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Vision Research 44 (2004) 2109–2128
Vision Research
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Differential latencies and the dynamics of the position computation process for moving targets, assessed with the flash-lag effect

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Received 7 November 2003; received in revised form 6 April 2004

Abstract

To investigate the dynamics of the position computation process for a moving object in human vision, we measured the response to a continuous change in position at a constant velocity (ramp-response) using the flash-lag illusion. In this illusion, flashed and moving objects appear spatially offset when their retinal images are physically aligned. The steady-state phase of the ramp-response was probed using the "continuous-motion" (CM) paradigm, in which the motion of the moving object starts long before the occurrence of the flash. To probe the transient phase of the ramp-response, we used the "flash-initiated cycle" (FIC) paradigm, in which the motion of the moving object starts within a short time window around the presentation of the flash. The sampling instant of the ramp-response was varied systematically by changing the luminance or the presentation time of the flashed stimulus. We found that the perceived flash misalignments in the FIC and CM paradigms were approximately equal when sampling of the ramp-response occurred after a relatively long delay from the onset of motion and, were significantly different when sampling of the ramp-response occurred at a relatively short delay. The systematic variations in the perceived misalignment between the moving and flashed stimuli as a function of stimulus parameters are compared to the predictions of our differential latency and to alternative models of position computation.

Keywords: Motion integration; Transient and steady-state phase; Model

1. Introduction

Position is a fundamental aspect of space perception which biological systems must compute accurately in order to interact successfully with the environment. The positions of objects relative to an observer can change frequently as objects and/or the observer moves. A system that must accurately track frequent changes in the positions of objects in the environment with respect to itself needs to carry out its computations rapidly and in real-time. However, signal transmission delays and intrinsic processing latencies in the human visual system put an upper limit on how fast position information can be updated in real-time. For example, assume that visual signals take 40 ms to travel from retina to cortex and that an additional 20 ms is required to compute the position information. A target traveling at 60 km/h will traverse 1 m during this 60 ms time interval. Predictive strategies by either perceptual or motor systems (or both) can be used to reduce the adverse effect of these delays. For example, if a moving target follows a predictable trajectory, the future positions of the moving target can be estimated and the position lag due to internal delays can be compensated. Our ability to interact with rapidly moving objects, such as in catching or hitting a baseball, suggests that with training our *sensorimotor* system is able to overcome the potentially

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doi:10.1016/j.visres.2004.04.003

disastrous effects of delays in the afferent visual pathways (Nijhawan & Kirschfeld, 2003).

Whether our *perceptual* system overcomes the adverse effect of afferent neural delays has been under intense debate. One major focus of this debate is the flash-lag illusion, in which a continuously moving object typically is perceived to lead in space a flashed object when the retinal images of the flashed and the moving object are aligned (e.g., Mackay, 1958; Metzger, 1932; Nijhawan, 1994; Walker & Irion, 1982). Nijhawan (1994) proposed that the perceptual system compensates for the lag that would result from afferent delays by extrapolating the perceived position of objects in predictable motion (extrapolation hypothesis). According to this hypothesis, the afferent delay for a flashed stimulus is not 'compensated' because the sudden and brief nature of the flash makes it unpredictable. The resulting percept is that of the flash lagging spatially behind the moving object. Following Nijhawan's work, the flash-lag illusion and its variants have been used by several researchers to study the position computation process in the human visual system (rev. Krekelberg & Lappe, 2001; Nijhawan, 2002; Whitney, 2002). As we summarize below in Section 7.1, numerous studies provided evidence against the motion extrapolation hypothesis.

In this study, we examine an alternative explanation for the flash-lag effect, viz., the differential latency model, which is an elaboration of the explanation proposed initially by Metzger (1932). We measured the flash-lag effect as a function of relative luminance and relative timing of the moving and the flashed stimuli. The results of our study provide insight into the dynamics of the position computation process of a moving object and are used to evaluate alternative models of the position computation process.

2. The differential latency model and its predictions

Metzger (1932) proposed that a flashed target that is presented in physical alignment with a continuously moving object appears to lag the moving target spatially because the flashed target takes a longer time to reach perception. Several subsequent investigators who observed the flash-lag effect (e.g., Mateeff & Hohnsbein, 1988; Mita, Hironaka, & Koike, 1950; Murakami, 2001a, 2001b; Whitney & Murakami, 1998) provided similar accounts. Our version of the differential latency model differs from other similar models for the flash-lag and related perceptual effects in several important ways. In particular, our differential latency model (Patel, Öğmen, Bedell, & Sampath, 2000; Purushothaman, Patel, Bedell, & Öğmen, 1998) is based on the following fundamental assumptions:

1. In general, flashed and moving stimuli are processed by *different* neural systems (or "channels"). These systems interact to provide a coherent perception of stationary and moving objects.
2. The latency of each processing system, from the onset of the stimulus to the perception that it generates, depends on the intrinsic dynamic properties of that system and on the attributes of the stimulus.
3. The computation of stimulus position and stimulus visibility are different processes with different dynamics.

In order to distinguish our model from other similar models, we will hereafter call our model a multiple-channel differential latency model. The basic components of the model are illustrated in Fig. 1. Before addressing the flash-lag effect specifically, it is important to highlight how the latency between the retinal input and the perceptual output can include a component that is produced by the processing dynamics of the system. To illustrate this point, consider a first-order linear time-invariant (LTI) system defined by the differential equation:

$$\tau \frac{\mathrm{d}y(t)}{\mathrm{d}t} + y(t) = Kx(t), \quad (1)$$

where $x(t)$, $y(t)$, τ, and K are the input, the output, the time-constant that describes the dynamics of the system,

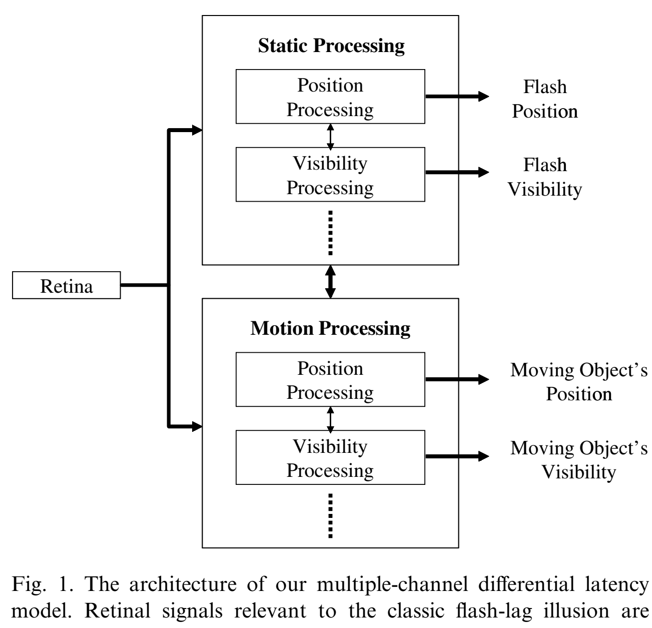

Fig. 1. The architecture of our multiple-channel differential latency model. Retinal signals relevant to the classic flash-lag illusion are concurrently processed by separate visual sub-systems: one sub-system processes static visual stimuli such as a brief flash and the other sub-system processes a moving stimuli such as a continuously rotating line. Within each sub-system, various stimulus attributes such as visibility and position are processed largely by separate modules. The modules within each sub-system and the two sub-systems may interact with each other to ensure that a coherent percept is generated at their outputs.

and the static gain of the system, respectively. In response to a ramp input

$$x(t) = atu(t), \tag{2}$$

where a is a constant that represents the slope of the ramp and $u(t)$ is a step function with unit amplitude, the output or ramp-response is given by

$$y_{\mathrm{ramp}}(t) = Ka(t - \tau + \tau e^{-t/\tau})u(t). \tag{3}$$

This function is plotted in Fig. 2. The *steady-state phase* of the system's response is given by

$$y_{\text{ramp-steady-state}}(t) = Ka(t - \tau)u(t), \tag{4}$$

and the transition from the initial state of the system to the steady-state asymptote is governed by the exponential term in Eq. (3). We refer to this transition as the *transient phase* of the response. As one can see from Eq. (4), if the static gain of the system is not unity ($K \neq 1$), then the ramp-response does not track the input accurately, i.e., the input and the output have different slopes. However, even for a unity-gain system ($K = 1$), at steady state one observes a constant temporal shift equal to the time-constant τ between the input and the output. This lag (or latency difference between the input and the output) is *not* a pure delay but is induced by the dynamics of the system. This simple example shows that latencies in a system's response can arise from its *dynamical properties* in addition to pure delays.

Application of the above results to our model indicates that each component in the model will exhibit a latency that is based on its dynamic properties, in addition to a pure transmission delay. Unfortunately, the dynamics of the position computation process for a moving object, particularly around the initial phase of motion, are largely unknown (but see Krekelberg & Lappe, 2000a; Whitney, Murakami, & Cavanagh, 2000b). In the following paragraph, we discuss how our multiple-channel differential latency model accounts for the classic flash-lag illusion, using a paradigm in which motion of the moving stimulus starts long before the presentation of the flashed stimulus.

The space–time diagram in Fig. 3 depicts the explanation of the flash-lag illusion according to our model. The star-shaped symbol at the origin and the oblique line that passes through the origin represent the flashed and the moving stimuli, respectively. The filled squares show the perceived position of the moving stimulus as a function of time. Here, we show a case in which the position computation process tracks the position of the moving object with a latency of d_{m}. The open circles on the time-axis depict processing of the flash before the flash becomes perceptually visible and the filled circle at $t = L_{\mathrm{f}}$ indicates the instant in time when the flash is initially perceived. If $d_{\mathrm{m}} < L_{\mathrm{f}}$, then at the time instant when the flash becomes visible, it appears to lag in space with respect to the moving object by

$$m = s(L_{\mathrm{f}} - d_{\mathrm{m}}), \tag{5}$$

where s is the speed of the moving object.

Data from a variety of experiments have been found to agree with the predictions of our multiple-channel

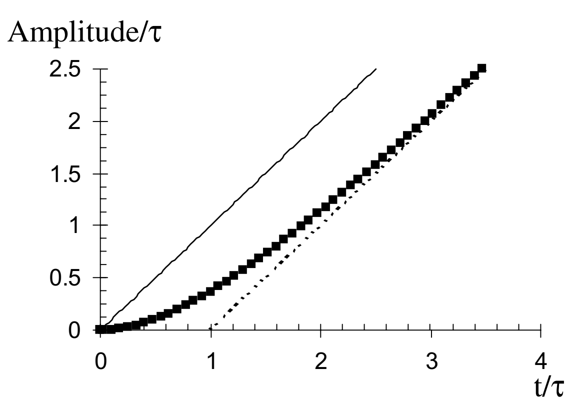

Fig. 2. Ramp-response of a first-order linear time-invariant system with unit static gain. The solid line represents the ramp input and the solid symbols represent the output of the system. The dotted line represents the asymptotic level for the system's output. The purpose of this example is to show that a system can exhibit dynamic delays even when it has no absolute (fixed) delay. The presence of fixed delays would shift the response curve to the right by the delay amount. At $t = 0$, the input and output overlap because there is no fixed delay and because we assumed the initial output to be zero. If we assume a different initial output, the input and output will not overlap at the origin.

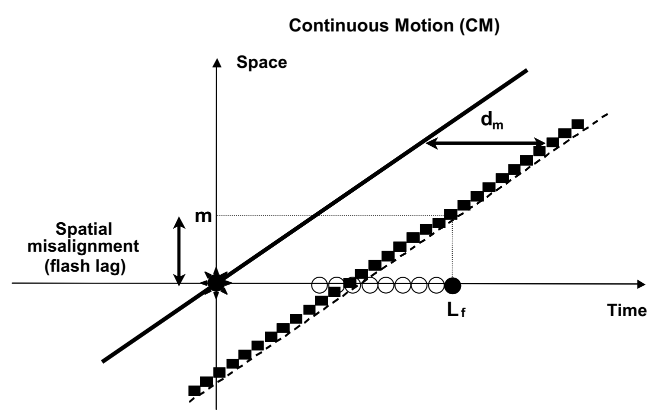

Fig. 3. Depiction of the classic flash-lag illusion according to the multiple-channel differential latency hypothesis. In this illustration, the motion of the moving object had started long before the occurrence of the flashed object. In the space–time diagram, the star-shaped symbol and the line crossing the origin represent the flashed and the moving object, respectively. The filled squares represent the perceived position of the moving object when it is visible. The open circles represent the processing of the flashed object before it becomes visible. The filled circle indicates the time instant at which the flash becomes visible. Symbol m represents the spatial misalignment between the position of the flashed and the moving object at the time when the flashed object becomes visible. L_{f} represents the latency of the flashed object and d_{m} is the latency of the moving object when the position computation process has reached steady state.

differential latency model. One can see from Eq. (5) that if we increase (decrease) the latency of the flash L_f, for example by decreasing (increasing) its detectability (e.g., Cattell, 1886; Mansfield, 1973; Maunsell et al., 1999; Roufs, 1974; Williams & Lit, 1983; Wilson & Anstis, 1969), then the flash-lag is predicted to increase (decrease). Furthermore, when the latency of the flash is short enough such that $L_f < d_m$, our model predicts that the flash-lag should turn into a *flash-lead*. These predictions have been found to agree with data (Purushothaman et al., 1998). If we increase (decrease) the latency of the moving object, d_m, for example by decreasing (increasing) its detectability, then the flash-lag is predicted to decrease (increase). These predictions also agree with data (Lappe & Krekelberg, 1998; Purushothaman et al., 1998). Moreover, according to our formulation, dividing the perceived misalignment by the speed of the moving object yields a perceptual offset in time units that is equal to the differential latency between the moving object and the flash $m/s = L_f - d_m$. Thus, if stimulus speed is changed in a manner such that all other aspects of the stimuli remain the same (to keep L_f and d_m fixed) one should observe a constant perceptual offset in *time units*. This prediction is also supported by data (e.g., Krekelberg & Lappe, 1999, 2001; Nijhawan, 1994).

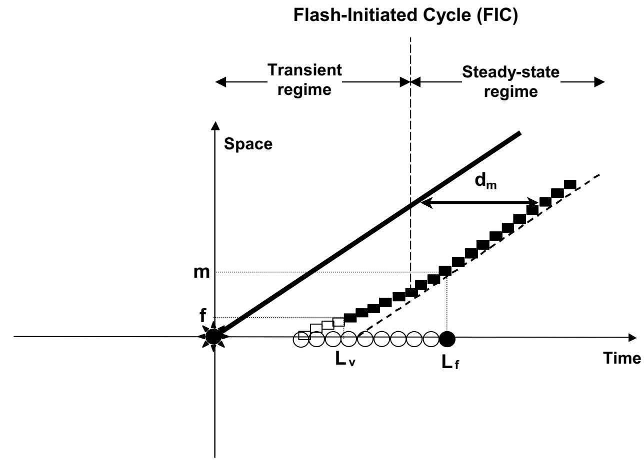

Fig. 4. Space–time diagram depicting the predictions of the multiple-channel differential latency model for the flash-initiated cycle paradigm. In this illustration, the motion of the moving object starts concurrently with the occurrence of the flashed object. In most respect, this figure is identical to Fig. 3. The unfilled squares represent the initial phase of position computation process during which the moving object is not visible. L_v represents the instant at which the moving object first becomes visible. Two distinct regimes of the ramp-response are shown: a *transient regime* in which the perceived position of the moving object is different from the asymptote (dotted line) and a *steady-state regime* in which the perceived position of the moving object is parallel to the asymptote.

3. Characterization of the position computation process using the flash-lag effect

How can one characterize the *complete* dynamics of the position computation process? In the case of a LTI system, the response to an impulse input (i.e., the impulse response) provides a complete description of the system. The experimental characterization of this type of system can therefore be based on the estimation of either the impulse response or its frequency domain transformation (the transfer function), using inputs such as step, ramp, or sinusoidal functions. Although the same types of inputs do not completely characterize a non-LTI system, the responses to these inputs still provide a wealth of information that can be used in modeling the system. Our approach in this paper is to study the ramp-response of the position computation process in order to gain insight into its transient and steady-state dynamics.

An object that moves with a constant velocity provides a ramp-input to the position computation process. The slope of this ramp input is equal to the velocity of the object. In order to measure the output of the position computation process (the perceived position of a moving object), a spatio-temporally localized stimulus (i.e., a briefly flashed thin line) is presented as a reference. The observer judges the perceived position of a moving object with respect to the perceived position of the reference *at the time instant that the reference is perceived*. Consequently, in addition to providing a spatial and temporal reference, the flashed stimulus also allows us to sample the motion system's position output, as illustrated in Fig. 4. In this figure, the perceived misalignment m corresponds to a sample of the ramp-response at the time, $t = L_f$.

In order to characterize the ramp-response of the position computation process, we need to obtain output samples at different time instants. As mentioned in the previous section, perceptual latency varies inversely with stimulus intensity, so that the time instant at which the position computation process is sampled can be changed by varying the luminance of the flash, as shown in Fig. 5A. As the flash luminance increases, its latency decreases and the resulting samples (assessed in terms of the magnitude of perceived misalignment between the flashed and moving objects) correspond to progressively earlier parts of the ramp-response. We will refer to this sampling technique as the "varying-luminance" technique. A second method to shift the sampling instant is to vary the temporal delay between the onset of the motion and the onset of the flash (i.e., the stimulus onset asynchrony, or SOA), as shown in Fig. 5B. We will refer to this second sampling technique as the "shifted-flash" technique. Both of these techniques were used in our study, to generate two independent characterizations of the position computation process.

We used two versions of the ramp input in conjunction with each of the above techniques. In the "contin-

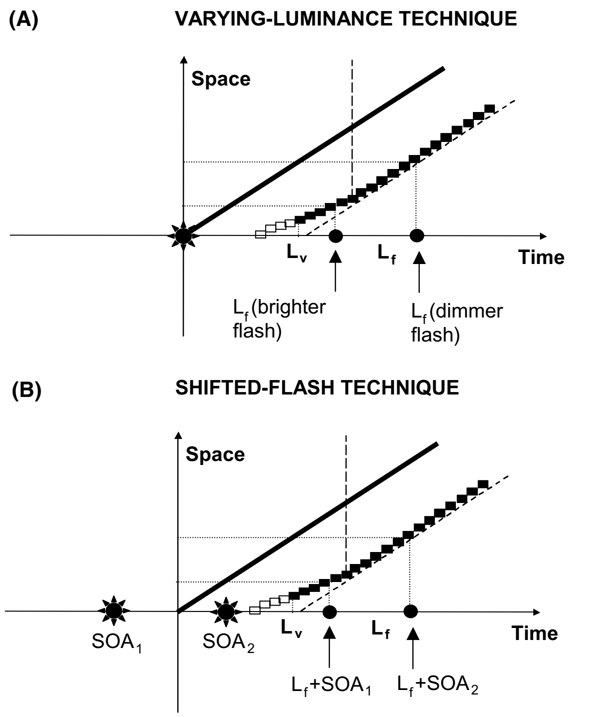

Fig. 5. Space–time diagrams illustrating techniques by which the ramp-response of the position computation process can be sampled in time. A. In the varying-luminance technique, the time instant at which the flashed object is perceived is varied by varying the detectability of the flashed object. B. In the shifted-flash technique, the presentation time of the flashed object relative to the time at which the flashed and the moving object are collinear (SOA), is varied to vary the instant at which the flashed object is perceived. Note that in this example SOA_1 is a negative number.

uous-motion'' (CM) paradigm (e.g., Nijhawan, 1994), the motion of the moving object starts long before the presentation of the flash, thereby allowing the position computation process for the moving object to reach *steady state* (Fig. 3). In the ''flash-initiated cycle'' (FIC) paradigm (Eagleman & Sejnowski, 2000a; Khurana & Nijhawan, 1995) the motion of the moving object starts at the same time instant that the flash is presented (Fig. 4). The results obtained using the FIC paradigm provide information about the *transient phase* of the position computation process when the perception of the flash occurs shortly after the onset of the motion. On the other hand, the results provide information about the *steady-state phase* of position computation when the perception of the flash occurs long after the onset of the motion.

The principal goal of our study was to characterize the transient and steady-state dynamics of the position computation process by measuring its response to ramp inputs. One important constraint in the characterization of the ramp-response by our methods is imposed by the Fröhlich effect. When a moving stimulus is turned on at the instant it starts moving, the spatial location at which it is perceived for the first time is displaced in the direction of motion, an illusion known as the Fröhlich effect (Fröhlich, 1923). In Fig. 4, the unfilled squares represent the initial phase of position computation process during which the moving object is not visible. L_v represents the instant at which the moving object first becomes visible. The position of the moving object at L_v corresponds to the Fröhlich effect. If the perception of the flash occurs before this ''Fröhlich point'', then the ramp-response will not be sampled validly because the observers cannot follow the instruction to match the perceived position of the moving object at the instant that the flash is perceived. Thus, the estimate of the ramp-response is only valid for the part of the response where $t \geqslant L_v$.

The second goal of the study was to experimentally test a critical prediction of our model which is illustrated in Fig. 6. The model predicts that the flash-lags measured in the FIC and CM paradigms should be equal if, in the FIC paradigm the latency of the flash is long enough so that it is perceived during the steady-state phase of the position computation process. On the other hand, if the latency of the flash is short enough for it to be perceived during the transient phase of the position computation process, then our model predicts that flash-lags measured in the FIC and CM paradigms should differ. Data collected previously for two combinations of detectability for the flashed and moving objects support

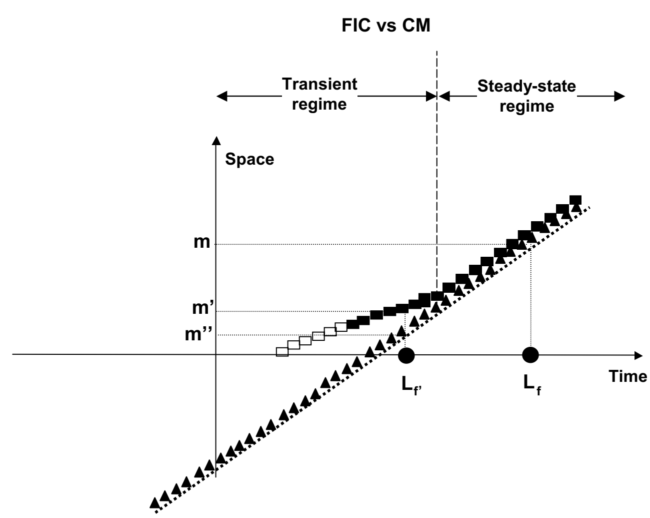

Fig. 6. A comparison of FIC and CM paradigms according to multiple-channel differential latency model. The perceived positions of the moving object in FIC paradigm are shown with filled squares and those in CM paradigm are shown with filled triangles. For simplicity, the stimuli are not shown. If the perception of the flash occurs during the steady-state regime of the position computation process (e.g., $t = L_f$) then FIC and CM paradigms should produce the same perceived misalignment (m). If the perception of the flash occurs during the transient regime of the position computation process (e.g., $t = L_{f'}$) then FIC and CM paradigms should produce different perceived misalignments (m' and m'', respectively).

these predictions (Patel et al., 2000). Here, we evaluate this prediction more systematically by covering a broad range of stimulus detectability values.

Finally, the third goal of this study was to use the data obtained in the FIC and CM paradigms to test alternative models of the position computation process and to evaluate alternative explanations of the flash-lag phenomenon in human vision.

4. Varying-luminance experiments

4.1. Methods

4.1.1. Apparatus and stimulus configuration

The stimulus, diagrammed in Fig. 7, consisted of a rotating line that was straddled by two horizontally aligned flashes, generated by green ultra-bright light-emitting diodes (LEDs). The rotating line was generated on a 19-inch Macintosh computer monitor with 640×480 pixel resolution and 66.6 Hz frame rate. The monitor was placed 200 cm from the observer and provided a background luminance of 0.1 cd/m^2. The rotating line was displayed using the green channel of the monitor so as to provide an approximate match between its color and the color of the LED flashes. The LEDs were mounted on a black rectangular board (16.5×11.5 cm) that contained a 2.35° diameter circular aperture, centered with respect to the rotating line. This board was glued permanently to the face of the computer monitor. Each LED was covered by a black mask with a central pinhole to restrict its angular size to 1.7′. During rotation of the line, the minimum gap between each LED and the end of the line was 17.2′. The luminance of each LED was controlled by an analog signal from a multifunction data acquisition board (MacADIOS, GW Instruments, MA) that was housed in the Macintosh computer. The luminance of each LED was calibrated separately using a photometer (Minolta, LS-100). The analog signals for both LEDs were updated synchronously with the vertical refresh signal for the monitor. The duration of the LED flashes was 1 video frame.

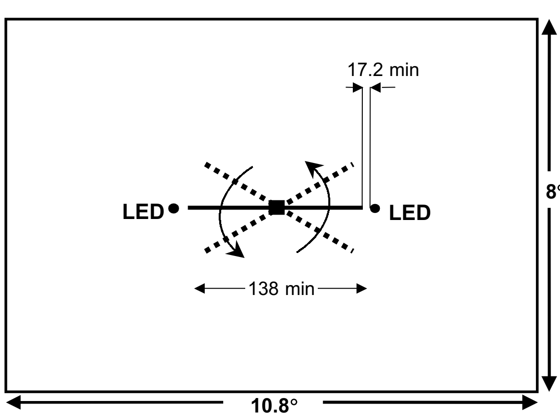

Fig. 7. The stimulus configuration used in our experiments is similar to that used by Nijhawan (1994). A dim fixation target indicated by a black square is presented in the center of a computer monitor. A line rotates in the anticlockwise direction with a constant speed (16.6 rpm) about the center of the fixation target. Two LEDs indicated by black dots straddle the rotating line in the horizontal direction. As indicated by the dotted lines, on various trials the line may appear either spatially ahead or behind the flashes at the time the flashes are perceived.

A head and chin rest were used to minimize head movements. At the start of each trial, an $8.8' \times 8.8'$ fixation rectangle (luminance = 23.8 cd/m^2) was presented at the center of the circular aperture. The rotating line, with dimensions $138' \times 8'$, rotated about the center of the fixation square. The duration of one full (360°) rotation of the line was 240 frames, corresponding to 16.6 revolutions-per-minute (rpm). At this speed, 1° of rotation angle corresponds to a duration of 10 ms. The direction of the rotation was always counter-clockwise. The luminance of the rotating line was set to 2.8 log-units above the average detection threshold (LU) of the three observers. For each observer, the luminance of the paired LED flashes was one of the following six values: 0.2, 0.5, 1, 2, 3, 4 LU above his/her individual detection threshold. Detection thresholds for the rotating line and for the LED flashes were measured separately for each observer in preliminary experiments.

Two of the authors and a naïve observer participated in the experiments. All had normal or corrected-to-normal vision.

4.1.3. Procedures for the continuous-motion (CM) paradigm

Observers were seated in a dark room and were dark-adapted for approximately 10 min at the beginning of each session. The observers were asked to fixate on the square at the center of the circular aperture throughout each trial. A continuously rotating line, centered on the fixation square, was presented 2 s after the onset of the fixation square. The flashes were presented for 15 ms after about one-and-a-half rotations of the rotating line. The rotating line always completed two full (360°) revolutions, and then disappeared. The onset time of the flashes relative to the instant of physical alignment with the rotating line varied randomly from trial to trial according to the method of constant stimuli. A single experimental session consisted of 45 trials (9 relative flash onset times $\times$ 5 times each). On each trial, observers reported with a keypad whether the rotating line was spatially ahead or behind the flashes at the time the flashes were perceived (two alternative forced-choice). When the observer pressed a key, the response was recorded and the next trial started automatically. Twelve sessions were conducted on each subject, to investigate the six different flash luminances, with each of these conditions run twice. The data from each session were used to construct a psychometric function, which plotted the percentage of rotating-line-in-front responses against the relative flash onset time. A cumulative Gaussian was fit to each function, from which the relative flash-onset time corresponding to the 50% level was defined as the perceived *temporal* flash misalignment.

4.1.4. Procedures for the flash-initiated cycle (FIC) paradigm

The experimental task, conditions and parameters were the same as in the CM paradigm, except that the flashes were presented concurrently with the onset of the motion of the rotating line. The initial position of the rotating line changed randomly from trial to trial using the method of constant stimuli. Nine initial positions of the moving line, that straddled the position of physical alignment with the flashes, were used to sample each psychometric function. The initial position of the rotating line with respect to the flashes that corresponded to the 50% level of the psychometric function was defined as the perceived spatial flash misalignment. Depending on the initial position, the duration of the rotating line corresponded to a little less or a little more than one half (180°) rotation. Note that in all the trials of CM and FIC experiments, the final position of the rotating line was always horizontal. In this and the following experiments, for cases where the flash was perceived before the onset of the rotating line, the observers judged the relative position of the *first visible point* of the rotating line with respect to the flash (see Section 3 for a discussion of the Fröhlich effect and how it can influence the results).

4.2. Results

4.2.1. Continuous-motion (CM) paradigm

The top panel in Fig. 8 shows the perceived temporal misalignment between the moving line and the flash as a function of the detectability of the flash in the CM paradigm. The detectability of the flash is plotted in decreasing magnitude along the abscissa in order to reflect the relative latency of the flash as increasing in magnitude. Positive (negative) values of temporal misalignment indicate a flash-lag (flash-lead). The different open symbols represent the data of the individual observers (±1 SEM) and the line indicates the average data across the three observers. The filled symbols show the average misalignment across the three observers in a condition where the detectability of the moving line was set to 0.5 LU above its detection threshold averaged across the three observers. In agreement with previous studies, we observe an increase in the perceived misalignment as the detectability of the flashes decreases

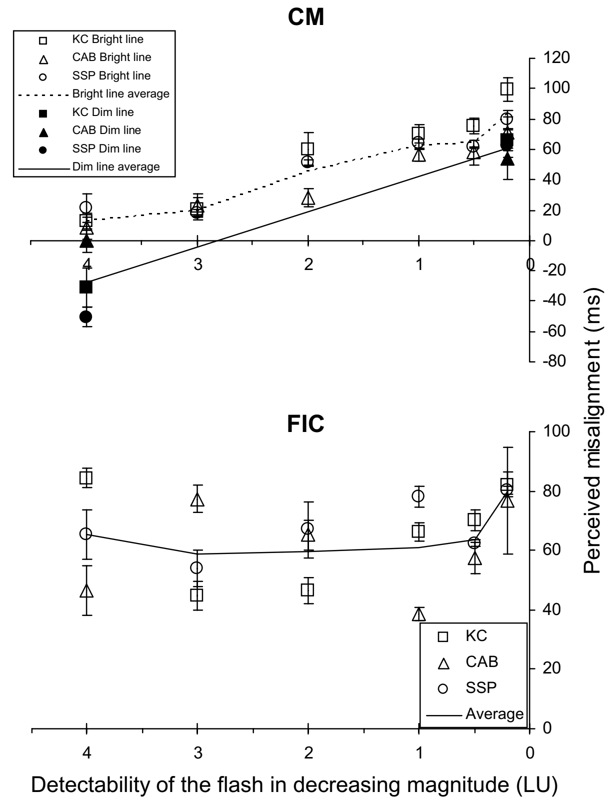

Fig. 8. Perceived misalignment between the moving line and the flash as a function of the detectability of the flash in the continuous-motion (CM; top panel) and the flash-initiated cycle (FIC; bottom panel) paradigms. The detectability of the flashed stimulus is plotted in decreasing magnitude. The perceived misalignments are expressed in temporal units (temporal misalignment = spatial misalignment/speed). Positive (negative) values of misalignment indicate a flash-lag (flash-lead). The data of the individual observers are shown with different open symbols and the average data are indicated by (dashed and solid) lines. The filled symbols in the top panel correspond to data collected with a dim rotating line of detectability 0.5 LU. In this and all other figures, the error bars represent ±1 SEM.

(Purushothaman et al., 1998), an increase in the perceived misalignment as the detectability of the moving line increases (Lappe & Krekelberg, 1998; Purushothaman et al., 1998), and a flash-lead when the detectability of the flash is high and the detectability of the moving line is low (Patel et al., 2000; Purushothaman et al., 1998). All of these findings are in agreement with the predictions of our multiple-channel differential latency model.

4.2.2. Flash-initiated cycle (FIC) paradigm

The lower panel in Fig. 8 shows the perceived misalignment between the moving line and the flash in the FIC paradigm. Flash detectability has different influences on perceived flash misalignment in the FIC and CM conditions. A repeated measures ANOVA (2 conditions × 6 flash detectabilities) indicates a significant effect of flash detectability ($F[5,10] = 10.8$; $p = 0.003$)

and a significant interaction between the flash detectability and condition (FIC/CM) ($F[5, 10] = 5.9$; $p = 0.02$). Unlike the CM paradigm, the perceived misalignment remains relatively constant when the detectability of the flashes is high. We observe an increase in the perceived misalignment, but only for the lowest detectability of the flashes.

4.2.3. Comparison of CM and FIC data

Fig. 9 plots the critical variable from the perspective of modeling the CM and FIC conditions, viz., the difference between the flash misalignments observed in these two paradigms. As predicted by our model, the difference between the flash misalignments in the FIC and CM conditions is approximately zero when the detectability of the flash is low. As outlined in Section 2 above, low flash detectabilities should correspond to a range of relatively long flash latencies for which the position computation process has already reached steady state. In particular, the same perceived flash misalignment is found in the FIC and CM conditions if the detectability of the flashed stimulus is 1.0 LU or less, when the detectability of the moving line is 2.8 LU (Fig. 9). Previously, Khurana and Nijhawan (1995) and Eagleman and Sejnowski (2000a) reported a difference between the flash-lags in the FIC and CM paradigms that was close to zero. Based on the data shown in Fig. 9, their results would be compatible with ours if the detectability of their flashed stimuli (which was not reported in either of these studies) was lower than that of the rotating stimuli by approximately 1.8 LU or more.

Fig. 9 shows also that the difference between the perceived misalignment in FIC and CM paradigms increases as the relative detectability of the flash (i.e., compared to the moving stimulus) increases. When the detectability of the flash is sufficiently high, we observe a substantial difference between the flash-lags obtained in

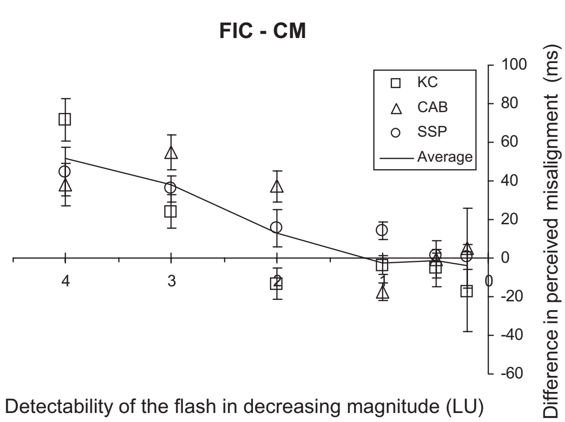

Fig. 9. The difference in the perceived misalignments observed in the FIC (Fig. 8 bottom panel) and CM (Fig. 8 top panel) paradigms as a function of the detectability of the flashed stimulus. The format and conventions of this figure are same as in Fig. 8.

the FIC and CM conditions. According to our model, this difference occurs because the position computation process requires time to reach its steady state and therefore is not expected to produce values equal to the steady-state output instantaneously.

Based on the assumption of transitivity, one could derive a prediction that a continuously moving object will be perceived *briefly* to lag a similar object that just started to move. This prediction assumes that the position computation for the two moving objects occurs independently. On the contrary, it is possible that the position computation process for the second object is influenced by the ongoing position computations within the motion system for the first moving object. Alternatively, in the FIC condition the presence of a nearby flash might influence the time and/or location at which the moving object first becomes visible. In other words, depending on whether or not a flash is present, the moving object may become visible at different times.

5. Shifted-flash experiments

5.1. Methods

The methods and procedures for this experiment were identical to those used in the FIC paradigm of the "varying-luminance experiment" with the following exceptions. The luminance of the flashes was 1 LU and the duration was 1 video frame. In contrast to the FIC condition, the delay between the onset of the moving line and the presentation of the flash (SOA) varied in 30-ms steps from −105 ms (flash occurs before motion onset) to 225 ms (flash occurs after motion onset). On each trial, either the flash or the line was presented first, depending on which SOA was being tested. Only a single SOA was tested in each session. The initial position of the rotating line, relative to physical alignment with the flash, changed randomly from trial to trial. Twenty-four sessions (12 SOAs × 2 times each) were conducted for each observer. For each SOA, the point of spatial subjective alignment (PSA) was specified as the initial position of the moving line in rotation angle with respect to the flash that corresponded to 50% "moving-line-in-front" responses on the psychometric function. Division of these spatial PSAs by the angular velocity of the moving line (1°/10 ms) converted these spatial PSAs to temporal misalignments, in ms.

5.2. Results

Fig. 10 shows the PSA between the moving line and the flash in rotation angle as a function of SOA. For comparison, the filled symbols at SOA = 0 ms show the perceived misalignments obtained in the FIC condition of the varying-luminance experiments when the detect-

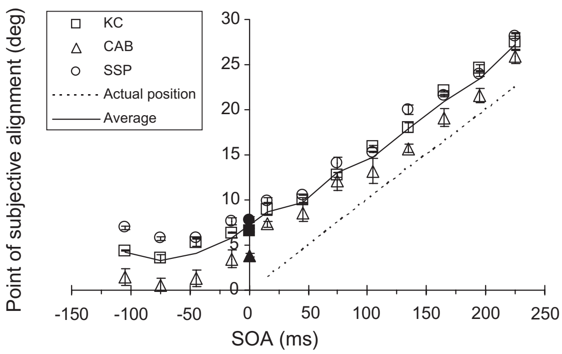

Fig. 10. The point of subjective alignment (PSA) between the moving line and the flash in degrees of rotation as a function of SOA in the shifted-flash paradigm. The dashed line indicates the actual position of the moving line. The data of the individual observers are shown with different open symbols and the average data are indicated by the black line. The filled symbols at SOA = 0 ms show the perceived misalignments obtained in the FIC condition of the varying-luminance experiments when the detectability of the flash was 1 LU.

ability of the flash was 1 LU. Note that these filled symbols are close to the values of spatial misalignment that were measured in the shifted-flash experiments for SOAs = −15 and +15 ms. When the SOAs are positive and large, we expect the flash to be perceived during the steady-state phase of the position computation process for the moving line. If so, then these data points should run parallel to the line that describes the physical position of the stimulus. Indeed, for SOA values greater than approximately +75 to +105 ms, the perceived misalignment does parallel the physical position of the stimulus (the dotted diagonal line in Fig. 10). As the SOA decreases, we expect a transition from the steady-state to the transient regime of the position computation process. Indeed, for SOAs less than approximately +75 to +100 ms the perceived misalignments deviate from parallelism with the diagonal stimulus line and levels off at a "minimum value". We interpret this minimum PSA value as a combination of two factors: First, as mentioned in Section 3, estimates taken before the Fröhlich point are likely to be set equal to the Fröhlich point. Second, the dynamics of the position computation process could also contribute to the PSAs obtained in relatively flat part of the curves (see for example the initial "flat" part of the response shown in Fig. 2).

Previously, Eagleman and Sejnowski (2000a) used the shifted-flash technique (with non-positive SOAs only) but instructed their observers to adjust the position of a flashed pointer line "to point to the *beginning of the trajectory*" (italics added) of the moving target, i.e., to the spatial position at which the moving target first became visible. As a result, they measured the position of the flashed target, not relative to the position of the moving target at the time the flash was perceived, but rather relative to the *initial visible point of the moving target's trajectory* (i.e., the Fröhlich point). As predicted by our model, they found that the perceived misalignment was independent of the SOA in the range that they used in their experiment (from −53 to 0 ms). In our experiments, the observers were instructed to judge the relative position of the moving line with respect to the flash at the instant the flash was perceived. As a result, we observe a systematic dependence of perceived misalignments on SOA, for SOA values larger than about −45 ms.

The vertical difference between the measured PSAs (data points in Fig. 10) and the physical position of the moving line (dotted line in Fig. 10) gives the magnitude of perceived misalignment between the flashed and the moving target. These perceived misalignments are converted from spatial to temporal units and plotted as a function of SOA in Fig. 11. For comparison, the perceived temporal misalignments obtained in the CM condition of the varying-luminance experiment are plotted as filled symbols at the right of the plot. As the SOA becomes large, sampling occurs during the steady-state phase of the position computation process and the perceived misalignment reaches a relatively constant value, which indicates that the position computation process tracks the input with a stable latency. In particular, note that the values of temporal misalignment obtained in the varying-luminance experiment (measured approximately 5.4 s after the onset of the moving line) agree with the steady-state misalignment values that were determined in the shifted-flash experiment. At small negative SOAs, we observe a significant increase in the perceived misalignments that are measured in the shifted-flash condition. At small SOAs, perception of the flash should occur more and more during the transient phase of the position computation process.

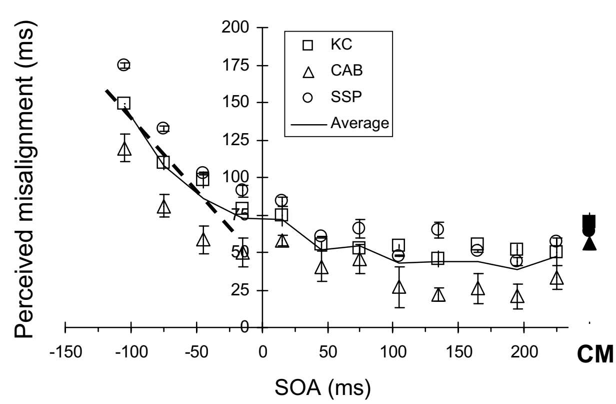

Fig. 11. The perceived misalignment between the flashed and the moving stimuli computed from the data of Fig. 10 by subtracting the actual position of the moving line (dashed line) from point of subjective alignment between the moving line and the flash. The differences are expressed in temporal units as in Figs. 8 and 9. For comparison, the filled symbols at the right of the plots show the perceived temporal misalignments obtained in the CM condition of the varying-luminance experiment. The conventions of this figure are same as in Fig. 10.

Consequently, we interpret the relatively large misalignments for small SOAs as the characterization of the transient dynamics, viz., the transition from the initial state of the position computation process to its steady-state asymptote. At large negative SOAs, the data fall close to a line with a slope of −1 which corresponds to the flat region of the data in Fig 10. As already noted above, the data obtained at large negative SOAs should yield the misalignments that can be predicted from the Fröhlich effect. In Fig. 11, we estimate the beginning of the transient phase of the position computation process as the time when the temporal misalignment data first deviate from a slope of −1. A conservative estimate of this time is approximately −15 ms.

Note that one can measure independently the SOA at which the flash and the moving line cease to appear simultaneous by a temporal-order judgment. Similarly, the Fröhlich point can be measured based on a purely spatial judgment. However, as we argue in this paper and elsewhere (Bedell, Chung, Öğmen, & Patel, 2003), these different estimates of the seemingly same phenomenon are likely to be different, because changing the task can cause the observer to use different neural signals to make these perceptual judgments. The deviations from theoretical asymptotes as discussed above, as well as the qualitative agreement from the varying-luminance experiments, as discussed in Section 6, provide evidence based on the *same* experimental task. Nevertheless, we measured the point of subjective simultaneity (PSS) between a 1 LU flash and the onset of motion of a 2.8 LU line (e.g., FIC paradigm) for our three observers and found the average PSS to be -78 ± 17 ms. In this control experiment, observers judged whether the flash was perceived before or after the moving line became visible, a task that is substantially different than the spatial localization task used in the main experiment. Regardless of how accurately the PSS judgments map onto judgments of spatial localization, this substantially negative value indicates that there is a differential latency between the visibilities of the flash and the moving object.

A similar argument can be applied to address the question whether the approximately constant lag for flashes with detectabilities of 4–1 LU in the FIC condition of the varying-luminance experiments (Fig. 8, bottom panel) occurs because these flashes are perceived before the moving object is visible. As mentioned above, the average PSS between a 1 LU flash and the onset of a 2.8 LU moving object is approximately −80 ms. Based on the data from the CM condition (Fig. 8, top panel), the flash-lag decreases by approximately 60 ms when the detectability of the flash decreases from 4 to 1 LU. From this result, we can infer that the PSS for a 4 LU flash would be approximately −20 ms. We can therefore conclude that none of the flashes that we presented in our FIC experiment are perceived before the moving object is visible. As we made no a priori assumptions about the dynamics of the position computation process in the transient regime, our finding of a constant flash-lag for flash detectabilities between 4 and 1 LU in the FIC condition of the varying-luminance experiment can be interpreted as a slow dynamic process around the initial motion trajectory.

In a study by Müsseler, Stork, and Kerzel (2002), a flashed stimulus was presented either at the onset of motion, at the offset of motion, or midway between the start and the end of motion. When the observers judged the position of the moving object at the instant that the flash was presented, a flash-lag was present in the motion-onset condition, a smaller flash-lag occurred in the midway condition, and a spatial flash-lead was found in the motion-offset condition. Quantitatively, all of the misalignments reported by Müsseler et al. (2002) were within +10 and −5 ms, which may differ from the values that we obtained because of differences in the stimulus parameters. However, in qualitative agreement with their findings, we find larger misalignments at or near SOA = 0 ms (motion-onset condition) when compared to misalignments near SOA = 135 ms (their midway condition). As mentioned above, these findings can be accounted for by our model if we assume that the flash in the motion-onset condition is perceived during the transient phase of the position computation process.

The predictions of our model for the motion-offset condition are based on the nature of the offset transient as well as on the time at which the flash is perceived relative to the offset transient. A small spatial flash-lead in the motion-offset condition (Müsseler et al., 2002) is consistent with our model because a transient phase of position computation should occur at the offset of motion. If we assume that at motion offset the position signal decays gradually to its last input value as depicted in Fig. 12, then our model predicts a small spatial flash-lead in the offset condition when the flash is used as a temporal reference. On the other hand, if the flash is perceived to occur when the position signal of the moving object has already decayed to its last input value, the predicted flash misalignment is close to zero, as reported by Nijhawan (1992) and Eagleman and Sejnowski (2000a). The observation that a moving object is perceived to occupy a position *ahead* of its terminal position (e.g., representational momentum; Fu, Shen, & Dan, 2001; Whitaker, Pearson, McGraw, & Banford, 1998) can be explained by our model if the position signal overshoots (e.g., second-order under-damped response) during its decay back to the terminal stimulus position.

When Müsseler et al. (2002) asked their observers to ignore the flash and judge the position of the moving target at its onset and at its offset, the perceived "misalignment" was reduced significantly in the motion-onset condition and was not significantly different from zero at the motion-offset condition. Note that for these condi-

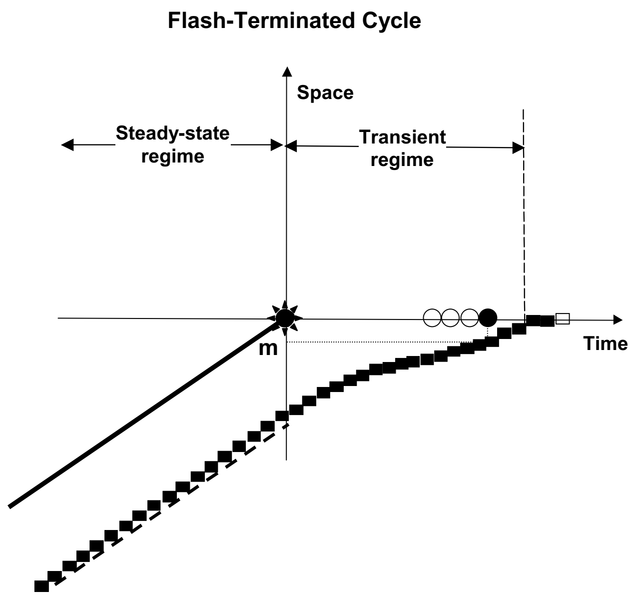

Fig. 12. In the flash-terminated cycle (FTC) paradigm, the flashed stimulus is presented concurrently with the cessation of the motion. In this example, the dynamics of position computation process at motion offset are shown as a simple monotonic decay to the final position of the moving object. If the observers are asked to judge the perceived position of the moving target when the flash is perceived, a spatial flash-lead equal to *m* is predicted if the flash is perceived during the transient regime of the position computation process. When the observers are asked to judge the final position of the moving target, they would use the last visible point, which in this example produces a zero misalignment error. If the visibility of the moving object ends before the final stimulus position is processed, then a spatial flash-lead would also be perceived. The transient regime for the position computation process near the time of motion offset can be quantified by applying the methods used in the paper to the FTC paradigm.

tions, the "misalignment" refers to the difference between the spatial position of the moving stimulus and its perceived position when the moving stimulus becomes visible or invisible for the first time. The change in perceived misalignment in the motion-onset condition that depends on whether the judgment is made with respect to the flash or with respect to the first position of the moving target can be explained by our model by considering that the former criterion measures the flash-lag (m in Fig. 4) whereas the latter criterion measures the Fröhlich effect (f in Fig. 4, which is smaller than m), as discussed above in the context of Eagleman and Sejnowski's (2000a) experiment. For the condition in which the observers ignored the flash, we interpret the lack of misalignment at motion offset to indicate that the moving stimulus becomes invisible at its final physical position.

6. Summary of experimental findings

Overall, the results from the shifted-flash experiments shown in Fig. 11 provide an estimate of the ramp-response for the position computation process. The steady-state asymptotic behavior that was seen in the shifted-flash experiments for large values of SOA (Figs. 10 and 11) agrees with the flash misalignment obtained using the CM paradigm in the varying-luminance experiments (Fig. 8, top panel). The results of the FIC paradigm in the varying-luminance experiment provide information about the transient (steady-state) regime, when the flash detectability is high (low). Qualitatively, because high detectabilities of the flash correspond to small SOA values (cf. Fig. 5A and B), the constant flash misalignment in the varying-luminance FIC paradigm (the flat part of the data in the bottom panel of Fig. 8) is compatible with the constant PSA in the shifted-flash paradigm (the flat part of the data in Fig. 10). The presence of a separate transient regime is confirmed by the significantly different outcomes of the FIC and CM paradigms in the varying-luminance experiment (non-zero values in Fig. 9). In the shifted-flash experiment, the presence of the transient regime is shown by the departure of the PSAs from parallelism with the moving target's trajectory (see Fig. 10). When the PSA values in Fig. 10 are converted to temporal flash misalignments (Fig. 11), this departure from parallelism is transformed to a deviation from the horizontal asymptote. Thus, the horizontal asymptotes in Figs. 9 and 11 theoretically indicate the steady-state regime. Consequently, the qualitatively similar shapes of the functions observed in Figs. 9 and 11 demonstrate agreement about the transition from a transient to a steady-state regime of position computation using two different psychophysical techniques.

7. Discussion: position computation models

In this section we will review several models proposed either to account for the flash-lag illusion or more generally for the position computation process in human vision. When applicable, we will use the data presented in the previous sections to evaluate the models.

7.1. Lag-compensation through extrapolation

According to this model, to compensate for delays of signal transmission, the perceptual system extrapolates the perceived position of moving objects whose trajectories are predictable (Nijhawan, 1994). We will consider two versions of this model and show that a wide-range of empirical evidence contradicts the predictions of both versions. In the first version, lag-compensation is accurate and the extrapolated trajectory of the moving line coincides with its physical trajectory (the "exact-extrapolation" model). In the second version, a compensation error is introduced so that the extrapolated trajectory of the moving line does not match exactly the physical trajectory (the "approximate-extrapolation" model). Clearly, the extrapolation error has to be small for the lag-compensation to have any practical significance.

(1) Assume that the latency of the flash is reduced, for example by increasing its luminance, while keeping the latency of the moving target fixed. The exact-extrapolation model predicts that the flash-lag will decrease with increasing luminance of the flash but can never become negative (i.e., a flash-lead). On the other hand, the approximate-extrapolation model predicts that a flash-lead can be observed. The value of the flash-lead puts a lower bound on the extrapolation error. The data shown in Fig. 8 as well as prior findings (Purushothaman et al., 1998) show that increasing the luminance of the flashes can change the flash-lag to a flash-lead as large as 40 ms. This finding contradicts the exact-extrapolation model and shows that the lower bound of the extrapolation error can be as high as 40 ms.
(2) Assume that the latency of the moving line is reduced, for example by increasing its luminance, while keeping the latency of the flash fixed. Since the latency of the flash is not changing, according to the exact-extrapolation model the flash-lag should remain constant. However, prior findings (Lappe & Krekelberg, 1998; Purushothaman et al., 1998) show that the flash-lag increases as the luminance of the moving target is increased. The approximate-extrapolation model could account for such an outcome by positing an additional hypothesis, i.e., that the extrapolation error becomes smaller as line luminance increases. However, a quantitative analysis of the data in Purushothaman et al. (1998) indicates that the minimum extrapolation error can be as large as 120 ms.
(3) According to the extrapolation model, unpredictable changes that occur in the trajectory of the moving line should result in "overshoot errors" in the position estimates. However, experiments with unpredictable changes in the direction (Eagleman & Sejnowski, 2000a; Whitney, Cavanagh, & Murakami, 2000a; Whitney & Murakami, 1998; Whitney et al., 2000b), and the speed—including sudden disappearance—(Baldo, Kihara, Namba, & Klein, 2002; Brenner & Smeets, 2000; Eagleman & Sejnowski, 2000a; Nijhawan, 1992; Whitney et al., 2000b) of the moving target all provided evidence against this prediction.
(4) According to the extrapolation model, the flash-lag effect occurs because the motion of the moving object is predictable and should therefore disappear if the motion is unpredictable. Contrary to this prediction, Murakami (2001a) showed a temporal flash-lag of approximately 60 ms when the path of the moving object is random.

Overall, given this large body of contradictory evidence, the lag-compensation through extrapolation model appears untenable.

7.2. Stimulus-triggered computation

7.2.1. Approaches based on the stimulus-triggered update of internal-models

Mackay (1958) proposed that the perceptual system uses an internal 'model' (in Mackay's terminology, an "internal state of organization, which implicitly represents the perceived world") and that this internal 'model' is updated only when the evidence for the occurrence of a change in the external world reaches a certain threshold level. In Mackay's (1958) observations, the stimuli consisted of stroboscopically lit and self-luminous objects and retinal motion was induced by externally moving the eyeball. Externally induced movement of the eyeball causes static objects to appear to be moving in the opposite direction of the eye's movement. Mackay (1958) reported that the "stroboscopically lit field is seen to move sluggishly to 'catch up' with the self-luminous objects, requiring several flashes to do so". In this paradigm, both the stroboscopically and continuously lit objects move on the retina; however the updated positions of the continuously lit objects are available continuously whereas the updated positions of the stroboscopically lit objects (i.e., flashed targets) are available only intermittently, during brief time intervals. According to Mackay's hypothesis, the positions of the continuously lit objects are updated as soon as the continuous stream of positional information reaches a critical level. However, for the stroboscopically lit objects, the positional update is delayed until sufficient evidence for positional change is obtained from several brief presentations. As a result, the stroboscopically lit (flashed) objects appear to lag behind the continuously lit (moving) objects.

The stimulus paradigm used by Mackay is similar to the one used by Krekelberg and Lappe (see Section 7.3) but differs from the paradigm used in most other studies of flash-lag, in which the flashed object does *not* move on the retina. Nevertheless, Mackay's hypothesis can explain the flash-lag effect for stationary flashes as follows: For the continuously moving object, continuous information is received by the visual system about changes in position and the visual system continuously updates the position of the moving target. For the flashed target, it will take a certain amount of time before the perceptual system detects a change (the appearance of the flash). During this time the position of the moving object would be updated to the locations it occupies *after* the presentation of the flash. As a result, the flash would appear to lag behind the moving target. However, this model would predict overshoots when the moving target suddenly changes its features, for the "conservative null assumption" (Mackay, 1958) would be the maintenance of the moving target's characteristics *until* the change is detected. As a result, this model is contradicted by the data cited in item (3) in Section 7.1.

Eagleman and Sejnowski (2000a) proposed a variant of this model that they called the postdiction model. According to this model, the visual system maintains an internal 'model' of the moving target, which dictates the perceived positions of the target. The occurrence of the flash signals a change in the external environment which in turn causes a re-assessment of the internal 'model'. In the original version of the model, Eagleman and Sejnowski (2000a) proposed that "the flash resets motion integration in the visual system, making motion after the flash effectively like motion that starts de novo". A temporally weighted spatial average of the positions occupied by the moving target *after* the flash is "postdicted" as the position of the moving target at the time of the presentation of the flash. [1] The predictions of this model include the following:

(1) In general, the trajectory of the moving object *before* the presentation of the flash should have no effect on the magnitude of the flash-lag illusion. In particular, the flash-lags observed in the CM and FIC paradigms should be equal. Eagleman and Sejnowski (2000a) tested this prediction by comparing the FIC paradigm to variants of the CM paradigm and, in support of their prediction, found the same magnitude of flash-lag. As mentioned above, the data of Khurana and Nijhawan (1995) appear to provide additional supporting evidence. However, in contradiction to this prediction, the results of the onset (i.e., FIC) and midway (i.e., CM) conditions in the study by Müsseler et al. (2002) show a small but a significant difference (see Section 5.2). Earlier, Patel et al. (2000) found significantly different magnitudes of flash-lag using FIC and CM paradigms for one combination of stimulus parameters. As shown above in Fig. 9, the predicted equality holds only when relative flash visibility is low. The significant differences found between FIC and CM when the flash visibility is increased (Fig. 9) provide evidence against this model. Furthermore, recently Chappell and Hine (2004) showed that if a target remains static for a period of time and starts moving concurrently with the presentation of a flash, the magnitude of the flash-lag decreases as the "pre-movement" exposure duration increases. Again, this shows that events occurring before the flash can influence the magnitude of the flash-lag.

(2) If the perceived position of the moving line is computed as a weighted average of positions occupied by the moving line *after* the flash, then the flash can never lead the moving line. Contrary to this prediction, the data in Fig. 8 as well as in our previous reports (Patel et al., 2000; Purushothaman et al., 1998) show that a flash-lead is possible in the CM condition.

(3) If the perceived position of the moving line is computed as a weighted average of positions occupied by the moving line *after* the flash, then the flash-lag in the shifted-flash experiment should be independent of the SOA. As mentioned in Section 5.2, Eagleman and Sejnowski (2000a) attempted to test this prediction by asking their observers to match position of the flashed stimulus to the *beginning of the trajectory* of the moving target. The matched positions were independent of SOA. However, their measures are more likely to correspond to the Fröhlich effect than to the flash-lag effect (Patel et al., 2000; Whitney & Cavanagh, 2000). Contrary to the prediction of the postdiction model, the data in Figs. 10 and 11 show a strong dependence on SOA when the observers are asked to judge the relative position of the moving line with respect to the flash, at the instant the flash is perceived. Moreover, Whitney and Cavanagh (2000) showed that a stationary cue reduced strongly the Fröhlich effect but not the flash-lag effect, providing against Eagleman and Sejnowski's (2000a) claim that the Fröhlich effect and the flash-lag effect are two expressions of the same phenomenon.

Eagleman and Sejnowski (2000b) proposed an expanded version of their model, in which a change in the environment does not completely reset the internal 'model'. Rather "the amount of information discarded will likely be graded and will depend on the salience of the transient stimulus: The greater the surprise, the less the internal 'model' is relied upon" (Eagleman & Sejnowski, 2000b). The aforementioned predictions can be reformulated for this new model as follows:

(1′) The trajectory of the moving object *before* the presentation of the flash should have less and less effect on the magnitude of the flash-lag as the transient stimulus becomes more salient. In particular the flash-lags observed in the CM and FIC paradigms should become more and more similar as the transient stimulus becomes more salient. Our findings in the varying-luminance paradigm are opposite to this prediction: As the detectability of the flash (and therefore the salience of the transient stimulus)

[1] Note that the authors do not make a clear distinction between the presentation time of the flash and the time at which it is perceived.

is increased, the flash-lags observed in the CM and FIC paradigms become more and more dissimilar (see Fig. 9 and note that the detectability of the flash is plotted in decreasing magnitude).

(2′) A flash-lead is possible when the "internal 'model' is more resistant to devaluation, such that more pre-flash information is carried over into the interpolated (postdictive) position estimation" (Eagleman & Sejnowski, 2000b). The internal model is devalued less when the salience of the transient stimulus is less. This would predict that, other parameters being identical, reducing the detectability (and therefore the salience) of the flash should lead to a flash-lead. Again, our data in Fig. 8 (note that the detectability of the flash is plotted in decreasing magnitude) and in Purushothaman et al. (1998) are in contradiction with this prediction. Reducing the detectability of the flash *increases* the flash-lag and increasing the detectability of the flash produces a flash-lead.

(3′) The prediction that the flash-lag in the shifted-flash experiment should be independent of SOA remains unchanged, as the salience of the flash remains constant in this experiment.

Overall, both the original and modified versions of the Eagleman and Sejnowski's model have difficulties in explaining empirical data. Although averaging and stimulus salience play a role in perceived misalignments, the idea of postdiction for position computation does not appear to have any empirical support when a broad range of parameter space is taken into account.

7.2.2. Approaches based on stimulus-triggered sampling of neural activities

Baldo and Klein (1995) proposed that the flash-lag effect results from a longer delay involved in the processing of the flash compared to the moving stimulus and suggested that this additional delay could be the result of the time required to capture or to shift attention so as to take a "snapshot" of the moving stimulus. This idea that the flash triggers a process whereby the position of the moving target is sampled was also proposed by Brenner and Smeets (2000). Furthermore, Cai and Schlag suggested that the sampling of a continuous stream of positions is also accompanied by a feedback process of (asynchronous) feature binding (Cai, 2003; Cai & Schlag, 2001).

Although some studies showed that attention *can* modulate the flash-lag illusion (Baldo & Klein, 1995; Baldo et al., 2002; Eagleman & Sejnowski, 2000b), others did not find any significant effect of attention on the flash-lag illusion (Khurana & Nijhawan, 1995; Khurana, Watanabe, & Nijhawan, 2000). Taken together, these results lead to the interpretation that delays generated by attentional/sampling shifts can be viewed as modulatory components that supplement those generated by lower-level sensory processing stages (Baldo et al., 2002). However, an explanation based *solely* on stimulus-triggered attentional/sampling shifts cannot explain the flash-lag effect, for these models also make the predictions discussed in items (1) and (2) in Section 7.2.1. These models cannot explain the dependence of flash-lag on the luminance of the moving target (Fig. 8 top panel; Lappe & Krekelberg, 1998; Purushothaman et al., 1998) without postulating additional mechanisms according to which the speed of attentional/sampling shifts would be a function of line luminance over a range of at least 2 LU.

7.3. Position persistence model

Walker and Irion (1982) proposed that the flash-lag illusion is attributable to a protracted visible persistence of the flashed stimulus. They favored the visible persistence model because they interpreted their data to be inconsistent with the differential latency model. However, as discussed in Section 7.4, their data are not inconsistent with the differential latency model. Further, more recent research showed that visible persistence does not appear to play a significant role in the flash-lag effect (Baldo et al., 2002; Whitney et al., 2000b). A model proposed by Krekelberg and Lappe (Krekelberg, 2001; Krekelberg & Lappe, 1999, 2000a, 2000b, 2001; Lappe & Krekelberg, 1998) is based on the persistence of a position signal after the offset of the stimulus, which is distinct from visible persistence. According to this model, the position of a target is based on a temporal average of this putative position signal. When a flash is presented, it generates a position signal that persists for some time at the location of the flash. During this time, the moving target occupies positions ahead of the flash. When averaged, the position of the moving target appears ahead of the flash. Krekelberg and Lappe estimated the persistence and averaging times to be in the order of 180 and 600 ms, respectively.

This model is similar to the original postdiction model (Eagleman & Sejnowski, 2000a) that was discussed in Section 7.2.1 in that both models posit that the flash-lag is a function of the average of positions occupied by the moving target *after* the flash. However, the position persistence model does not use a "reset" mechanism and it does not assume that the perceived positions are postdicted backward in time (Krekelberg & Lappe, 2000b). For the basic flash-lag experiments, this model makes the predictions (1) and (2) discussed in Section 7.2.1 and a modified version of prediction (3) as follows:

> If the perceived position of the moving line is computed as a weighted average of positions occupied by the moving line *after* the flash, then the flash-lag

in the shifted-flash experiment should be independent of SOA for positive SOAs and should decrease for negative SOAs. Our data in Fig. 10 stand in contradiction to both aspects of this prediction.

This model played an important role in highlighting the role of averaging in position computation. However the lack of a distinction between specialized systems to process the moving and the flashed stimuli and their differential latencies leads to qualitative and quantitative difficulties in explaining the flash-lag data.

7.4. Challenges for the differential latency models

The notion that the flash-lag phenomenon can be explained by the differential latencies of flashed and moving targets goes at least back to Metzger (1931, as cited in Mateeff & Hohnsbein, 1988). More recently, as discussed in Section 7.2.2, Baldo and Klein (1995) proposed that the flash-lag effect results from a longer delay involved in the processing of the flash compared to the moving stimulus and suggested that this additional delay could be the result of attentional mechanisms in addition to perceptual mechanisms. Whitney et al. (2000b) proposed a first-order LTI system, as described in Eq. (1), with unit static gain, a time-constant of 50 ms, and an additional pure delay. They suggested that the latency advantage of moving targets over flashed targets originates from a mechanism of temporal facilitation. Bachmann and Põder (2001) attribute the temporal facilitation for an item in a continuous stream to a perceptual "retouch" mechanism carried out by a nonspecific and slow thalamic signal.

In explaining his flash-lag data for random motion (Murakami, 2001a, 2001b); Murakami (2001b) concluded that, on average, observers compare the position of a moving object with the position of a flash that was presented approximately 60 ms earlier. However, Murakami's flash-lag data (2001a, 2001b) show substantial temporal variability. According to our multiple-channel differential latency model, at least part of this temporal variability can be attributed to the range of the temporally integrated motion signals in his experiment. Specifically, at various times within a random motion sequence, the instantaneous motion signal can be (1) continuous in one direction, (2) reversing in direction, or (3) approximately zero, when the random position steps exceed the value of $D_{\max}$. Clearly, the magnitude and direction of flash-lag would be expected to differ for these conditions (e.g., Whitney et al., 2000b). For example, a flash that reaches perception concurrently with a continuous motion signal requires the comparison of position signals in the static and motion systems. On the other hand, a flash that reaches perception when the motion signal is instantaneously zero may involve a comparison of two position signals in the static system (see Fig. 1).

Our multiple-channel differential latency model (Patel et al., 2000; Purushothaman et al., 1998) has already been outlined in Section 2. In this section, we will address data that have been interpreted in the literature to contradict the differential latency model.

(1) Walker and Irion (1982) tested the differential latency hypothesis by changing jointly the luminance of the moving target and the background. They suggested that in one of their experiments the flash-lag increased as the luminance of the moving target was reduced, apparently in contradiction with the prediction of the differential latency hypothesis. However, as they decreased the background luminance simultaneously with the luminance of the moving target, the ratio of the luminances and hence the detectability of the moving target should have remained almost constant. In such a case, our differential latency hypothesis would predict a nearly constant flash-lag. Indeed, their data indicate a maximum flash-lag difference between any two moving target's luminance conditions of about 10 ms. More recent data (Lappe & Krekelberg, 1998; Purushothaman et al., 1998) as well as data in this manuscript show systematic effects of luminance on the flash-lag effect as predicted by the differential latency hypothesis.

(2) Eagleman and Sejnowski (2000a, 2002) argued that their shifted-flash experiment provides evidence against the differential latency hypothesis because, according to the differential latency-hypothesis, changing the timing of the flash should modulate the perceived misalignment. As argued in Krekelberg and Lappe (2002), Patel et al. (2000), Whitney and Cavanagh (2000) as well as in Section 5.2, Eagleman and Sejnowski's (2000a) experiment most likely measured the Fröhlich effect and not the flash-lag effect. The results of our shifted-flash experiments show a clear dependence of flash-lag on SOA, as predicted by the differential latency hypothesis. We already addressed in Patel et al. (2000) how the differential latency model can account for all the data presented in Eagleman and Sejnowski (2000a).

(3) It has been suggested that according to the differential latency hypothesis, if the perception of the flash is delayed with respect to that of the moving stimulus, then a similar illusion should also be found in other tasks involving the relative timing of these stimuli. For example, it was suggested that if the observers were asked to judge the relative timing between the halt of a moving stimulus and a flash, the differential latency would predict a perceived asynchrony between these two events (Eagleman & Sejnowski, 2000c). The tacit assumption in deriving this prediction is that the judgment of temporal order is based on identical neural substrates as the judgment of relative position. Our model includes no such assumption, as an important

part of the model is the multiple-channel structure of the visual system. The judgment of the temporal order of events can be based on different neural substrates than those used to determine their relative positions. For example a transient signal, generated when the moving stimulus stops, that is not involved in coding position can be used to carry out the temporal-order judgment. Even similar tasks such as temporal-order judgments and reaction time differ in their dependence on stimulus characteristics, such as luminance (Jaśkowski, 1992) and rise-time (Jaśkowski, 1993), suggesting that they do not involve identical neural substrates. Williams and Lit (1983) showed that the dependence of Hess and Pulfrich effects on stimulus luminance is different from the dependence of reaction time on stimulus luminance. A task-dependent perceptual asynchrony is also found for other perceptual dimensions such as color and motion. The perception of motion appears to temporally lag the perception of color when the observers are asked to report the predominant color during one phase of a stimulus in repetitive motion (Arnold & Clifford, 2002; Arnold, Clifford, & Wenderoth, 2001; Bedell et al., 2003; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002; Viviani & Aymoz, 2001) but this lag is substantially reduced or eliminated when the observers are asked to report the temporal order of color changes relative to changes in the direction of motion (Bedell et al., 2003; Nishida & Johnston, 2002). Similar task-dependent results were obtained when color changes were paired with orientation changes (Clifford, Arnold, & Pearson, 2003). These findings can be explained by assuming that different tasks invoke different neural activities with different relationships between the resulting latencies (Bedell et al., 2003). A recent fMRI study confirmed that the hemispheric engagement in the human brain is determined largely by the task of the observer rather than by the attributes of the stimulus (Stephan et al., 2003).

(4) Eagleman and Sejnowski (2002) suggested that the differential latency model has difficulty in explaining the results of the FIC paradigm, for "the moving object will suffer the same delay as the flash, as it suddenly appears from nowhere". As noted by Krekelberg and Lappe (2002), this argument oversimplifies the spatio-temporal dynamics of visual processing. During the short time interval immediately following the onset of the stimuli, similar activities will be generated by moving and flashed targets, for the stimuli are either identical (the first frame in the case of apparent/sampled motion) or very similar (in the case of continuous motion). However, while the flashed stimulus remains at the same location and disappears, the moving stimulus activates neighboring locations thereby generating a different activity profile. According to our model, this difference causes the two stimuli to activate *different* neural sub-systems. Although the latencies of the *initial* responses generated by the two stimuli may be similar, the latency at the perceptual level can be quite different (Fig. 13).

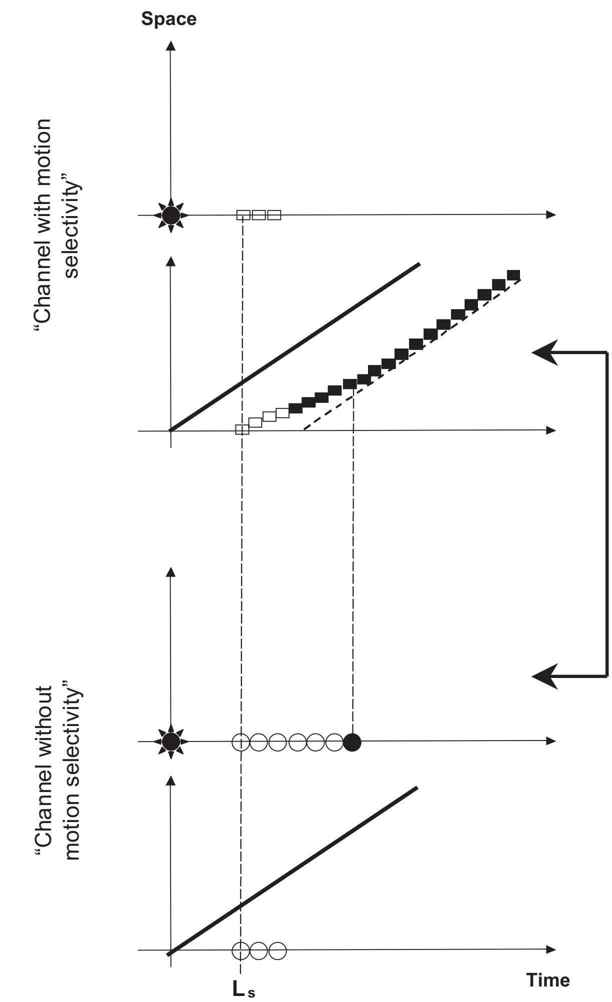

Fig. 13. More detailed depiction of processing timing according to our model. The top (bottom) pairs of panels illustrate the responses of a channel with (without) motion selectivity to a flashed and moving stimulus. In all cases, the processing starts with a latency of L_s. However, the flashed stimulus does not reach visibility in the channel with motion selectivity, and the moving stimulus does not reach visibility in the channel without motion selectivity. Therefore, responses underlying perceptual judgments come from the two middle panels as depicted in the previous figures. That the flash does not reach visibility in the channel with motion selectivity can be explained in a variety of ways, such as inhibitory interactions between mechanisms tuned to opponent directions of motion, or a poor overlap with the spatio-temporally oriented summation field of motion mechanisms. Similarly, the failure of the motion stimulus to reach visibility in the channel without motion selectivity can be explained by a poor overlap with the unoriented spatio-temporal summation field of this channel. Mutual inhibition between channels with and without motion selectivity is also possible.

(5) Krekelberg and Lappe (2001) provided a review of neurophysiological data indicating that moving stimuli have a small latency advantage (~15 ms) with respect to flashed stimuli in cat LGN, but flashed stimuli have a slight advantage (~5 ms) over moving stimuli in monkey

MT. We agree with Krekelberg and Lappe (2001) that these data do not provide direct support for the differential latency hypothesis and that more extensive neurophysiological studies are required, that take into account a broader range of brain areas (cf. Eagleman & Sejnowski, 2002; Krekelberg & Lappe, 2002) as well as the details of task-related neural-coding leading to perceptual decisions (Bedell et al., 2003; Clifford et al., 2003; Stephan et al., 2003).

(6) Some critiques of the differential latency model are based on the notion that latencies correspond to fixed delays. We fully agree that fixed delays cannot explain the flash-lag phenomenon in particular, or perceptual asynchronies, in general. Indeed the data on which our model for flash-lag (Patel et al., 2000; Purushothaman et al., 1998) and perceptual asynchronies (Bedell et al., 2003) is based exhibit *changes* in differential latencies as the stimulus parameters or the task change. Alais and Burr (2003) showed that a flash-lag effect exists in the auditory system as well as cross-modally between auditory and the visual systems. Their data suggest that the latency in judging relative spatial position is shortest for their auditory motion stimulus (AMS) and approximately 56 ms longer for their visual motion stimulus. The latency of the visual flash stimulus was ranked third at approximately 69 ms longer than the latency of AMS. Finally, the auditory "flash" had the largest latency at 169 ms longer than the latency of AMS. Alais and Burr (2003) interpreted these findings as evidence against the differential latency model by considering that (i) the latencies for audition are shorter than those for vision when measured by reaction times or evoked potentials and (ii) the auditory system has poorer sensitivity to spatial motion than the visual system. Considering the second point first, it is not clear why poorer sensitivity should imply a longer latency. With regard to the first point, as discussed above, latencies measured by reaction times or neural signal timing do not necessarily reflect the perceptual latencies that are relevant to a specific task. Alais and Burr (2003) note that integration time is substantially longer for audition than for vision, but they do not relate integration dynamics to latencies. As the example in Section 2.1 shows, leaky-integration (equivalently, low-pass filtering and averaging) induces latencies. In a study that is related to the one by Alais and Burr (2003), Hine, White, and Chappell (2003) asked their observers to judge the position of a moving visual stimulus with respect to a fixed visual stimulus when an auditory click (cf. "auditory flash") was heard. In this case, the auditory stimulus serves as a temporal reference point and the relative position judgment is carried out in the visual domain. Accordingly, the auditory detection task in the experiment by Hine et al. involves much simpler processing of the auditory stimulus than the azimuthal localization task (based on interaural delays) in the experiment by Alais and Burr. Consequently, one would expect that the latencies for auditory signals would be shorter for the experimental task in Hine et al. than in Alais and Burr. In agreement with this analysis, Hine et al. (2003) reported a flash *lead* in their experiment.

Arnold, Durant, and Johnston (2003) used the simultaneous tilt-contrast illusion to evaluate whether differential latencies play a role in the flash-lag illusion. In their first task, Arnold et al. (2003) determined when a flashed test grating appeared to be physically vertical. A surrounding annular grating rotating either clockwise or anti-clockwise at 0.5 Hz induced illusory tilt in the test grating, the direction of which depended upon the relative orientations of the two gratings. The authors' logic was that the test grating should appear to be vertical if, at the instant it reaches perception, the surround grating is perceived simultaneously to be vertical so that no tilt contrast is induced. The results indicated that in order for the test grating to appear vertical, it had to be flashed approximately 15–20 ms before the rotating grating was physically vertical. In the second, "flash-lag" task, Arnold et al. (2003) determined when a flashed central test grating was perceived to match the orientation of the rotating surround grating. In this task, perceived alignment between the two gratings occurred when the test grating was flashed approximately 75 ms before the orientation of the rotating grating was in physical alignment.

The authors considered the 15–20 ms delay that they found in their first task to be a more valid indicator of the difference in neural latencies between the flashed and rotating targets. Consequently, they concluded that differential latency between flashed and rotating targets accounts for only a small portion of the 75-ms flash-lag that they measured in their second experiment. However, their data are not inconsistent with our differential latency model. First, note that the observers' task in the two experiments is not the same. In the first experiment, observers judged the orientation of the flashed grating relative to physical vertical, whereas in the second experiment the observers judged the relative orientation of the flashed and rotating gratings. Second, the author's interpretation of their data assumes that the tilt-contrast illusion depends on the orientation of the surround grating at the instant that this grating is perceived. In other words, the magnitude and sign of the tilt-contrast illusion in the test stimulus is assumed to be instantaneously determined from the difference in the perceived orientation between the rotating and flashed stimuli. The tilt-contrast illusion is usually attributed to lateral inhibitory interactions between cortical orientation-tuned neurons (e.g., Carpenter & Blakemore, 1973). Thus, the induction of tilt-contrast illusion is a dynamic process which presumably takes time to develop. Consequently, at the time that the flashed grating is perceived, the accompanying tilt-contrast illusion may not be due to the perceived orientation of the rotating grating at that instant, but rather the orientation of the surround grating that was perceived at some earlier time. We therefore interpret the 20 ms flash misalignment in their first experiment as the lag of the perceived orientation of the flash with respect to the *inducing* orientation of the rotating grating rather than with respect to the *perceived* orientation of the rotating grating. Under the assumption that the dynamics of the tilt-contrast illusion play a minimal role in their second experiment, the 75 ms flash misalignment obtained in this experiment can be interpreted as the lag of the perceived orientation of the flash with respect to the perceived orientation of the rotating grating. Note also that because of the presence of a dynamic tilt-contrast illusion, it is possible that the perceived spatial alignment between the flashed and the rotating gratings in their second experiment occurs at an orientation different from vertical.

(7) Although Krekelberg and Lappe (2001) concluded that "the influence of differential latencies on the perception of moving objects, however, is undeniable" they offered the following challenges to the differential latency hypothesis:

(i) As discussed in Section 7.2.1, Mackay (1958) conducted experiments in which the retinal images of *all* targets were in motion; motion information was available continuously for self-luminous objects, but only briefly and intermittently for the objects that were illuminated stroboscopically. Similarly, Lappe and Krekelberg (1998, 2001) conducted a series of experiments to measure the perceived misalignment between moving objects that were continuously visible and moving objects that were visible intermittently. In the latter case, the visibility of the moving stimulus was modulated by a periodic waveform where each period consisted of a temporal interval of visibility of duration T_{on} and a temporal interval of invisibility of duration T_{off}. We will refer to this stimulus as the "sampled moving-stimulus". They showed that the perceived misalignment between the continuously moving stimulus and the sampled moving-stimulus decreased when T_{on} increased or when T_{off} decreased (Lappe & Krekelberg, 1998; Krekelberg & Lappe, 2001). Krekelberg and Lappe (2001) suggested that the differential latency hypothesis cannot explain this finding. When T_{on} is small, the sampled moving-stimulus approximates a flashed stimulus and thus our model predicts that the perceived misalignment should be similar to the flash-lag obtained under similar conditions. When T_{on} is large, Krekelberg and Lappe effectively presented two moving stimuli and thus the comparison was no longer between a flashed and a moving stimulus but between stimuli with different parameters of apparent motion (AM). In this case, both stimuli activate the motion channel and our model predicts, in agreement with their findings, a zero or a very small misalignment (which can result from the fact that not all parameters (e.g., eccentricity; "goodness" of AM) of the two stimuli are identical). According to our multiple-channel model, as T_{on} is increased gradually, the sampled moving-stimulus progressively excites the system that processes static stimuli less (i.e., the system processing the flash) and excites the system that processes moving stimuli more. As a result, perceived misalignment results less from a comparison between the positions computed in separate systems that process flashed and moving stimuli, and more from a comparison between the positions computed within the system that processes moving stimuli. This explains why the perceived misalignment decreases as T_{on} increases. Following the same logic, a decrease in T_{off} results in a more effective stimulus for the motion system, thereby decreasing the perceived misalignment.

(ii) Krekelberg and Lappe (2001) suggested that because flash-lag-like phenomena occur in other stimulus dimensions, independent evidence for substantially larger differential latencies that are found in those studies is needed to support the differential latency hypothesis. A particular study highlighted by Krekelberg and Lappe (2001) was by Sheth, Nijhawan, and Shimojo (2000) in which briefly presented objects were found to lag continuously changing objects within color, luminance, spatial frequency, and entropy dimensions. As shown in Bedell et al. (2003), the conceptual basis of the differential latency hypothesis can be extended to other dimensions. An important point to consider, as we highlighted throughout this paper, is that latency is *not* a fixed delay but can arise from the dynamics of the system. As a result, differential latencies can change substantially as the observer's task changes and as the stimulus parameters change (as shown by the data presented here and in Lappe & Krekelberg, 1998; Patel et al., 2000; Purushothaman et al., 1998), even within the same processing system. In this regard, it is noteworthy that Sheth et al. (2000) reported that, when the observers' task was changed from judging the stimulus color at the time of a flash to judging the temporal order between the onsets of the continuously changing and the flashed stimuli, the temporal misalignment was substantially reduced. In addition, if we note that continuously changing objects and briefly flashed objects generate ramp and pulse responses, respectively, then it should not be surprising that these two responses differ in their time-course.

8. Conclusions

Substantial evidence supports the involvement of differential latencies in the flash-lag illusion. We highlighted the fact that latency is not just a pure fixed delay and can also be induced by system dynamics, for example at the onset and offset of motion. This clarifies the relationship between leaky-integration (or equivalently averaging, and low-pass filtering), a mechanism that is used in many models, and the latencies it generates in response to dynamic inputs. The multiple-channel system approach that we have presented shows how the flash-lag illusion can be used to probe the dynamics of the position computation process. By using this approach, we characterized the ramp-response of the position computation process for unidirectional motion. In a LTI system, the ramp-response that is shown in Fig. 10 would contain all the information needed to characterize the system. However, in the case of the position computation process, the ramp response does not generalize to all stimulus conditions. For example, comparing the data in Whitney et al. (2000a) to the data in Whitney et al. (2000b), one can see a clear difference in system dynamics depending on whether the motion reverses direction (180°) or makes an orthogonal turn (90°). The explanation in our multiple-channel differential latency model is based on a change in system dynamics that depends on the extent to which motion opponency mechanisms are engaged (Bedell et al., 2003). Therefore, additional studies are required to broaden our understanding of the neural processing mechanisms that affect perceived position in human vision.

Acknowledgements

This work was supported by NIH grants R01-MH49892, R01-EY05068, and P30-EY07551. We thank the anonymous reviewers for comments and suggestions on the manuscript.

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