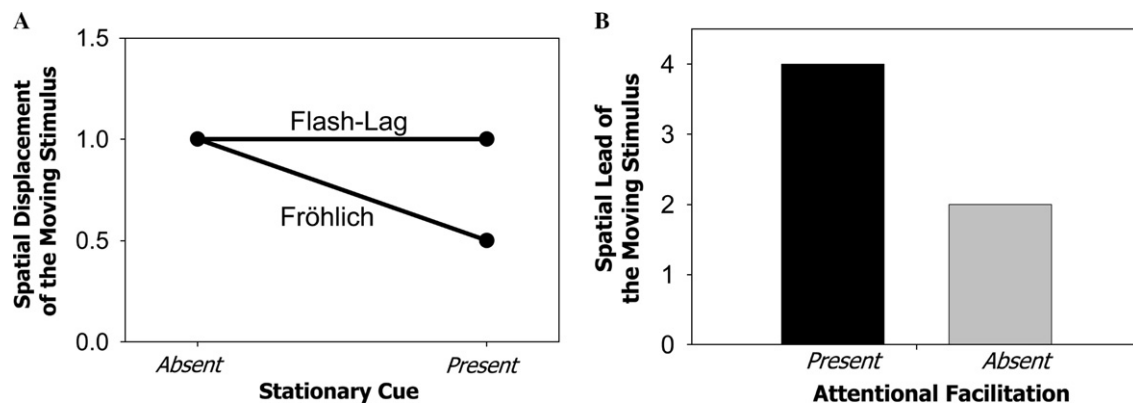


Fig. 5. The magnitude of both flash-lag and Fröhlich effects as a function of priming and attention. (A) The presentation of a cue preceding the moving stimulus (*Present*) in comparison to the absence of visual cueing (*Absent*) reduces the Fröhlich effect with no consequences on the FLE. (B) In comparison to the condition where no previous activation is provided (*Absent*), the magnitude of FLE was reduced (*Present*) by previous activation (4% of the stimulus amplitude) of neurons in the hidden layer whose receptive field in the input layer was stimulated by the stationary stimulus; this pre-activation mimics the likely influence of the deployment of attention to a specified region of the visual field.

spatial locations (Baldo & Namba, 2002; Namba & Baldo, 2004). In the present model, we assumed that either a higher spatial predictability or a previous spatial cueing might lead to a top-down facilitation of neurons belonging to the neural circuitry. The attentional facilitation of the stationary stimulus' processing was hence implemented by pre-activating a set of neurons located, in the hidden layer, along the path recruited by the stationary stimulation. A small pre-activation (only 4% of the stationary stimulus' intensity) of three neurons in the hidden layer whose receptive field, in the input layer, was stimulated by the stationary stimulus was enough to halve the magnitude of the FLE (Fig. 5B). Although not a primary cause of the FLE, attentional mechanisms do manifest a modulatory influence on this perceptual phenomenon, therefore calling for their inclusion in any conceptual or mathematical model offered to spell it out.

4. Predictions of the model

The present model was far from being complete and, as such, it is not yet geared up to predict empirical findings with quantitative accuracy. Nonetheless, it is already capable to foresee a few phenomena we should expect from experimental procedures.

A straight prediction of the model tackles the relationship between the FLE and temporal order judgments (TOJ). In the FIC condition, both stationary and moving stimuli are abruptly presented at the same time. Despite the presence of a clear perception of spatial misalignment (the FLE), our model predicts that no temporal asynchrony would be required. According to our simulations (for $I_{stat}/I_{mov} = 1$), the activities generated in the output layer by both stationary and moving stimuli cross the threshold at the same time, although displaying a clear spatial misalignment (a similar experimental result has been previously reported by Eagleman & Sejnowski (2000c) concerning the flash-terminated cycle condition). In fact, our model predicts that for some I_{stat}/I_{mov} ratios above unity an evident FLE could be observed even in a condition where a TOJ would indicate the precedence of the stationary stimulus (a prediction at odds with the allegation according to which the differential latency account of the FLE implies the temporal precedence of the moving stimulus in TOJ tasks).

Another prediction refers to the modulation of the FLE by interfering with the stationary stimulus presentation. Presenting a cue shortly before the presentation of the stationary stimulus, at the same location in the visual field, should decrease the magnitude of the FLE under the CM condition, with no effect under the FIC condition.

5. General discussion

The present model was able to capture several findings related to the flash-lag effect reported over the last decade. A summary of the replicated experimental results includes: (i) the standard FLE; (ii) the standard Fröhlich effect; (iii) the properties of the FLE when the moving stimulus stops or reverses direction at the moment of the flash; (iv) the emergence of a clear FLE when moving and flashing stimuli are presented at the same time in the visual field (flash-initiated cycle, FIC); (v) the dependence of the FLE on the luminance ratio between flashing and moving stimuli (the flash-lag may even turn into a flash-lead for high enough ratios); (vi) the dissociation of the outcomes produced on the flash-lag and Fröhlich effects by a brief stationary cue presented just before the appearance of the moving stimulus; and (vii) the modulatory role of attention on the magnitude of the FLE.

Among the components that forge the present mathematical model, our simulations have shown that the divergent/convergent lateral connections stand up as possibly the most important ingredients of the network. These connections provide the spatial integration of facilitatory and inhibitory inputs that seems to play a crucial role not only in generating those perceptual phenomena themselves but also in providing an important functional substrate for their modulation. The facilitation generated by spatial interactions along the pathway of a moving object can be seen as the root of an incipient mechanism of motion extrapolation (Nijhawan, 1994, 1997, 2002).

However, the facilitatory and inhibitory effects brought about by the divergent connections can only manifest themselves if the neural circuitry is endowed with an appropriate architecture, which allows the integration of neural activity throughout several synaptic stations. This sequential integrative process includes the summation of excitatory and inhibitory inputs over successive processing levels, entailing nonlinear rules (such as exponential leak, intrinsic threshold, and firing behavior).

The existence of a sequence of processing steps naturally includes intrinsic temporal delays not only for the neural activity to proceed from one layer to another (transmission delays) but also for the activity in a given neuron to build-up from a sequence of inputs before reaching its threshold (activation delays). According to our model, these delays can influence not only the magnitude of the FLE but the very nature of the perceptual effect as well, for instance, turning a flash-lag into a flash-lead effect. This conclusion lies at the very core of the differential latencies account (Baldo & Klein, 1995; Murakami, 2001; Patel et al., 2000; Ögmen et al., 2004; Purushothaman et al., 1998; Whitney & Murakami, 1998; Whitney et al., 2000).

Since transmission delays are generally constrained by the characteristic times of synaptic transmission and the axonal speed of action potentials, it is the activation delay the parameter most likely affected by the stimulation environment. In our simulations, variations in the luminance ratio between stationary and moving stimuli ($I_{\text{stat}}/I_{\text{mov}}$) acted upon the activation delays of neurons belonging to the hidden and output layers. Similarly, the pre-activation of neurons in the hidden layer, which mimics a mechanism of attentional facilitation, also decreased the magnitude of the simulated FLE by reducing the activation time of the pre-activated neurons (Baldo & Namba, 2002; Baldo et al., 2002; Namba & Baldo, 2004).

The temporal dynamics inherent to the present model also helps us to realize that its computation does integrate postflash information, predicting that the percept might be changed by a stimulus presented after the flash but before the processing completion (Eagleman & Sejnowski, 2000a, 2000b, 2000c). For instance, a stimulus delivered to the input layer after the presentation of a previous stimulation could be able to catch up with the ongoing neural activity produced by the preceding stimulus and modify it before its perceptual actualization.

In summary, our model points to some components whose role may be dominant in generating the perceptual phenomena under examination. Lateral connections give rise to divergent and convergent inputs that naturally define, for each neuron, a corresponding receptive field. The structured summation over excitatory and inhibitory inputs may lead to both facilitation and suppression of spatial activity: the former seems critical for the emergence of the FLE whereas the latter may contribute to the genesis of the Fröhlich effect. The build-up of the neuronal activity depends on the overall input summation in a given processing level (a layer, in the present model), which is then passed on to a next level by means of nonlinear computation. The time consumed within these transmission and activation processes define temporal latencies that characterize the dynamics of the network. These temporal latencies can be modified by either external (for example, stimulus luminance and eccentricity) or internal factors (attentional deployment) resulting in a modulatory influence on the final perceptual outcome.

Whereas some authors have proposed conceptual, non-mathematical, schemes in agreement with certain findings of the present work (Kirschfeld & Kammer, 1999; Müsseler et al., 2002), other studies have also addressed the mathematical modeling of the FLE (Berry et al., 1999; Erlhagen, 2003; Erlhagen & Jancke, 2004; Krekelberg & Lappe, 2000b; Rao, Eagleman, & Sejnowski, 2001). Berry et al. (1999) complemented their experimental work with a phenomenological model based on a contrast-gain control mechanism, where an effective gain function is convoluted with a spatio-temporal filter.

Their model, being the first attempt to formalize on mathematical grounds the underlying mechanisms responsible for the FLE, was able to explain the advance of the moving stimulus over the flash. Other models were also successful in capturing the essence of the FLE (Erlhagen, 2003; Erlhagen & Jancke, 2004; Krekelberg & Lappe, 2000b; Rao et al., 2001) but, similarly to the approach chosen by Berry et al. (1999), these models also rely on a more global description involving black-box filters and mean field equations. Even though these models represented an important step toward an understanding of the fundamental dynamics underlying the FLE, the present model offers greater simplicity and biological realism. Phenomenological properties necessary for generating the FLE, such as filters and kernels (Berry et al., 1999; Krekelberg & Lappe, 2000b; Rao et al., 2001) or mean field phenomena (Erlhagen, 2003; Erlhagen & Jancke, 2004), should emerge from the collective behavior of interacting realistic units.

Accordingly, an important contribution of the proposed network (due to its greater simplicity) is the possibility to look inside the neural circuitry and search for the fundamental elements that are responsible for the emergence of the FLE and a broad set of related phenomena. Its greater neural realism while still mathematically simple allows us to recognize in a more intuitive way the essential elements underlying the genesis of those perceptual phenomena. In addition, the simplicity of the model makes easier the comparison between observed properties emerging from its simulation and real behaviors observed in experimental approaches, such as those found in electrophysiological recordings. As a further original contribution of the present approach, our model has been able to replicate a variety of empirical designs not addressed by those earlier mathematical attempts, reproducing several experimental findings and helping us see more clearly their underlying mechanisms.

Even though the perceptual details underlying the flash-lag and Fröhlich effects may rely on different internal representations (Kreegipuu & Allik, 2003), the neural network we have studied reveals the gist of these perceptual phenomena in a unifying perspective, bringing them to a more physiologically realistic ground. Our results show that the core not only of the FLE, but also of several other perceptual phenomena, already emerges as a manifestation of collective properties of neurons interacting through quite simple dynamical rules. The strength of this conclusion has been substantiated by additional simulations we have carried out employing, in a similar network architecture, neurons described by the FitzHugh–Nagumo (FHN) model (e.g., Koch, 1998), instead of the simpler leaky LIF neurons here described. In the FHN model, the neurons are defined by coupled first order ordinary differential equations characterizing the continuous evolution of the membrane potential. Although the FHN continuous

model displays quite different features in comparison to the discrete LIF model, it was also able to replicate the standard flash-lag and Fröhlich effects. The coherence we observed when implementing both models points to the dependence of the present findings on more fundamental properties of the underlying network, regardless the minute details or precise arrangement of its structure.

Here, we offer a model that is still crude and provisional and does not address more elaborate experimental results such as those involving multichannel visual patterns (Cai & Schlag, 2001; Nijhawan, 1997; Sheth et al., 2000), crossmodal processing (Alais & Burr, 2003; Schlag et al., 2000) or motor behavior (Nijhawan & Kirschfeld, 2003). Therefore, it should be considered a starting point from which biologically realistic refinements may eventually lead to a broader comprehension of the neural basis of the FLE and related phenomena. However, our approach already points toward clear directions in which the model can be systematically extended by adding ingredients that would bring it closer to the anatomy and physiology of the nervous system. These additional ingredients might include, for instance, feedback connections, multicompartamental neurons, and crossmodal sensory interactions, permitting the computational exploration of a larger perceptual scenario in which the FLE has been empirically observed. Moreover, we should keep in mind that perception has to be understood in the context of adaptive behaviors. Therefore, the present model, still confined to the first stages of sensory processing, is open to be further elaborated to the level of representing action as well. The generality of the FLE could be thus scrutinized not only within perceptual limits but also in the realm of the interactions between perception and action.

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