



Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flashed stimuli

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Abstract

A flash that is presented adjacent to a continuously moving bar is perceived to lag behind the bar. One explanation for this phenomenon is that there is a difference in the persistence of the flash and the bar. Another explanation is that the visual system compensates for the neural delays of processing visual motion information, such as the moving bar, by spatially extrapolating the bar's perceived location forward in space along its expected trajectory. Two experiments demonstrate that neither of these models is tenable. The first experiment masked the flash one video frame after its presentation. The flash was still perceived to lag behind the bar, suggesting that a difference in the persistence of the flash and bar, does not cause the apparent offset. The second experiment employed unpredictable changes in the velocity of the bar including an abrupt reversal, disappearance, acceleration, and deceleration. If the extrapolation model held, the bar would continue to be extrapolated in accordance with its initial velocity until the moment of an abrupt velocity change. The results were inconsistent with this prediction, suggesting that there is little or no spatial compensation for the neural delays of processing moving objects. The results support a new model of temporal facilitation for moving objects whereby the apparent flash lag is due to a latency advantage for moving over flashed stimuli. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

When a brief flash is presented adjacent to a moving stimulus (referred to as a 'bar'), the bar appears to spatially lead the flash. This illusory flash lag phenomenon can be traced at least as far back as Metzger (1932), although related phenomena were noted by Hazelhoff (1923, 1924) and Fröhlich (1929; c.f., Roufs, 1974). Recently, a resurgence in research on this illusion has prompted several new explanations for the effect (MacKay, 1958; Nijhawan, 1994).

One possibility is that there are differences in the persistence of flashed and moving stimuli. According to this hypothesis, the perceived duration of the flash is longer (Efron, 1970; Hogben & Di Lollo, 1974) than that of the bar because of processes which shorten the persistence of the moving stimulus (e.g. deblurring; Burr, 1980). Therefore, when a flash is presented

aligned with a moving bar, the bar's trace is quickly suppressed while the longer lasting flash appears to lag behind the bar.

Another possibility, according to Nijhawan (1994, 1997a) and Khurana and Nijhawan (1995), is that the illusory lag phenomenon is the result of a spatial extrapolation mechanism. During neural latencies of 50–100 ms (DeValois & DeValois, 1991; Nijhawan, 1994; Cavanagh, 1997), a significant distance can be traveled by the moving bar, resulting in a dissociation between its perceived location and its actual physical location. The extrapolation model argues that to overcome this discrepancy, the bar's perceived position is extrapolated forward to its physical location based on its past velocity and neural latency (Fig. 1). That is, during the neural latency, the bar has continued through its trajectory; in order to compensate, the visual system extrapolates the bar forward in space. The bar is therefore perceived where it is expected to be after the neural delay, whereas the flash is seen where it actually is. Thus, the bar appears ahead of the flash (Fig. 1A).

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Recently, Whitney and Murakami (1998) revived an alternative explanation based on the relative difference in the neural latencies for moving and flashed stimuli (Fig. 2A). If the neural delay for the moving bar is shorter than that for the flash, the bar should naturally appear to lead the flash. Though proposed early in this century (Metzger, 1932; c.f., Hazelhoff, 1923, 1924; Fröhlich, 1929), this account lost favor when the persistence and extrapolation explanations, mentioned above, were introduced. The idea of differential neural delays, however, is consistent with a growing body of literature which suggests that latency varies with a variety of stimulus attributes such as luminance contrast and velocity (Pulfrich, 1922; Rogers & Anstis, 1972; Hohnsbein & Mateeff, 1992; Gawne, Kjaer & Richmond, 1996; Allik & Kreegipuu, 1998; Mechler, Victor, Purpura & Shapely, 1998; Purushothaman, Patel, Bedell & Ogmen, 1998). Further, a few recent studies have used differential latencies to explain anisotropic sensitivity to direction of motion (Mateeff & Hohnsbein, 1988; Mateeff, Bohdanecky, Hohnsbein, Ehrenstein & Yakimoff, 1991b; Mateeff, Yakimoff, Hohnsbein, Ehrenstein, Bohdanecky & Radil, 1991a).

The purpose of the following experiments is to test the persistence, extrapolation, and differential latency explanations for the illusory flash lag phenomenon. The first experiment will test whether a differential persistence of the flash and moving bar is responsible for the illusory flash lag by presenting a mask one frame after the flash, greatly reducing the flash's persistence (and leaving the bar's persistence unchanged). If the judgment of the flash's location is made after its persistence, and this persistence is reduced when the mask is presented, then the illusory flash lag should be reduced. Whereas if the flash's location is judged by its initial appearance, and there is a differential latency for the initial appearance of the flash and the moving bar, then the illusory flash lag should remain unchanged. The second set of experiments will introduce an unpredictable change in velocity, such as a reversal, a stop, an acceleration, or a deceleration, for which the extrapolation and differential latency models generate clearly different predictions. This novel stimulus will be introduced for two primary reasons. First, although constant and predictable motion trajectories have been employed in the past to study the illusory flash lag phenomenon, natural motion is rarely so predictable.

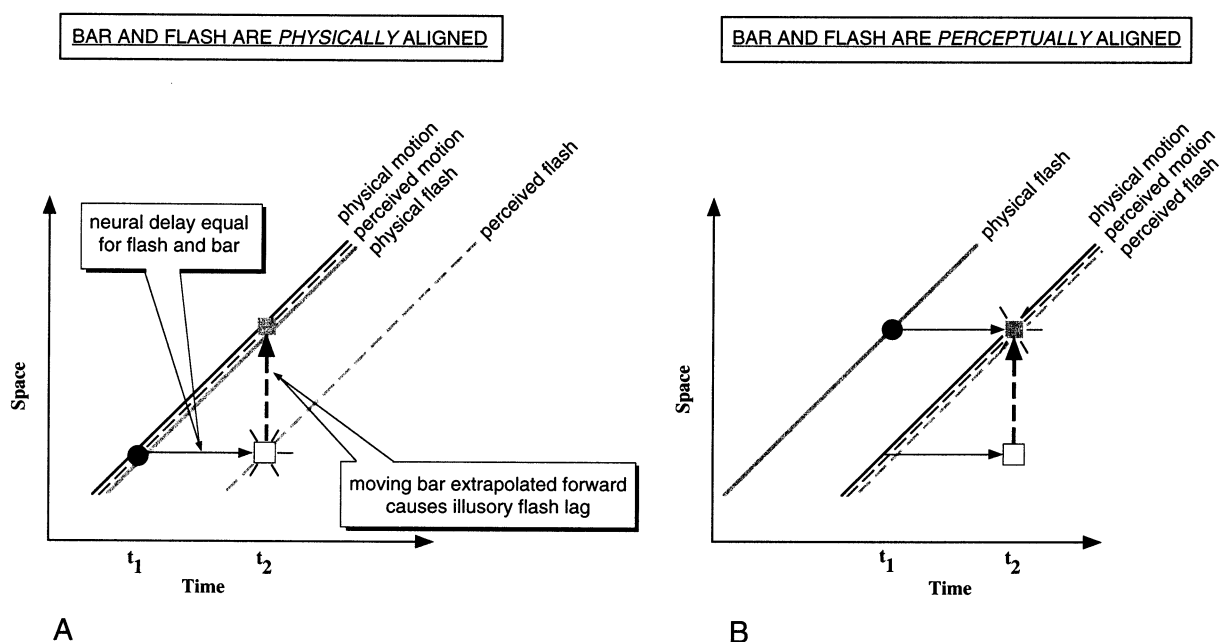


Fig. 1. Spatial extrapolation model. (A) The solid black line represents the physical motion of the bar, and the dashed black line depicts the perceived motion of the bar. Note that these two are superimposed. The filled circle shows the physical location of a flash that is presented aligned with the bar at a particular time. A family of such flashes across time are represented by a solid gray line. By definition, it is superimposed upon the physical motion line. The black arrow spanning from t_1 to t_2 is the neural latency of the flash and the bar. The open square depicts the perceived bar (presented at t_1) one would expect without extrapolation; the radiating lines around it depict the perceived time and position of the flash. The dashed gray line illustrates a family of such perceived flashes. The dashed arrow is the distance that the bar is extrapolated forward (extrapolated distance = past velocity \times neural delay). The filled square is the perceived position and time of the bar from t_1 (but perceived at t_2). Therefore, the length of the dashed arrow is the perceived misalignment between the flash and the bar. (B) Identical to (A), except that the gray lines are shifted to the left, meaning that the flash is presented ahead of the bar in order for it to appear aligned with the bar. Note that the extrapolated distance (dashed arrow) is identical to the distance between the physical positions of the flash and bar. Therefore, the flash alignment setting measures the extrapolated distance and the neural delay for the flash and bar.

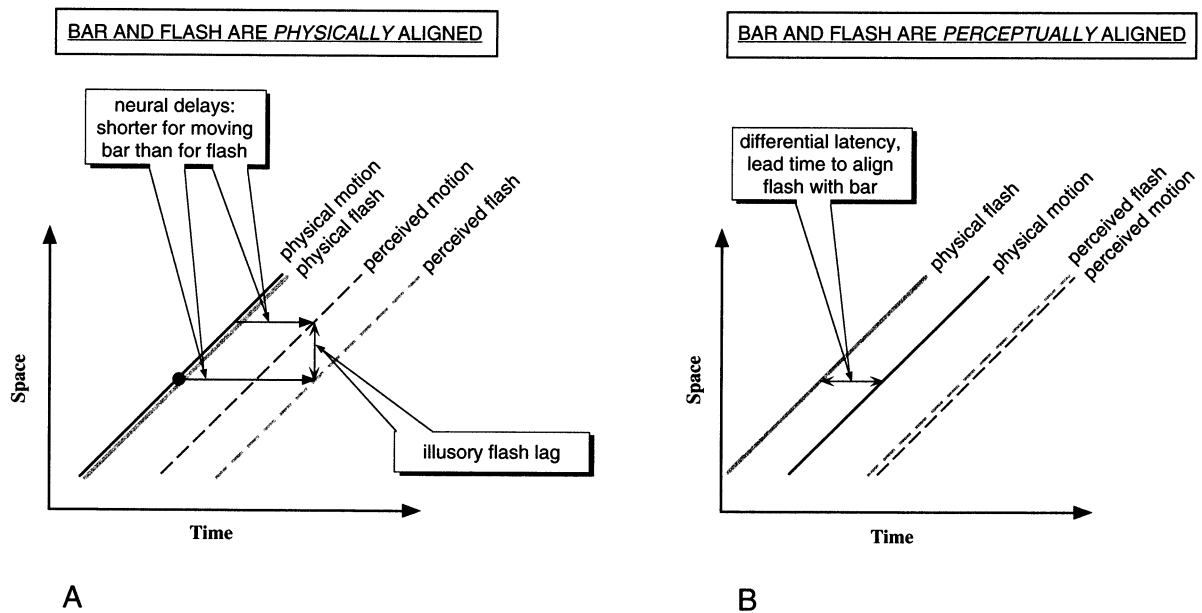


Fig. 2. Differential temporal latency model. (A) The solid lines represent the physical motion of a bar (black) and where flashes are presented (gray). The dashed black line shows the perceived motion of the bar after a constant latency. The dashed gray line shows the perceived positions of the flashes. Because the latency for the flash is longer than the latency for the bar, the bar is perceived ahead (in space) of the flashes at any moment in time. The distance (in space) between the dashed black and gray lines is the perceived misalignment between the flash and bar (double arrow). (B) To perceive the flash aligned with the bar, the flash must be presented ahead of the bar (in time), on the gray line. The horizontal distance between the gray line and the black line is the difference in the neural delay for the flash and the bar.

Second, using continuous and predictable motion does not adequately distinguish between the predictions made by the extrapolation and differential latency models.

2. Experiment 1: masking the flash

2.1. Methods

Three subjects participated in the experiment. Each had normal or corrected-to-normal vision. Subjects were seated in a darkened experimental booth with a chin rest 57 cm from a Macintosh high resolution CRT whose refresh rate was 66.7 Hz. A pair of vertically aligned white (34.5 cd/m^2) squares translated horizontally 5.04° above a white (34.5 cd/m^2) fixation point on a dark background (0.01 cd/m^2). Each square subtended 0.90° (Fig. 3). The distance between the squares (1.80°) was constant, and they moved concurrently at $11.84^\circ/\text{s}$. For the sake of consistency with the previous literature (Nijhawan, 1994, 1997a,b; Khurana & Nijhawan, 1995), we will call this pair of squares a 'bar'. The bar was presented within a 23.04° horizontal window (within 12.57° of fixation). On each trial the bar's motion was randomly presented as either moving from the left to the right, or right to left. After an initial translation ($\geq 3.6^\circ$), a small white disk (34.5 cd/m^2) subtending 0.36° was flashed for one video frame (15

ms) between the moving squares. The eccentricity of the flash, and therefore the duration of the bar's movement before the flash, was randomly varied. A mask was presented one video frame after the flash and remained on the screen for the duration of the trial. The mask was the same height, color, and luminance as the flash and extended across the entire presentation area (thus entirely covering the flash).

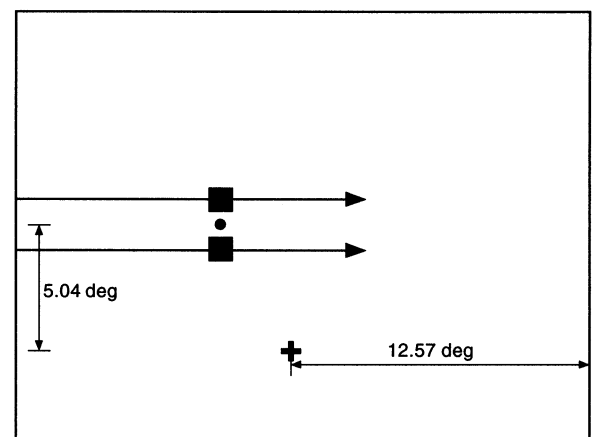


Fig. 3. Stimulus display used in the experiments. Two squares (referred to as a 'bar') translated horizontally across a CRT. A flash was presented between the squares at various horizontal offsets. Subjects judged whether the flash was located to the left or right of the bar (method of constant stimuli). The initial direction of the bar was randomized, as was the eccentricity and duration of the bar's motion before the flash.

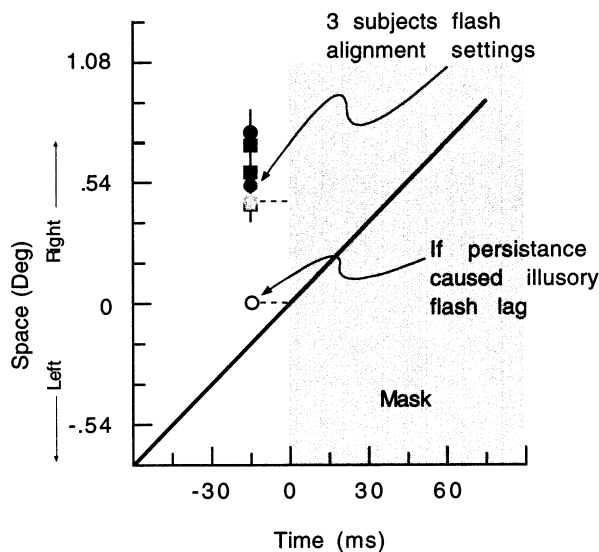


Fig. 4. Experiment 1 results. The solid black line is the bar's physical motion. The solid squares show perceived flash alignment settings when no mask was presented. The solid circles show perceived flash alignment settings when a mask was presented one frame after the flash. The shaded area represents the mask. If there were differential persistence for the flash and the bar, the flash alignment settings (solid circles) should have been located near the open circle, or at least the flash alignment settings should have differed from those when no mask was presented. There was no significant difference between the flash alignment settings with and without a mask. (The graph implies that the neural delay for the flash is equal to that for the bar, but this is not necessary, and is only for illustrative purposes.)

The observers were asked to judge whether the flash appeared spatially offset to the left or right of the moving bar (method of constant stimuli — 2AFC task). By varying the position of the flashed dot relative to the bar, a psychometric function was calculated for a given time that yielded a setting of perceived alignment where the flashed dot appeared aligned with the bar (c.f. Figs. 1B and 2B). There were at least 20 trials for each of the six positions of the flash. Psychometric functions were fitted to the data from the logistic function $y = \{1 + \exp[-a(x - b)]\}^{-1}$, where b estimates the flash setting that appears spatially aligned with the bar. For example, when the dot was flashed aligned with the bar, it appeared to lag behind the bar; in order to offset the apparent lag, the flash had to be presented ahead of the bar.

2.2. Results

The data points (solid circles) in Fig. 4 show flash settings that appeared aligned with the moving bar (flash alignment settings). The data for the right-to-left condition were flipped and merged with the data for the left-to-right condition so that physical motion is always displayed in the figures as moving rightward. Lines through the data points are 95% confidence intervals,

(c.f., Finney, 1947; McKee, Klein & Teller, 1985). The solid black line is the physical motion of the bar. The shaded region is the mask, which was presented one video frame after the flash. The open circle in Fig. 4 is the predicted flash alignment setting if differential persistence for the flash and bar were entirely responsible for the illusory flash lag phenomenon (the more that persistence contributes to the illusion, the closer the flash alignment settings should be to the open circle). This prediction is based on the fact that masking after 15 ms reduces visual persistence (Castet, 1994; Francis, 1996). So if the judgment of the flash's location were made after its persistence, which is shortened with the mask, the flash alignment setting should be located nearer to the physical motion of the bar (open circle). The actual data points (solid circles) for the three subjects are significantly different from the differential persistence model's prediction (least significant point is for subject DVW: $t_{(19)} = 3.14$, $p < 0.005$).

For the sake of comparison, Fig. 4 also shows the flash alignment settings when no mask is presented (solid squares). The results are not significantly different from those when a mask is presented ($t_{(4)} = 1.8$, $p > 0.05$), demonstrating that although the addition of the mask reduces persistence, it does not alter the illusory flash lag phenomenon. It should be noted that no assumption is made about the relative neural delays for the flash and bar; if persistence were contributing to the illusory flash lag, then reducing the persistence would reduce the illusion regardless of the relative neural delay.

In this experiment, which employed continuous linear motion, the flash had to be presented before the moving bar at a particular location in order for it to appear aligned with the bar, irrespective of whether a mask was presented (solid circles and squares in Fig. 4). These results are consistent with previous studies that used continuous predictable motion trajectories without a mask, suggesting that a difference in the persistence for the flash and the bar does not account for the illusory flash lag phenomenon. Indeed, these results confirm previous claims that the illusory flash lag should not be the result of a persistence difference because although the duration of the flashed dot would seem longer (Efron, 1970; Hogben & Di Lollo, 1974), its *initial* position should appear aligned with the bar (Cavanagh, 1997; Nijhawan, 1997a,b).

3. Experiment 2: velocity manipulations

3.1. Methods

The methods used in this experiment were identical to those in the first experiment, except that a mask was not presented and at an unpredictable point along the

moving bar's trajectory the bar abruptly changed velocity. There were four velocity manipulations: in Condition 1, the bar reversed direction; in Condition 2, it disappeared; in Condition 3, it abruptly accelerated to $26.05^\circ/\text{s}$; in Condition 4, it abruptly decelerated to $2.37^\circ/\text{s}$. The eccentricity of the velocity change, and therefore the duration of the movement before the change was randomly varied. Positions of the flash that appeared aligned with the bar were measured for each of the 13–15 video frames (195–225 ms) around the velocity change. These aligned flash settings trace out the perceived trajectory of the bar.

3.2. Results

The data points in Figs. 5 and 7–9 show flash settings that appeared aligned with the moving bar. They therefore reflect the perceived locations of the bar in space but not in time (*when* the bar is perceived is in question). Lines through the data points are 95% confidence intervals, (c.f., Finney, 1947; McKee et al., 1985). The space-time graphs in Figs. 5 and 7–9 show the physical motion of the bar (solid black line), the alignment data, and the alignment settings that would be predicted by the extrapolation model (dashed lines). The solid gray lines through the data points are the output of a spatio-temporal filter that will be modeled in the discussion.

To determine the predicted flash alignment settings according to the extrapolation model (dashed lines), the average of the distances between the alignment data and the physical motion curve (solid black line), during continuous motion, was calculated. That is, the first few data points in each graph (i.e. during continuous motion) were averaged, because this measures precisely the distance that the extrapolation mechanism aims to offset.

Potential effects of duration and eccentricity (location) of the stimulus were examined in order to rule out the possibility that expectations about the bar's motion may have influenced the perception of the stimulus. Since the initiation of the bar's motion was from the edge of the screen, shorter duration presentations correspond to larger eccentricities. To examine any effects of duration of the bar's motion before the velocity change, the results were divided into six blocks of increasing presentation duration. It was found that there were no systematic effects of presentation duration on the perceived location of the flash relative to the moving bar. Similar analysis also excluded any effect of eccentricity. The initial direction of the bar (left versus right) also had no effect on the perceived location of the flash, which justifies flipping the data for purposes of presentation.

3.2.1. Condition 1: motion reversal

According to the extrapolation model (Fig. 1), the perceived position of the moving bar is extrapolated forward in space to its physical location, whereas the flashed dot is perceived where it is presented. Thus, in

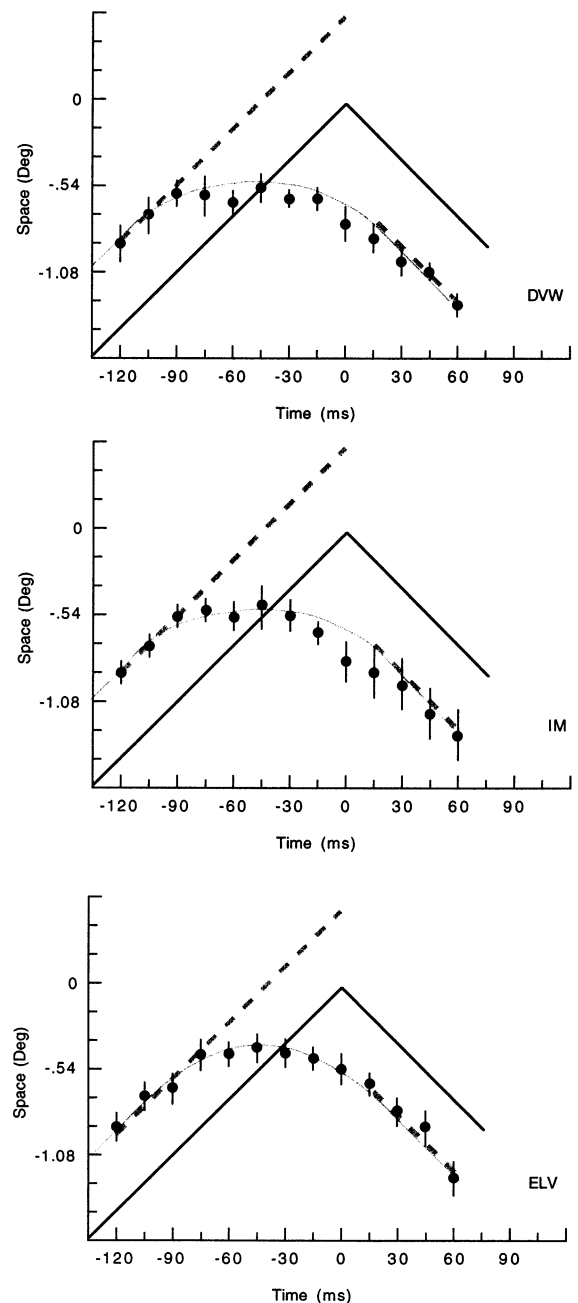


Fig. 5. Condition 1 results: motion reversal. The solid black line shows the bar's trajectory. The unpredictable reversal (at 0 ms) is centered on 0° although the actual reversals were randomized at various positions on the screen. Flash alignment settings were calculated from psychometric functions, and lines through the data points show 95% confidence intervals. The dashed line shows the predicted flash alignment settings according to spatial extrapolation theory. The data points begin to deviate significantly from extrapolation's prediction ~ 75 ms before the reversal.

the extrapolation model, to perceptually align the flash with a continuously moving bar the flash must always be presented ahead of the bar (Fig. 2B, dashed line in Figs. 5 and 7–9). For example, at -45 ms in Fig. 5 the flash should be presented ahead of the bar in order to perceive the flash aligned with the bar. This logically follows because the visual system does not know when or where the bar will reverse direction. Therefore, just prior to the reversal (e.g. -45 ms) the visual system must still treat the bar as if it were simply moving along a continuous trajectory.

However, the results of this experiment do not support such spatial extrapolation. First, since the data points in Fig. 5 (filled circles) show where the flash was physically presented in order to perceptually align it with the moving bar, they reflect the perceived locations of the bar (i.e. they trace out the bar's perceived trajectory). Contrary to extrapolation's prediction, the alignment settings, and therefore the perceived trajectory of the bar, never overshoot the actual reversal point. Spatial extrapolation's predicted flash alignment settings were significantly different from the actual data between -75 and 0 ms for subjects IM and DVW, and between -60 and 0 ms for subject ELV (the least significant of these points was at -60 ms for subject ELV: $t_{(9)} = 4.79$, $p < 0.0025$, Bonferroni adjusted for four observations). Further arguments will be considered later in the discussion section.

As Fig. 5 shows, it is when the flash alignment settings are shifted roughly 45 ms that they best match the physical trajectory of the bar. This simply means that the flash has to precede the bar at each location by about 45 ms to appear aligned, which strongly suggests a differential neural delay of 45 ms between the bar and the flash (temporarily ignoring the rounding of the data). Therefore, the reason the data in Fig. 5 seem to cross over the physical trajectory of motion about 45 ms before the physical reversal is because the flash has a longer latency. This is more easily seen in the schematic of the differential latency model (Fig. 6), where the flash and bar trajectories (solid lines) are presented temporally offset in order to create their perceptual alignment (dashed lines). Although the differential latency model alone (Fig. 6) does not explain the rounding of the data in Fig. 5, further analysis in the discussion section will show that a typical spatio-temporal filtering mechanism models this rounding well, and that it does not influence the interpretation of the data.

3.2.2. Condition 2: disappearance

Data in Fig. 7 show flashes that appeared aligned with the moving bar when the bar disappeared at a random point on the display. (An alternative method, using a stationary reference at the point of disappearance, has been used in the past by Mateeff et al. 1991a,

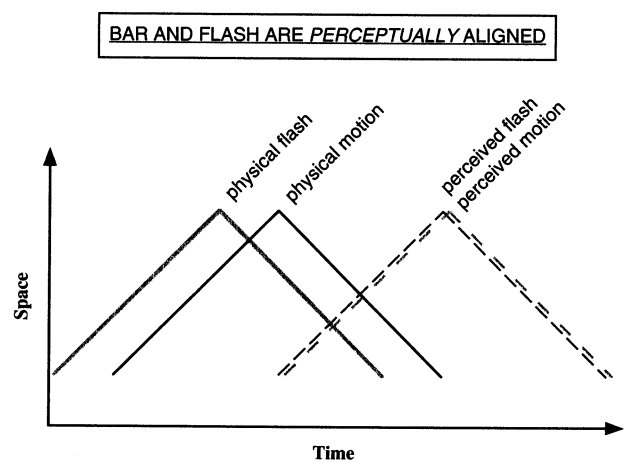


Fig. 6. Schematic diagram of motion reversal according to the differential latency model. The solid black line marks the physical trajectory of motion. The solid gray line shows the physical flash alignment settings. The dashed black and gray lines are the perceived trajectories of the bar and the flash respectively (accumulated over many trials). The perceived trajectories of the flash and bar are superimposed because this was the goal of the subject's task. If there were a difference in the neural delay for moving and flashed stimuli, there would be a necessary temporal offset between the physical motion and physical flash trajectories in order to align the perceived motion trajectory with the perceived flash trajectory. The physical trajectories for the bar and flash therefore cross over each other simply because there are differential latencies for the flash and bar. Note that the principal difference between this figure and Fig. 5 is the addition of the perceived flash and bar trajectories.

who found a systematic bias toward the fovea when localizing the moving stimulus. For purposes of comparison to the extrapolation literature, and because a stationary reference is a different task with potentially different results, e.g. Whitaker, Person, McGraw & Banford, 1998, we chose to use a flash as a reference stimulus.)

Spatial extrapolation theory predicts that the flash alignment settings must be located at a constant distance in front of the bar up to its disappearance, because the bar continues to be extrapolated forward in space until that point. The data indicate that, on the contrary, to perceive the flash aligned with the bar, the flash must be offset in front of the bar less and less as the point of disappearance is approached. There is no offset required at the point of disappearance. The flash alignment settings deviated significantly from extrapolation's prediction between -60 and 0 ms (the least significant of these data points was at -60 ms for subject ELV: $t_{(2)} = 3.62$, $p < 0.05$). Similar to the data in the motion reversal condition, these data reflect a perceived velocity decrease near the bar's disappearance. In the discussion section, the same spatio-temporal filter that was used to model the reversal condition will be used to model the data from this condition as well.

3.2.3. Conditions 3 and 4: acceleration and deceleration

Figs. 8 and 9 show the flash alignment settings when the bar's velocity abruptly accelerated or decelerated, respectively. Extrapolation theory predicts that the flash alignment settings should remain constant up to the point of velocity change because the visual system cannot predict when or where the change in velocity will take place. The data, however, show that the flash

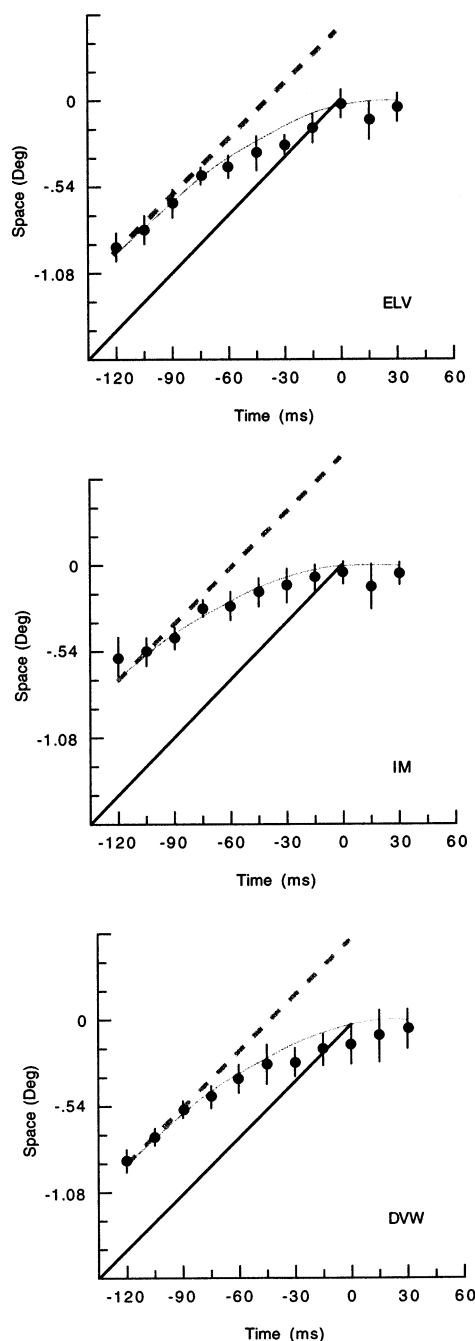


Fig. 7. Condition 2 results: motion disappearance. The solid black line shows the bar's trajectory: it translated linearly across the screen and disappeared at a random point. The dashed line shows spatial extrapolation's prediction. Flash alignment settings began to deviate from the prediction ~ 60 ms before the bar's disappearance.

alignment settings deviated from extrapolation's prediction *prior* to the velocity change. For example, when there was an abrupt increase in velocity (Fig. 8) the alignment setting shifted rightward at around -30 ms (flashes had to be presented further to the right in order to cancel the apparent lag). The data for each subject are significantly different from extrapolation's prediction between -30 and 0 ms (least significant of these points in Fig. 8 is -30 ms for subject ELV: $t_{(6)} = 2.08$, $p < 0.05$). Likewise, when there was an abrupt velocity decrease (Fig. 9) the flash alignment settings shifted leftward before the velocity change occurred. The data for each subject are significantly different from extrapolation's prediction between -45 and 0 ms (least significant of these points in Fig. 9 is -45 ms for subject DVW: $t_{(2)} = 3.33$, $p < 0.05$).

According to the differential temporal latency model, the flash alignment settings are a temporally shifted version of the physical motion curve, and the horizontal distance between the physical motion curve and the data points reflects the difference in latency for moving and flashed stimuli. Since this horizontal distance is roughly constant across all subjects and velocities, it is likely that there are shorter neural delays for moving than for flashed stimuli.

4. Discussion

The first experiment demonstrated that a reduction in the persistence of the flash, by presenting a subsequent mask, does not affect the apparent position of the flash relative to the moving bar. A differential persistence for the flash and bar is therefore unable to account for the illusory flash lag phenomenon. The second experiment employed unpredictable changes in the velocity of the bar. The illusory flash lag measured in these conditions revealed an inconsistency between the overshoot expected by spatial extrapolation and the actual data, which more closely followed the trajectory of the bar.

The experiments did support a differential temporal latency model, however, where the moving stimulus is processed faster than the flash. Consistent with this model, the data were approximated in general as temporally shifted versions of the physical motion trajectories (the rounding of the data will be explained in the next section). Although the differential latency model's prediction was similar to that of the extrapolation model in the case of continuous predictable motion, the two models' predictions diverged in the case of unpredictable motion. For example, in the extrapolation model, the spatial offset required to align a flash with a moving bar should have been constant up to the point of velocity change, whereas this offset would shift prior to the velocity modulation according to the differential latency model.

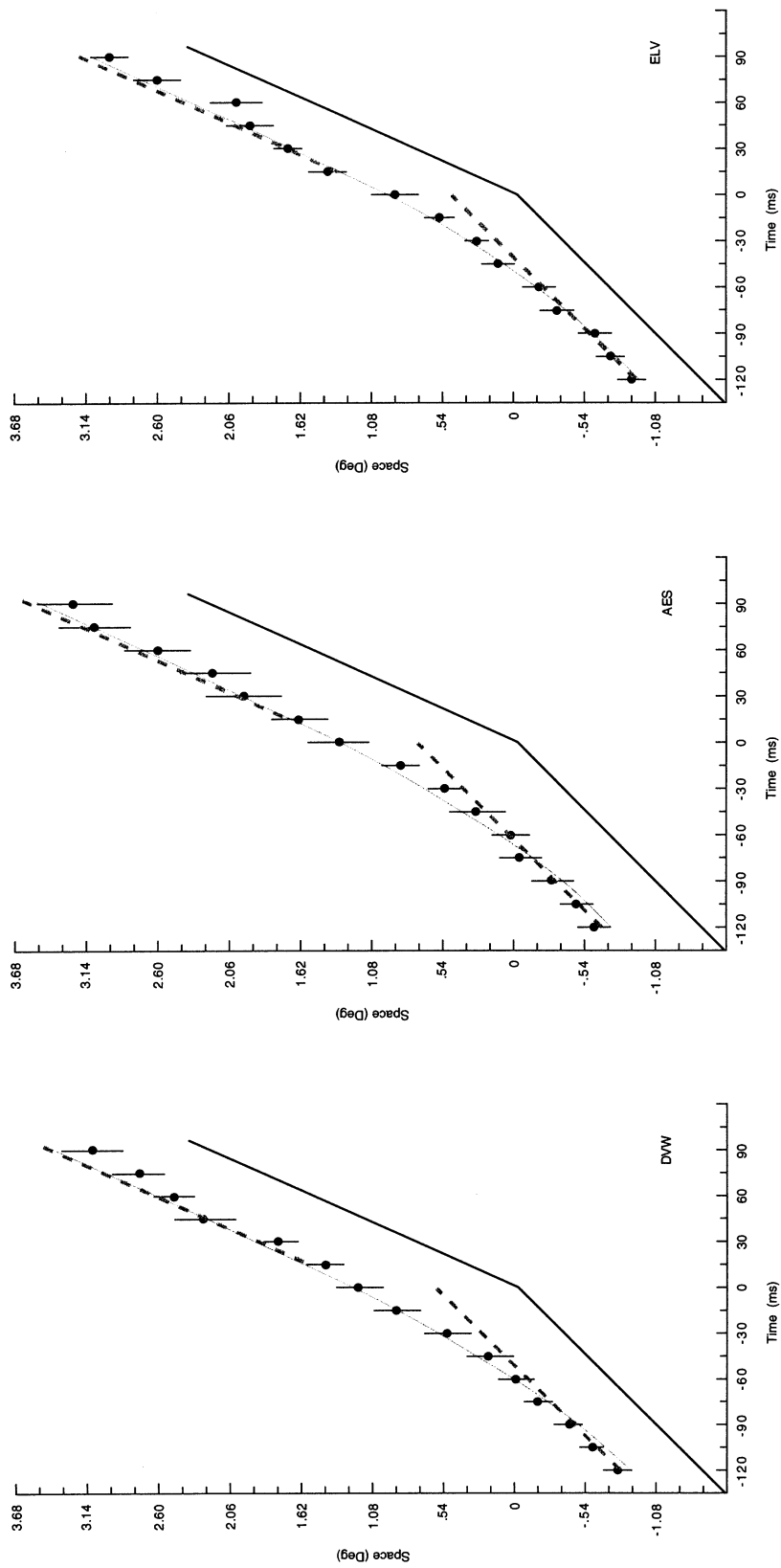


Fig. 8. Condition 3 results: motion acceleration. The solid black line shows the bar's physical trajectory. The bar's velocity changed from 11.84 to 26.05°/s at a random point on the screen. The dashed line shows extrapolation's predicted flash alignment settings. The actual alignment settings shift rightward before the change in velocity indicating that the flash had to be presented further in front of the bar in order to align the two.

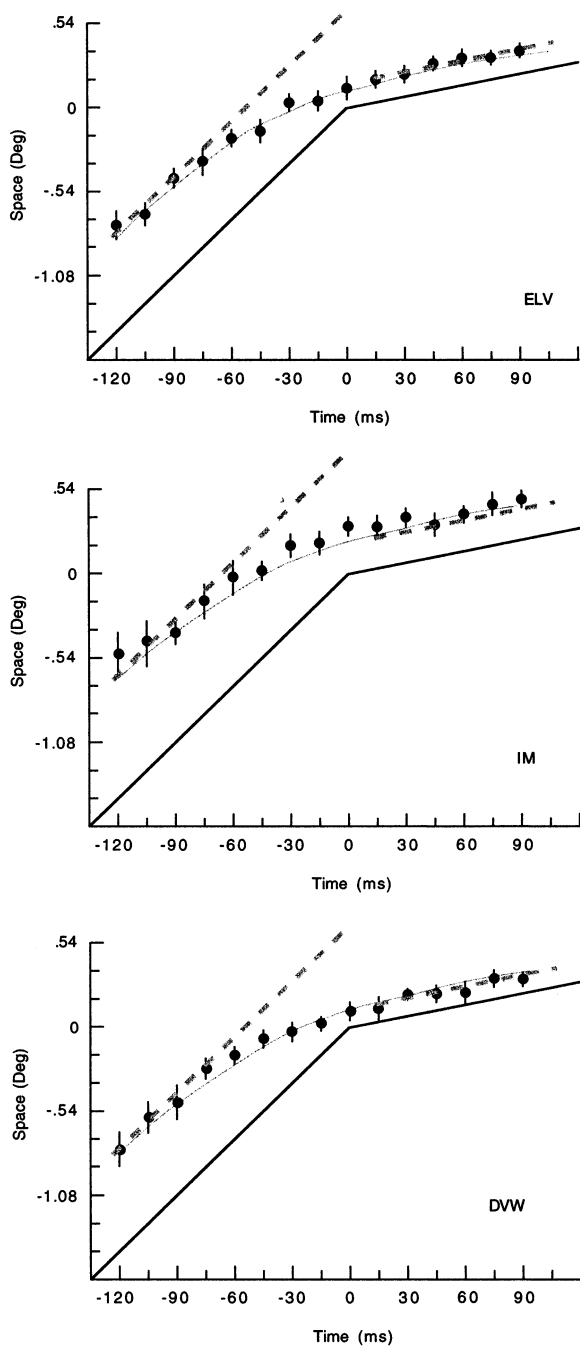


Fig. 9. Condition 4 results: motion deceleration. The solid black line shows the bar's physical trajectory. The bar's velocity changed from 11.84 to 2.37°/s. The dashed line shows extrapolation's predicted flash alignment settings. The data show that in order to align the flash with the bar the flash had to be presented closer to the bar just prior to the deceleration. The dashed line shows extrapolation's predicted flash alignment settings.

Although the differential latency model does account for the results better than the extrapolation or differential persistence explanations, there are facets of the data which are not addressed by the differential latency model. For example, in the reversal and disappearance conditions the data are rounded near the velocity

change. We will test whether this rounding could be attributed to plausible filtering properties of the motion response to the moving bar. We will then examine whether the filtering could affect the interpretation of the results presented earlier, and whether the alternative models might benefit from such a filtering mechanism. In addition, we will consider other phenomena that have been noted in the literature that may be a product of differential latencies. Lastly, we will discuss possible biological mechanisms that may underlie the differential latency model.

4.1. Perceptual blunting

An interesting characteristic of the data, most obvious in Fig. 5, is that there is a perceptual smoothing or blunting of the perceived velocity change. For example, in the motion reversal condition, the data curve is rounded near the bar's reversal point, possibly reflecting a spatio-temporal averaging (Morgan, 1979), filtering, or integration process. (An analogous observation supporting the idea that the perceived trajectory of motion is actually blunted is found when two vertically offset bars move toward each other and reverse direction just at the point when they are physically aligned. Rather than appearing as they are presented, the bars appear to reverse before ever aligning, mimicking the shape of the data in Fig. 5).

There have been many filtering models proposed in both the spatial and temporal domains, including linear probabilistic summation over space (Lappin & Bell, 1976; van Doorn & Koenderink, 1984; Fredericksen, Verstraten & van de Grind, 1994c), and temporal summation or averaging over time (Gottsdanker, 1956; Watamaniuk, Sekuler & Williams, 1989; Watamaniuk & Duchon, 1992; Fredericksen, Verstraten & van de Grind, 1994a,b; Todd & Norman, 1995). Nakayama and Silverman (1984) coined the term 'temporal recruitment' to describe the visual system's ability to average or integrate velocity information over time (or space, Snowden & Braddick, 1989a,b, 1990; but c.f. Welch & McKee, 1985).

Given that the flash alignment settings in Fig. 5 reflect a temporally shifted version of the perceived motion trajectory, we examined whether the curvature in the perceived motion (i.e. that the data reveal) could be the result of a spatio-temporal integration. By convolving the physical position of the bar with a biologically realistic leaky integrator (Fredericksen et al., 1994a,b), the shape of the data (also the perceived trajectory) was closely matched. [The convolution is formalized as $\tilde{f}(x) = \sum_{p=0}^{\infty} f(x - 15p)g(15p)$, where $f(x)$ is the physical motion trajectory and $g(x)$ is the leaky integrator characterized as a decaying exponential function $g(x|x \geq c) = d^{-1} \exp[-(x - c)d^{-1}]$ 15p corresponds to each display frame. The two free parameters

of $g(x)$ are d , an index of the integration window over which the integrator operates, and c , the temporal offset between the alignment data and the output of the filter.] The filter was optimized so that the sum of the squared residuals between the filter and the data was minimized. The average temporal integration window d for the leaky integrator in all four velocity change conditions was 44.7, 51.9, and 54.9 ms for subjects ELV, IM, and DVW, respectively. The average temporal offset c between the alignment data (data points in Figs. 5 and 7–9) and the output of the filter was 79.2, 108.2, and 92.9 ms for subjects ELV, IM, and DVW, respectively. Because this number indicates the minimum amount of time required between the alignment data (physical flash that appeared aligned with the moving bar) and the filter output (perceived motion trajectory), it also estimates the minimum latency for the flashed stimulus. That is, the temporal offset c between the alignment data and the output of the filter includes the differential latency for the flash and the moving bar (approximately 45 ms as reported earlier) and an inherent minimum delay for the leaky integrator to function.

The curved gray line in each of Figs. 5 and 7–9 shows the predicted flash alignment settings according to the differential latency model when the leaky integrator is incorporated. The r^2 between the output of the leaky integrator model and the data in Fig. 5 are 0.934, and 0.975, 0.957 for ELV, IM, and DVW, respectively. Further, the integration periods suggested by this analysis are consistent with those reported in previous studies (Morgan, 1980; Nakayama & Silverman, 1984; Welch & McKee, 1985). Thus, the smoothing of the perceived motion trajectory is well modeled by a spatio-temporal filter of typical properties.

4.2. Filtering and extrapolation?

If we are allowing both filtering and differential latencies to estimate our results in the velocity change experimental conditions, could one of the alternative models, such as spatial extrapolation, also be amended with a spatio-temporal filter in order to fit the data? According to the extrapolation model, the perceived location of the moving bar should match its physical location (during continuous motion). Therefore, the temporal misalignment between the flash and the bar that creates an apparent spatial alignment also measures the neural delay being corrected by extrapolation (the flash and bar have the same neural delay in the extrapolation model). During the continuous motion segments in Figs. 5 and 7–9, the delay between the presentation of the flash and the presentation of the bar (the horizontal offset between the data points and the black line

marking the physical trajectory) is about 45 ms. Therefore, 45 ms is the neural delay according to extrapolation, and this places an absolute constraint on the moment at which the data can start to reflect the reversal of motion. Any deviation from the expected trajectory during continuous motion (dashed line in Figs. 5 and 7–9) occurring at -45 ms or earlier refutes extrapolation theory, because this would imply that the perceived change in velocity precedes the physical change. As Figs. 5 and 7 show, however, the data begin to deviate earlier than -45 ms, demonstrating that any extrapolation model that assigns equal delays to the flash and bar is untenable even if a filter is added.

In fact, because the perceived motion cannot begin to curve (change velocity) before the actual change in velocity, and the data begin to curve at about -75 to -60 ms in Figs. 5 and 7, the shortest possible neural delay for the flash is about 75 ms. This estimate is in agreement with the estimate c from the leaky integrator above. Further, since the difference between the data and the physical motion curve (~ 45 ms) is the differential latency, the shortest possible neural delay for the moving bar is about 30 ms. It should be noted that the only absolute measurement in these experiments is the differential latency (~ 45 ms) and that the estimates for the flash and bar latencies given here are only *minima*; they are derived from the constraint imposed by causality.

4.3. Additional phenomena due to differential latencies

The differential temporal processing model not only accounts for the illusory flash lag phenomenon, but can also explain the apparent depth mislocalization of strobed stimuli relative to stimuli moving continuously in stereoscopic depth (Nijhawan, 1997b). Since there is motion across the retina, the processing time for the moving object is reduced relative to the flashed stimulus. This causes the moving object to be perceived ahead of the flash in its trajectory and therefore in a different depth plane.

The differential latency model also explains the perceived misalignment between a stationary object and an aligned flash during smooth pursuit (Nijhawan, 1998). When a pursued target is tracked, the image of a physically stationary object moves across the retina. Although the physically stationary object is not perceived to move, the retinal motion will certainly trigger motion detectors with their decreased latency. Thus, when a flash is presented aligned with the physically stationary object, it takes longer to perceive and results in a perceived misalignment between the flash and the stationary object. Similar arguments can be made to explain the color decomposition effect (Nijhawan, 1997a).

4.4. Neural mechanisms

Why should the latencies for moving stimuli be shorter than for flashed stimuli? Both have very similar temporal frequency components, especially within small regions. The underlying mechanism for the rapid response to moving stimuli could take the form of facilitatory connections to receptive fields that lie along the trajectory of motion, i.e. paths that are defined by highly correlated patterns of firing. For example, a ‘gated-enhancer’ facilitation model proposed by Grzywacz and Amthor (1993) suggests that in the rabbit retina there are excitatory connections to amacrine cells that in turn have facilitatory connections to directionally selective ganglion cells. The forward facilitatory connections alone do not cause the ganglion cell to fire, but rather prepare the ganglion’s response to direct stimulation. Therefore a sustained input, such as a moving bar, is required for the facilitation to occur, whereas a brief flash does not result in facilitation of a forward position. The authors note that facilitation can be elicited in both the preferred and null directions when GABA antagonists are used. This suggests that facilitation could become bidirectional by a slight modification to their gated enhancer model.

Although the ‘gated enhancer’ model does not rule out facilitation of any adjacent position, many alternative theories suggest that facilitation occurs only along predictable trajectories of motion (Welch & McKee, 1985; Snowden & Braddick, 1989a,b). In other words, the facilitation, or decreased latency if it is the result, should be strongest for future points along the established direction of motion. The experiments presented here have demonstrated clear evidence for facilitation along expected trajectories (linear motion) in the form of a shorter latency for moving than flashed stimuli. However, for velocity changes or reversals, the rounding of the data prevent any strong conclusion about whether the latency for the moving bar remained constant around the velocity change. If the bar’s latency had remained constant in the motion reversal condition, this would support facilitation of positions behind as well as in front of the bar. There are at least two possible explanations for why the data do not unequivocally support this form of facilitation. First, these experiments may not have been sensitive enough to detect small changes in latency. Second, the facilitation may be limited to future positions along the expected trajectory of motion. By extending the illusory flash lag paradigm to direction change experiments, the alternative forms of motion facilitation can be examined in future studies.

Another possible neural mechanism for the data reported here was recently proposed by Berry, Brivanlou, Jordan and Meister (1999). According to these authors, cells (rabbit and salamander retinal ganglion cells)

showing peak firing to small moving bars have receptive field centers just at or ahead of the leading edge of the stimulus. This ‘anticipatory’ firing could result in a perceptual response to moving targets that precedes (spatially or temporally) the response to an adjacent flash. Based on previous psychophysical literature, it seems more likely that if this mechanism contributes to the illusory flash lag, it does so by more rapid processing of moving stimuli (Whitney & Murakami, 1998; Whitney, Murakami & Cavanagh, 1998; Purushothaman et al., 1998).

A related issue is whether the latency advantage of moving objects is velocity dependent. When the velocity of the bar was 11.84°/s, the difference between the latency for moving and flashed stimuli was approximately 45 ms, consistent across all experimental conditions. When the velocity of the bar was altered to either 2.37 or 26.05°/s (Conditions 3 and 4, respectively), however, there was a slight change in the differential latency, i.e. alignment settings shifted so that less than 45 ms was present between the alignment settings and the physical motion curve. This difference was not significant, however, which suggests that the latency of the response to the bar is not changing dramatically in the range of velocities used in these experiments (most significant difference was $t(13) = 1.001$, $p > 0.05$ for subject ELV in the acceleration condition). Although the relative velocity independence in the current experiments is inconsistent with Berry et al. (1999), who found that the anticipatory response of ganglion cells becomes a lagging response at high velocities, it is consistent with the results of Mateeff et al. (1991b). Similarly, Tynan and Sekuler (1982) reported that the reaction times to velocities between 4 and 16°/s were relatively constant. On the other hand, Tynan and Sekuler (1982) also noted that the reaction times changed dramatically for velocities between 25 and 4°/s, a range for which we only had one test (2.37°/s), which is insufficient to draw a strong conclusion. Further experiments will directly address the effect of velocity on the neural latency of moving objects.

5. Conclusions

The experiments presented here have demonstrated that neither the persistence difference nor the spatial extrapolation model are viable as the sole mechanism underlying the illusory flash lag phenomenon. Rather, there is a temporal facilitation for moving targets in the form of shorter latencies for moving than for flashed stimuli. Therefore, although moving objects are not perceived where they really are, they are perceived more accurately than would be possible without the reduced latency.

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